

Origin, evolution and stratigraphic significance of the superfamily Deshayesitaceae STOYANOW, 1949

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Abstract

The idea that monomorph Deshayesitaceae descended from heteromorph Heteroceratidae is confirmed. This transition from *Heteroceras* and further to *Turkmeniceras* is based upon a similar type of suture line morphogenesis and sculpture in late *Colchidites* and early *Turkmeniceras*. A zonal subdivision of Lower Aptian in areas of the eastern and also partially of the western hemispheres is suggested mainly in accordance with the development of the Deshayesitaceae. The Lower Aptian ammonite zones of the Middle Volga region, of the Northern Caucasus and of Turkmenistan are characterized. Biozones of Barremian and Aptian boundary deposits from the Mediterranean and Boreal realms are compared. Seven genera of the superfamily Deshayesitaceae (family Deshayesitidae) are described: *Turkmeniceras* TOVBINA, 1962; *Deshayesites* KAZANSKY, 1914; *Paradeshayesites* KEMPER, 1967; *Obsoleticeras* BOGDANOVA & MIKHAILOVA, 1999; *Dufrenoyia* KILIAN & REBOUL, 1915; *Burckhardtites* HUMPHREY, 1949, *Neodeshayesites* CASEY, 1964; diagnoses of known species are given and three new species are erected: *Turkmeniceras tovbinae* sp. nov., *Deshayesites caseyi* sp. nov. and *D. kemperi* sp. nov.

Key-words: Europe, Turkmenistan, Ammonites, Deshayesitaceae, Lower Aptian.

Résumé

L'idée que les Deshayesitaceae monomorphes sont issus des Heteroceratidae hétéromorphes est confirmée. Cette transition d'*Heteroceras* à *Turkmeniceras* est basée sur un type semblable de morphogenèse de la ligne de suture et de la sculpture chez les derniers *Colchidites* et les premiers *Turkmeniceras*. Une subdivision zonale de l'Aptien inférieur dans l'hémisphère est et une partie de l'hémisphère ouest est proposée essentiellement sur base du développement des Deshayesitaceae. Les zones d'ammonites de l'Aptien inférieur de la région de la Volga moyenne, du nord du Caucase et du Turkmenistan sont caractérisées. Des biozones des dépôts au voisinage de la limite du Barrémien et de l'Aptien dans les domaines méditerranéen et boréal sont comparées. Sept genres de la superfamille des Deshayesitaceae (famille Deshayesitidae) sont décrits: *Turkmeniceras* TOVBINA, 1962; *Deshayesites* KAZANSKY, 1914; *Paradeshayesites* KEMPER, 1967; *Obsoleticeras* BOGDANOVA & MIKHAILOVA, 1999; *Dufrenoyia* KILIAN & REBOUL, 1915; *Burckhardtites* HUMPHREY, 1949, *Neodeshayesites* CASEY, 1964. Les diagnoses des espèces connues sont données et trois nouvelles espèces sont fondées: *Turkmeniceras tovbinae* sp. nov., *Deshayesites caseyi* sp. nov. et *D. kemperi* sp. nov.

Mots-clés: Europe, Turkmenistan, Ammonites, Deshayesitaceae, Aptien inférieur.

Резюме

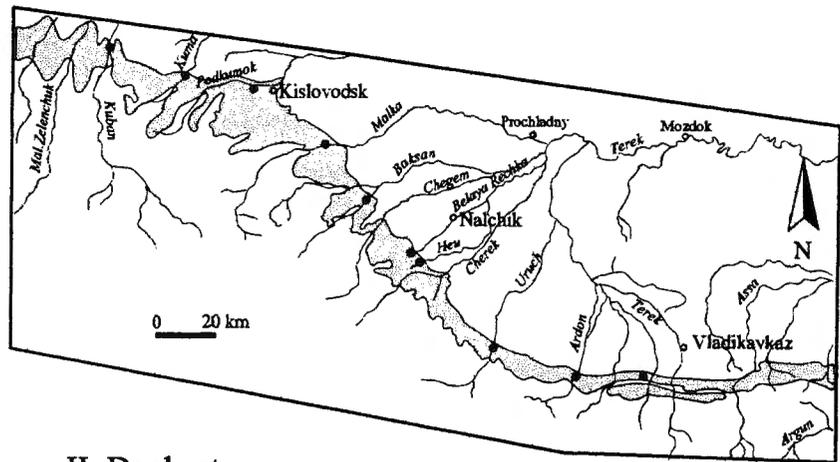
Подтверждено мнение о том, что предками мономорфных Deshayesitaceae являлись гетероморфные Heteroceratidae. Этот переход от *Heteroceras* к *Colchidites* и далее к *Turkmeniceras* базируется на едином типе морфогенеза лопастной линии и сходстве скульптуры поздних *Colchidites* и первых *Turkmeniceras*. Расчленение нижнего апта на зоны в районах восточного и частично западного полушария проведено главным образом в соответствии с развитием данного надсемейства. Приведена характеристика аммонитовых зон нижнего апта Среднего Поволжья, Северного Кавказа и Туркменистана. Дано сопоставление зонального расчленения пограничных отложений баррема и апта Средиземноморской и Бореальной областей. Описано 7 родов надсемейства Deshayesitaceae (семейства Deshayesitidae): *Turkmeniceras* TOVBINA, 1962; *Deshayesites* KAZANSKY, 1914; *Paradeshayesites* KEMPER, 1967; *Obsoleticeras* BOGDANOVA & MIKHAILOVA, 1999; *Dufrenoyia* KILIAN & REBOUL, 1915; *Burckhardtites* HUMPHREY, 1949, *Neodeshayesites* CASEY, 1964; даны диагнозы известных видов и установлены 3 новых вида: *Turkmeniceras tovbinae* sp. nov., *Deshayesites caseyi* sp. nov. и *D. kemperi* sp. nov.

Ключевые слова: Европа, Туркменистан, аммониты, Deshayesitaceae, нижний апт.

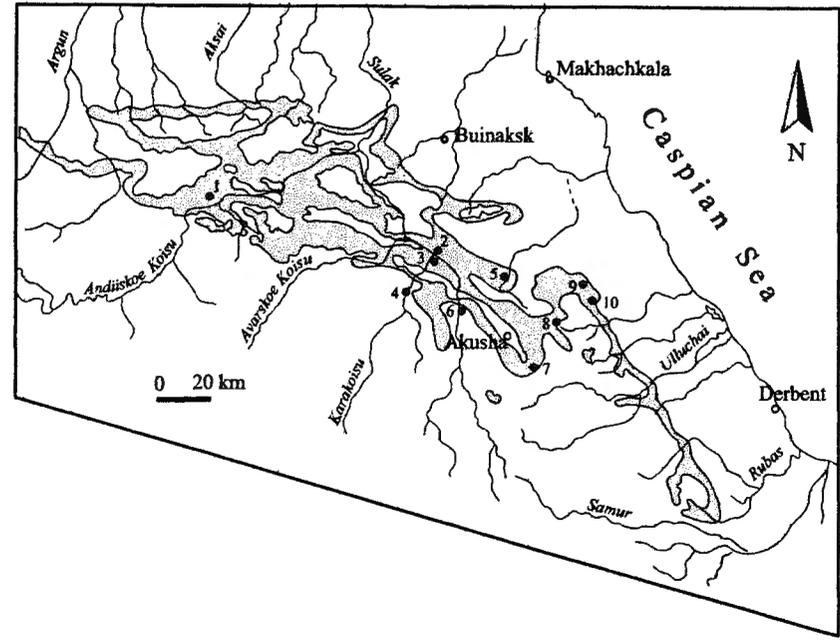
Introduction

In a previous paper BOGDANOVA & MIKHAILOVA (1999) revised the superfamily Deshayesitaceae STOYANOW, 1949. They discussed the origin, generic composition and evolution of this superfamily and confirmed the idea that monomorph deshayesitids were descended from heteromorph heteroceratids. The authors proposed, as was suggested already in MIKHAILOVA (1983), that the new superfamily Deshayesitaceae should include one family the Deshayesitidae. This family includes undoubtedly *Turkmeniceras* TOVBINA, 1962; *Deshayesites* KAZANSKY, 1914; *Paradeshayesites* KEMPER, 1967; *Dufrenoyia* KILIAN & REBOUL, 1915; *Obsoleticeras* BOGDANOVA & MIKHAILOVA, 1999 and *Burckhardtites* HUMPHREY, 1949. The genus *Neodeshayesites* CASEY, 1964 can apparently be assigned to this family and perhaps also *Kuntziella* COLLIGNON, 1962, but this remains highly hypothetical.

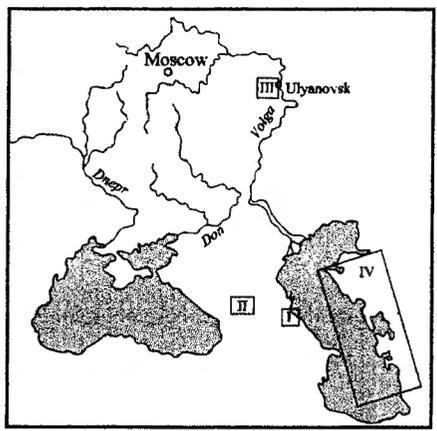
I. Northern Caucasus (rivers Mal. Zelenchuk - Assa)



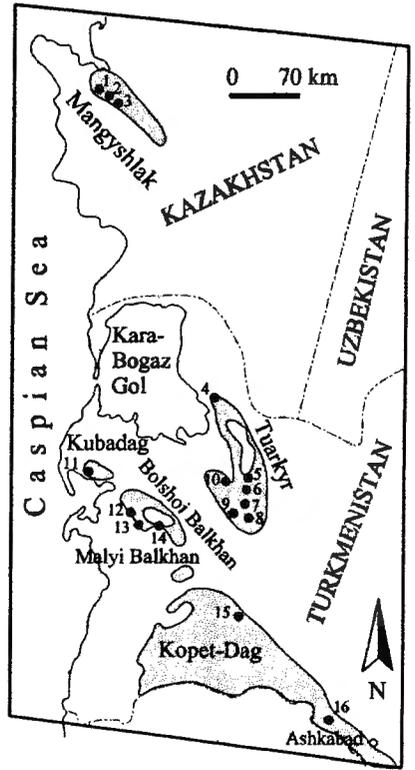
II. Daghestan



III. Ulyanovsk Region



IV. West Central Asia



Legend

- Daghestan:
- 1- Botlik
 - 2- Gergebel
 - 3- Murada
 - 4- Gunib
 - 5- Lavashi
 - 6- Tsudakhar
 - 7- Butri
 - 8- Verkhnie Mulebki
 - 9- Vanashimakhi
 - 10- Burdeki
- West Central Asia:
- 1- Chirchili
 - 2- Karashimrau
 - 3- Shair
 - 4- Babashi
 - 5- Geokdere
 - 6- Lausan
 - 7- Mirisinky
 - 8- Tekedzhik
 - 9- Gobekadzhi
 - 10- Umokdere
 - 11- Jangadzha
 - 12- Bordzhakly
 - 13- Utuludzha
 - 14- Oglanly
 - 15- Chalsu
 - 16- Sekizjab

Fig. 1 — Geographical location of the sections mentioned in the text.

In many areas of the Boreal and Tethys realms of Eurasia the zonal subdivision of the Lower Aptian is based on the change of species assemblages of the family in geological sections (and hence with time), and therefore the Deshayesitidae are of major importance for stratigraphy. Long-standing studies allowed the authors to present results of the subdivision of Lower Aptian deposits in regions such as the Northern Caucasus (including Dagestan), Turkmenistan (Kopet-Dag, Tuarkyr, Bolshoi and Malyi Balkhan, Kubadag), Mangyshlak, and the Middle Volga Region (Fig. 1).

The relationship and stratigraphic position of all zonal units characterized by the deshayesitids is best established in detail in Turkmenistan, where there is a complete succession of Lower Aptian deposits (BOGDANOVA, 1978), and therefore it was adopted as zonal standard for the Mediterranean Tethys (HOEDEMAEKER & BULOT, 1990; HOEDEMAEKER & COMPANY, 1993), and later for the general stratigraphical scale of Russia (RESOLUTION, N° 29, 1997). In fact according to the Tethyan standard the Turkmenian zonation is used for the zonation of the stratotype area sections of La Bédoule (Bouches-du-Rhône, France). The authors revised and studied their own collections from Turkmenistan, the Northern Caucasus and the Volga Region as well as collections in palaeontological museums of Moscow, St. Petersburg and the Natural History Museum in London.

The most representative Russian collections are kept in the CNIGR Museum, St. Petersburg (Sinzow, 10910, 11063, Renngarten, 334, Luppov, 6136, Sazonova, 11805, Glazunova, 8196, Tovbina, 8293, Bogdanova, 9442, 10096, 10367, 12730 and so on).

Following abbreviations are used to indicate collections:

BM – The Natural History Museum, London, England

GIG – Geologisches Institut, Universität Göttingen, Germany

GSM – Formerly Geological Survey Museum, London, England; now: British Geological Survey, Keyworth, Nottingham, England

CNIGR Museum – F.N. Chernyshev Central Research Geological Museum, St. Petersburg, Russia

MSU – Museum of Moscow State University, Moscow, Russia

RGM – National Museum of Natural History (Nationaal Natuurhistorisch Museum, Naturalis), Leiden, The Netherlands

Museum PUM – Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, USA

PIM – Museum of the Palaeontological Institute, Moscow, Russia

Mus. Nat. d'Hist. Nat. – Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, France

MAFI – Geological Museum of the Geological Institute of Hungary

The transliteration of the name of I.A. Mikhailova has been spelled differently over the years; in this paper it is uniformly written as MIKHAILOVA, also the spelling KAZANSKY, GLAZUNOVA, SAZONOVA is used for KASANSKY, GLASUNOVA, SASONOVA.

Stratigraphy

The study of Cretaceous deposits of Russia (including the Northern Caucasus and Turkmenistan) was begun in the 19th

century. In the 20th century successful studies were undertaken in the Caucasus by RENNIGARTEN (1951). He presented a palaeontological basis for the Lower Cretaceous zonal subdivision and compared it to the standard scale of MÜLLER & SCHENCK (1943). The Cretaceous deposits and fauna in the region of the Middle Volga are discussed in TRAUTSCHOLD (1865), SINZOW, (1870, 1872, 1898) and others. Later investigations of NATSKY (1915, 1918) and LUPPOV (1936, 1956) in the Transcaspian area contained the future zonal subdivision of Aptian-Albian deposits of the region.

After World War II systematic studies of Lower Cretaceous deposits were undertaken in the USSR, because large-scale geological mapping required detailed legends. Generalized results of these studies and zonal charts were presented in LUPPOV (1956), ERISTAVI (1962), GLAZUNOVA (1953, 1973), EGOIAN (1964), DRUSHITS, MIKHAILOVA (1966) and many others. This research was co-ordinated by the Cretaceous Commission of the Interdepartmental Stratigraphic Committee (ISC); the results of discussing boundaries and the volume on Lower Cretaceous stages and especially on the Aptian are given in RESOLUTIONS of this Committee (1981, 1987, and 1997).

Results of the study of the Cretaceous system in the USSR are given in "STRATIGRAPHY of the USSR. Cretaceous system" (1986 and 1987). A group monograph ("ZONES...", 1989) deals with the Lower Cretaceous zonal subdivision of this area.

CASEY (1961), FABRE-TAXY *et al.* (1965), DELANOY (1995), DELANOY *et al.* (1997), KEMPER (1967, 1995), MOULLADE *et al.* (1998) 2000) presented detailed and substantiated subdivisions of Lower Aptian deposits for individual areas of Western Europe.

RENNIGARTEN (1951), ERISTAVI (1962), TOVBINA (1963), BOGDANOVA (1978), KAKABADZE (1981), MIKHAILOVA (1983), MIKHAILOVA, BARABOSHKIN (2001), BARABOSHKIN, MIKHAILOVA (2002) are of great importance for the zonal subdivision of the Lower Aptian in Russia and former USSR countries.

Turkmeniceras turkmenicum Zone

Table 1 shows that the deshayesitid zonal subdivision in Turkmenistan begins with the *Turkmeniceras turkmenicum* Zone. Marls, clayey limestones, calcareous siltstones and sandstones, layers of glauconite, oolitic detrital sandstones and siltstones represent deposits of this zone in Turkmenistan with coquina interlayers from 7-10 to 70 m thick. *Turkmeniceras turkmenicum* TOVBINA, 1962 – Pl. 1, Figs. 1, 2; *T. geokderense* TOVBINA, 1962 – Pl. 1, Figs. 5, 6; *T. multicostratum* TOVBINA, 1963 – Pl. 1, Fig. 9; *T. rarecostatum* BOGDANOVA, 1971 – Pl. 1, Fig. 4; *T. tovbinae* sp. nov. – Pl. 1, Fig. 7, Pl. 11, Fig. 1 were found in this zone. The species *T. tumidum* BOGDANOVA, 1971 – Pl. 1, Fig. 8 occurs both in the *T. turkmenicum* Zone and in the overlying *Paradeshayesites tuarkyricus* Zone.

The *Turkmeniceras turkmenicum* horizon was established by TOVBINA (1963) and she assigned it to the Barremian. BOGDANOVA (1971) gave it zone rank.

In Turkmenistan the *Turkmeniceras turkmenicum* Zone replaces the levels with *Colchidites* (first established in Georgia). Later on *Colchidites* was found on continents of the Northern and Southern hemispheres (Western Europe, Africa, and South America) (KAKABADZE & THIEULOY, 1991; KAKABADZE & HOEDEMAEKER, 1997). *Turkmeniceras* species were initially only known from Turkmenistan, but were later also found in the Northern Caucasus, yet their affinity may be questionable (G.A. Tkachuk, oral communication 1980).

While correlating Turkmenian, North-Caucasian and Georgian sections it was shown that the volume of the *Turkmeni-*

TABLE I. CORRELATION OF LOWER APTIAN ZONATION OF BOREAL AND TETHYAN REALMS

STAGE	SUBSTAGE	CASEY, 1961 England		KEMPER, 1995 Germany	BOGDANOVA, 1978 Turkmenistan	MIKHAILOVA, 1983 Northern Caucasus	MIKHAILOVA, BARABOSHKIN, 2001 Ulyanovsk	
		ZONE	SUBZONE	SUBZONE	ZONE	ZONE	ZONE	
APTIAN	MIDDLE (part)	Chelonicerias (Epicheloniceras) martinioides (part)	Epicheloniceras debile	Tropaeum drewi + Tropaeum tenuinodosum	Epicheloniceras subnodosocostatum	Epicheloniceras subnodosocostatum – Colombicerias crassicosatum	Aconecerias nisum	
	LOWER	Tropaeum (Tropaeum) bowerbanki	Chelonicerias meyendorffi	Tropaeum bowerbanki + Dufrenoyia furcata	Dufrenoyia furcata	Dufrenoyia furcata – Dufrenoyia subfurcata	Tropaeum bowerbanki	
			Dufrenoyia transitoria					
		Deshayesites deshayesi	Deshayesites grandis	Deshayesites deshayesi	Deshayesites deshayesi	Deshayesites deshayesi	Deshayesites dechyi – Deshayesites deshayesi	Deshayesites deshayesi
			Chelonicerias parinodum					
		Deshayesites forbesi	Deshayesites callidiscus		Paradeshayesites weissi	Paradeshayesites weissi	Paradeshayesites weissi - Procheloniceras albrechtiaustriac	Deshayesites volgensis
			Deshayesites kiliani					
			Deshayesites fittoni					
	Proadeshayesites fissicosatus	Proadeshayesites obsoletus	Deshayesites tenuicostatus		Paradeshayesites tuarkyricus	Paradeshayesites tuarkyricus	Deshayesites tenuicostatus	
		Proadeshayesites bodei	Deshayesites bodei					
BAR	UPPER	WEALDIAN FACIES		Parancycloceras bidentatum	Turkmenicerias turkmenicum	Matheronites ridzewskyi	Oxyteuthis (Oxyteuthis) lahuseni	

ceras turkmenicum Zone corresponds to the “*Matheronites ridzewskyi*” Zone. The *M. ridzewskyi* Zone was first recognised by RENNIGARTEN (1951) in the Caucasus and assigned to the base of the Aptian, as shown in Table 1. Establishment of the *Turkmeniceras turkmenicum* Zone in Turkmenistan resulted in a longstanding discussion on the Barremian-Aptian boundary: namely should it be drawn at the top or at the base of *T. turkmenicum* Zone? Advocates of both viewpoints advanced their opinions on this problem (TOVBINA, 1963, 1982; MIKHAILOVA, 1970, 1983; BOGDANOVA, 1978, 1983; KAKABADZE, 1981; EGOIAN, 1989; BOGDANOVA & PROZOROVSKY, 1999; RESOLUTIONS..., 1981, 1997). The present authors’ viewpoint as to the position of this boundary also differs: MIKHAILOVA draws it at the base of the *T. turkmenicum* Zone, and BOGDANOVA places it at the top.

It is regrettable that the controversial position of the *Turkmeniceras turkmenicum* Zone resulted in the gradual disappearance in the Tethys scale of this undoubtedly independent zonal subdivision. The authors consider that the *Turkmeniceras turkmenicum* Zone was unnecessarily lowered to the rank of a horizon in the Tethys scale and placed at the top of the *Martelites sarasini* Zone (HOEDEMAEKER & BULOT, 1990). This happened because ammonites of the genus *Turkmeniceras* are poorly known beyond Turkmenistan and their stratigraphic position between the *Colchidites* level and the overlying levels are not clearly understood by Western European palaeontologists.

In the Tethys chart, published by HOEDEMAEKER & COMPANY (1993), *Turkmeniceras* was replaced by *Hemihoplites* (“*Matheronites*”). By this replacement the zonal succession of Barremian-Aptian boundary deposits for the Northern Caucasus of RENNIGARTEN (1951) was reintroduced. It should be emphasized that RENNIGARTEN (1951) placed the zone with *Matheronites ridzewskyi* at the base of the Aptian and in HOEDEMAEKER & COMPANY (1993) it is at the top of the Barremian. Later work on Lower Aptian deposits, revealed a stratigraphic level (or a horizon) with *Pseudocrioceras waagenoides* (KAKABADZE & KOTETISHVILI, 1995; DELANOY *et al.*, 1997; ROPOLLO *et al.*, 2000a; GONNET *et al.*, 2000). This has since been transformed into a subzone (CECCA *et al.*, 1999 b; ROPOLLO *et al.*, 2000 b; CECCA *et al.*, 2000). At the Vienna workshop on Lower Cretaceous ammonites in 2000, Kakabadze suggested that *Hemihoplites ridzewskyi* horizon (subzone) should be replaced by *Pseudocrioceras waagenoides* (HOEDEMAEKER & RAWSON, 2000), and the unit itself given the status of a zone. According to us the sequence of Barremian and Aptian boundary layers in the Tethyan realm is as follows (generic affinity is given according to the authors of the present paper) (from top to bottom):

Paradeshayesites tuarkyricus Zone

Pseudocrioceras waagenoides Zone

Martelites (= *Colchidites* according to Kakabadze) *sarasini* Zone

The recognition of the *Pseudocrioceras waagenoides* horizon (subzone) followed BUSNARDO (1984) for strata with *Pseudocrioceras* in France – presumably of Aptian age.

DELANOY *et al.* (1997) considered that *Pseudocrioceras* co-occurs with Barremian heteromorph ammonites in the upper *Martelites sarasini* Zone and partially coexists with the first deshayesitids of the *Paradeshayesites tuarkyricus* Zone. CECCA *et al.* (1999 b) stated that *Pseudocrioceras* only occurs in the *Martelites sarasini* Zone, but that the ammonite fauna in the *P. waageni* subzone is different from that of the independent underlying *M. sarasini* Zone and from that of the overlying *Paradeshayesites tuarkyricus* Zone.

The authors of the present paper think that the *Turkmeniceras turkmenicum* Zone is valid, the characteristic assemblage of the

earliest deshayesitid member (i.e. a phylogenetic series Heteroceratidae – Deshayesitidae) is preferable and better based for recognizing a zone, than the replacement by the *Hemihoplites ridzewskyi* horizon (subzone) first, followed by the *Pseudocrioceras waagenoides* horizon (subzone) afterwards.

In relation to this problem the findings of *Turkmeniceras* in Western Europe are extremely important. In the 1990’s, *Turkmeniceras* was reported from the Aptian stratotype area in southern France (AUTRAN & DELANOY, 1987, oral communication of G. Conte (1996) and examination of moulds from his collection). AUTRAN & DELANOY (1987, pl. 1, fig. 1) depicted as *Deshayesites* sp. (pl. 1, fig. 1) an ammonite that belongs undoubtedly to the genus *Turkmeniceras*. The shells depicted by AUTRAN & DELANOY (1987) were found in a condensed level, so their exact position in the section, where *Turkmeniceras* has been found, remains unclear. Later *Deshayesites antiquus* was found in the Les Caniers and Le Brigadan (Bouches-du-Rhône, France) sections (CECCA *et al.* 1999b, pp. 269, 270). The present authors restudied the generic affinity of the species *D. antiquus* and they consider this species as belonging to the genus *Turkmeniceras* (see p. 201). The occurrence of *T. antiquus* together with ammonite species of the *Paradeshayesites tuarkyricus* Zone does not solve the presence of an independent *Turkmeniceras turkmenicum* Zone in SE France. Thus, the problem of placing the Barremian-Aptian boundary in Western and Eastern European sections remains unsolved.

Paradeshayesites tuarkyricus Zone

Defined by BOGDANOVA (1971, 1983); its stratotype is on the northern slope of the Bolshoi Balkhan, 1-1.5 km west of the Utuludzha wells.

- In Turkmenistan deposits of this zone consist of silty clays, clayey siltstones, oolitic-glaucconitic sandstones and unconsolidated calcareous sandstones of about 50 m thick. They contain: *Paradeshayesites tuarkyricus* (BOGDANOVA, 1983) – Pl. 7, Fig. 7; *P. oglanlensis* (BOGDANOVA, 1983) – Pl. 7, Fig. 4; *P. weissiformis* (BOGDANOVA, 1983) – Pl. 7, Fig. 3; *P. planicostatus* (BOGDANOVA, 1991) – Pl. 7, Figs. 5, 6; *Turkmeniceras tumidum* BOGDANOVA, 1971 – Pl. 1, Fig. 8.
- In England the equivalent of the *P. tuarkyricus* Zone are deposits of the “*Prodeshayesites*” *fissicostatus* Zone with two subzones – “*Prodeshayesites*” *bodei* and “*Pr.*” *obsoletus*.
- In Germany the *P. tuarkyricus* Zone is compared with *Deshayesites bodei* and *D. tenuicostatus* zones though the specific composition of the zones in Germany differs from that in Turkmenistan.
- In the Middle Volga region (Saratov area, Russia) deposits of the *D. tenuicostatus* Zone were established on the occurrence of *D. tenuicostatus* (VON KOENEN, 1902) – Pl. 2, Fig. 7; *D. subfissicostatus* (SINZOW, 1898) – Pl. 2, Fig. 10 – and *D. aff. bodei* (VON KOENEN, 1902) – Pl. 2, Fig. 2; *D. consobrinoides* (SINZOW, 1898) – Pl., Figs. 4 – 6 also occurs in this association.

The *D. tenuicostatus* Zone was established by the presence of the species *D. tenuicostatus* [= *Hoplites bodei* var. *tenuicostatus* VON KOENEN (1902, p. 221-223, pl. 9, fig. 2)].

CASEY (1964), when revising the species *D. fissicostatus* (PHILLIPS, 1829), selected its neotype and regarded *Hoplites bodei* var. *tenuicostatus* VON KOENEN, 1902 as a synonym of the former species. In our opinion, both *D. fissicostatus* (PHILLIPS, 1829) and *D. tenuicostatus* (VON KOENEN, 1902) are valid species. The specimen from the Volga according to its general aspect and sculpture is identical with VON KOENEN’s species and is cited in German literature (KEMPER,

1995). However, we can identify the specimen from the Volga region (Pl. 2, fig. 7) neither with the drawing from the paper by PHILLIPS (1829, pl. 2, fig. 49), nor with its neotype in CASEY (1964, p. 356, pl. 58, fig. 2).

- In Mangyshlak, the equivalent of this zone is probably the upper part of the lagoon-continental strata (Kugusem Fm.).
- In the Caucasus deposits of the *tuarkyricus* Zone have not been confirmed faunally; the lower part of the overlying *Paradeshayesites weissi* – *Procheloniceras albrechtiaustriacae* Zone can possibly be assigned to them.

Correlation of the Tethyan *Paradeshayesites tuarkyricus* Zone with its Boreal equivalents (Middle Volga region, Germany, England) is very difficult, because the zonal assemblages have virtually no common elements. The correlation of the present authors is valid from the stratigraphic point, since the overlying deposits contain a representative complex of common species (see below).

Recently French palaeontologists gave a detailed description of the *P. tuarkyricus* Zone from stratotype sections in the Cassis – La Bédoule (Bouches-du-Rhône, France) area. According to GONNET *et al.* [1998 (2000)] the zone is represented by limestones and marls (sections: des Caniers – beds 81-92, des Fourniers – 101-109) and contains a rich zonal assemblage of deshayesitids similar to that of Turkmenistan. CECCA *et al.* (1999b; 2000) published an extensive list of ammonite species from the section Le Brigadan with the new species *Deshayesites bedouliensis*.

Paradeshayesites weissi Zone

The name of this zone comes from VON KOENEN (1907, p. 9) and KILIAN (1907-1913, table on p. 287). In Germany monomorph ammonites, including deshayesitids, poorly characterize this interval of the section. Gradually the *P. weissi* Zone disappeared from the zonal schemes of German scientists as shown in KEMPER (1967, 1976). In other regions the species – *Paradeshayesites weissi* (NEUMAYR & UHLIG, 1881, p. 51, pl. 46, fig. 1, 1a) – was identified only on the basis of illustrations. Later it became clear that the ammonite assemblage from this interval was poor and not as characteristic, as had previously been thought. Besides, the original material of NEUMAYR & UHLIG (1881) and VON KOENEN (1907) is lost (Casey, 2001, written communication). This does not allow a modern revision of this zonal species. Therefore, the zonal name “*weissi*” should be considered unacceptable and should be replaced in the Tethyan realm.

- In Turkmenistan *Paradeshayesites topleyi* (SPATH, 1930) – Pl. 7, Fig. 2, Pl. 9, Fig. 1; *P. callidiscus* (CASEY, 1961) – Pl. 10, Fig. 1; *P. similis* (BOGDANOVA, 1991) – Pl. 10, Fig. 2; *Deshayesites pappi* BOGDANOVA, 1991 – Pl. 3, Fig. 5; *D. dechyi* (PAPP, 1907) – Pl. 3, Fig. 6; *D. kemperi* sp. nov. – Pl. 4, Fig. 5, Pl. 10, Figs. 4 – 6 occur in beds (clayey and sandy siltstones, clay stones, and sandstones with interlayers of oolitic calcareous sandstones, thickness: 15 to 80 m).
- Since Renngarten it is known from the Northern Caucasus, including Daghestan, that *Procheloniceras albrechtiaustriacae* occurs along with *Paradeshayesites weissi* (NEUMAYR & UHLIG, 1881). Furthermore, the ammonite assemblage of this zone consists of *Deshayesites dechyi* PAPP, 1907, *D. consobrinus* (D’ORBIGNY, 1841), *Procheloniceras pschechaensis* LUPPOV, 1952, *Cheloniceras cornuelianum* (D’ORBIGNY, 1841) and others (DRUSHITS, MIKHAILOVA, 1966; EGOIAN, 1989).
- In the zonal scheme of the Middle Volga region this interval is designated as the *Deshayesites volgensis* Zone (BARABOSHKIN, MIKHAILOVA, 2002). Near Ulyanovsk, *Deshayesites volgensis* SAZONOVA, 1958 – Pl. 3, Figs. 3, 4; *D. forbesi* CASEY,

1961 – Pl. 3, Fig. 2; *D. gracilis* CASEY, 1964 – Pl. 6, Figs. 5, 6; *D. saxbyi* CASEY, 1964 – Pl. 6, Fig. 4; *D. aff. vectensis* SPATH, 1930 – Pl. 6, Fig. 3; *Paradeshayesites imitator* (GLAZUNOVA, 1968) – Pl. 6, Figs. 1, 2; *P. callidiscus* (CASEY, 1961) – Pl. 8, Figs. 1, 2; *Obsoleticeras levigatum* (BOGDANOVA, 1991) – Pl. 11, Fig. 3 were found in shales (thickness 7-12 m), with nodule horizons. This complex contains rare Turkmenian forms along with typical English forms. The index species *D. forbesi* and *D. volgensis* (description of the latter is given below) are also rather close; moreover, in the Volga region both species were found together.

Deshayesites deshayesi Zone

The name of the zone is taken from KILIAN (1907-1913, table on p. 287).

- In Kopet-Dag in Turkmenistan, deposits of this zone consist of silty clays with interlayers of orbitolinid limestones (thickness: 15 to 78 m), in the Bolshoi Balkhan of clayey siltstones (thickness 2 to 20 m), and in Tuarkyr of sandstones (thickness upto 7 m). Faunal content: *Obsoleticeras levigatum* (BOGDANOVA, 1991) – Pl. 11, Fig. 2; *Deshayesites kudrjavzevi* MIKHAILOVA, 1958 – Pl. 5, Fig. 6; *D. consobrinus* (D’ORBIGNY, 1841) – Pl. 4, Fig. 2; *D. dechyi* (PAPP, 1907) – Pl. 3, Fig. 6; *D. deshayesi* (D’ORBIGNY, 1841), *D. babaschensis* BOGDANOVA, 1977, *Paradeshayesites terminalis* (BOGDANOVA, 1979).
- In the Northern Caucasus (including Daghestan) deposits of the *Deshayesites dechyi* – *D. deshayesi* Zone are characterized by a diverse deshayesitid assemblage: *D. dechyi* (PAPP, 1907) – Pl. 3, Figs. 7, 8; *D. consobrinus* (D’ORBIGNY, 1841) – Pl. 4, Fig. 3; *D. lavaschensis* KAZANSKY, 1914 – Pl. 8, Figs. 3, 4; *D. kudrjavzevi* MIKHAILOVA, 1958 – Pl. 5, Figs. 4, 5; *D. robustocostatus* MIKHAILOVA, 1958 – Pl. 6, Figs. 7, 8; *D. kemperi* sp. nov. – Pl. 4, Fig. 4; *D. caseyi* sp. nov. – Pl. 5, Figs. 1, 2; *D. michailovae* BOGDANOVA *et al.*, 1979. Some of these taxa appeared somewhat later in this region than in Turkmenistan.
- In the Middle Volga region deposits of the *Deshayesites deshayesi* Zone consist of silts with sand and clay alternation of about 5 m thick. An assemblage of large ammonites is similar to the taxa characteristic of the zone of the same name in England, but their identification is not completed yet. Most likely *Deshayesites deshayesi* LEYMERIE (in TRAUTSCHOLD, 1865) – Pl. 2, Fig. 3 – was found in this zone.

Dufrenoyia furcata Zone

JACOB (1907, p. 163 – the section of Vesc (Drôme, les “Baronnies”) p. 170 – the “la colline du Teil” section (Le Teil, Ardèche, France); p. 291 – one of the index fossils of the lower subzone of the Gargasian) erected the biounit with the index species *Hoplites furcatus*. The *Dufrenoyia furcata* Zone and, respectively, its position at the Lower/Middle Aptian boundary at the base of the Gargasian, was generally accepted in western Europe. ROCH (1927) studied the Bedoulian stratotype section and placed its upper boundary at the base of the beds with “*Parahoplites*” *dufrenoyi*. RENNGARTEN (1951 – p. 55) presented the zone with *D. furcata* as the top zone for the Lower Aptian. The position of the boundary between Bedoulian and Gargasian, proposed by ROCH continued to be used in France until CONTE (1994) separated “...in the so-called “Gargasian base formation...” (p. 321) the lower part of the beds containing *Aconeceras nisum*, *Dufrenoyia furcata* and *Cheloniceras* (*Epi-cheloniceras*) *martini*. This lower part contains: *Cheloniceras cornuelianum*, *Dufrenoyia* sp. gr. *transitoria-discoidalis*, *Tropaeum* cf. *bowerbanki* etc (p. 324, fig. 2). CONTE transferred this

part into the Lower Aptian (Bedoulian) with the rank of the *Dufrenoyia* spp. and *Tropaeum bowerbanki* Zone. CASEY *et al.* (1998) commented and reviewed the position of the upper boundary of the Lower Aptian and supported the conclusions of CONTE (1994). In a recent comprehensive volume on the stratotype of the Bedoulian (MOULLADE *et al.*, 2000) the level with *Dufrenoyia* was included into the Lower Aptian and was renamed the *Dufrenoyia furcata* Zone: "...en accord avec la terminologie du découpage standard méditerranéen." (ROPOLO *et al.*, 2000b, p. 171).

- In Turkmenistan this zone is composed of loose sandstones up to 25 m thick (Tuarkyr), siltstones up to 25 m thick (Bolshoi Balkhan) and up to 33 m thick (Malyi Balkhan), sandstones, clays and siltstones up to 150 m thick (Kopet-Dag).
- In Western Turkmenistan a conglomerate bed with phosphorite and glauconite pebbles is present at the base of this zone, and in some sections the zone is limited to this bed. Faunal content: *Dufrenoyia furcata* (J. de C. SOWERBY, 1836), *D. dufrenoyi* (D'ORBIGNY, 1841), *D. lurenensis* (KILIAN, 1888), *D. sinzowi* LUPPOV, 1949, *D. scalata* CASEY, 1964 – Pl. 12, Fig. 5, *D. fursovae* BOGDANOVA, 1991, *Burckhardtites palumbes* HUMPHREY, 1949 – Pl. 12, Fig. 11, *B. gregoriensis* HUMPHREY, 1949 – Pl. 12, Fig. 12.
- In the Northern Caucasus (including Daghestan) deposits of the corresponding *Dufrenoyia furcata* – *D. subfurcata* Zone are often washed out (Pl. 12, Figs. 3, 6).
- In the Volga region the *Tropaeum bowerbanki* Zone corresponds to the *Dufrenoyia furcata* Zone (BARABOSHKIN, MIKHAILOVA, 2002, pl. 3, fig. 4). The *Tropaeum bowerbanki* Zone is correlated to the upper Lower Aptian in boreal regions (Germany, England).

Taxonomy

In the descriptions the authors use the terms accepted in Russian literature. In the tables of the main parameters the following letter symbols are used: *shell diameter* – D, *umbilicus diameter* – Du, *whorl height* – H, *whorl width* – W.

The shell diameter is not always maximal; it is often measured at some distance from the aperture, when this is more convenient for measuring other dimensions. Ratios of umbilicus diameter, whorl height and width to diameter (Du/D, H/D, W/D) are given for each shell characteristic.

In the description of the degree of overlapping of one whorl by another all shells are subdivided into four groups depending on Du/D ratio:

- Shells involute Du/D up to 0.2
- Shells semi-involute Du/D from 0.2 to 0.3
- Shells semi-evolute Du/D from 0.3 to 0.4
- Shells evolute Du/D over 0.4

All Deshayesitidae have semi-evolute or semi-involute shells and the Du/D ratio allows the characterization of relative umbilicus dimensions:

very wide umbilicus	0.40
wide umbilicus	0.34 – 0.40
moderately wide umbilicus	0.26 – 0.35
relatively narrow umbilicus	0.21– 0.25

All dimensions are given in mm. For uniformity they were taken at the top of the ribs; exceptions are stated.

Suture line. Two highly developed terminologies and systems of symbols exist: one developed by SCHINDEWOLF (1929) and the other by RUZHENTSEV (1949). We consider that the place, way and succession of appearance of new elements is

reflected more precisely in the RUZHENTSEV terminology. It clearly shows the phylogenetic variety of ammonoids.

Terminology used herein: V – ventral lobe; L – lateral lobe; U – umbilical lobe; I – internal lateral lobe; D – dorsal lobe.

Jurassic-Cretaceous Ammonitida descended from the evolutionary branch of those Palaeozoic ammonoids that had no lateral lobe L.

Class Cephalopoda

Subclass Ammonoidea

Order Ammonitida

Suborder Ancyloceratina WIEDMANN, 1966

Herein the suborder Ancyloceratina is restricted to four superfamilies: Ancylocerataceae MEEK, 1876; Deshayesitaceae, STOYANOW, 1949; Douvilleicerataceae PARONA & BONARELLI, 1897 and Parahoplitaceae SPATH, 1924.

The first superfamily had heteromorph shells and was the ancestor of the three other superfamilies. This accounts for the similarity of appearance of Deshayesitaceae and some Parahoplitaceae (genus *Parahoplites*).

Herein the superfamily Deshayesitaceae is considered as containing only one family, the Deshayesitidae, and the superfamily Parahoplitaceae contains only the family Parahoplitidae.

Heteromorph Turrilitaceae were arranged in the suborder Turrilitina (BESNOV, MIKHAILOVA, 1983), assigned to the order Lytoceratida based on morphogenic features of the suture line, a predominantly bifid umbilical lobe and early siphon displacement towards the ventral side.

Family Deshayesitidae STOYANOW, 1949

Description. Shell is disk-shaped, semi-involute to semi-evolute. Whorl section varies from high trapezoidal to rounded-rectangular. The earliest forms sometimes have an umbilical perforation.

Initial chamber and three first whorls are smooth. Sculpture appears as faintly visible ribs at the beginning of the fourth whorl. Later ribs become distinct, first closely spaced, then the space between them increases. In the adult stage, sculpture consists of main and intermediate ribs, the latter occurring either between the main ribs singly or in two. The main ribs begin at the seam, have an S-shaped bend on the flanks, are directed forward on the venter and often become weaker there. Sometimes ribs form bundles at their base.

The primasuture is unstable, five-lobe (VUU¹ID). Lobe U¹ is reduced on the first whorl and number of lobes is reduced to four (VUID). Later on new elements appear at the expense of inner saddle division (I/D) and should be denoted as I¹, I², etc.

Formula of the suture line: (V₁V₁)UU¹ID → (V₁V₁)UID → (V₁V₁)(U₂U₁U₂)I I¹D.

Composition. *Turkmeniceras* TOVBINA, 1962; *Deshayesites* KAZANSKY, 1914; *Paradeshayesites* KEMPER, 1967; *Obsoleticeras* BOGDANOVA & MIKHAILOVA, 1999; *Du-*

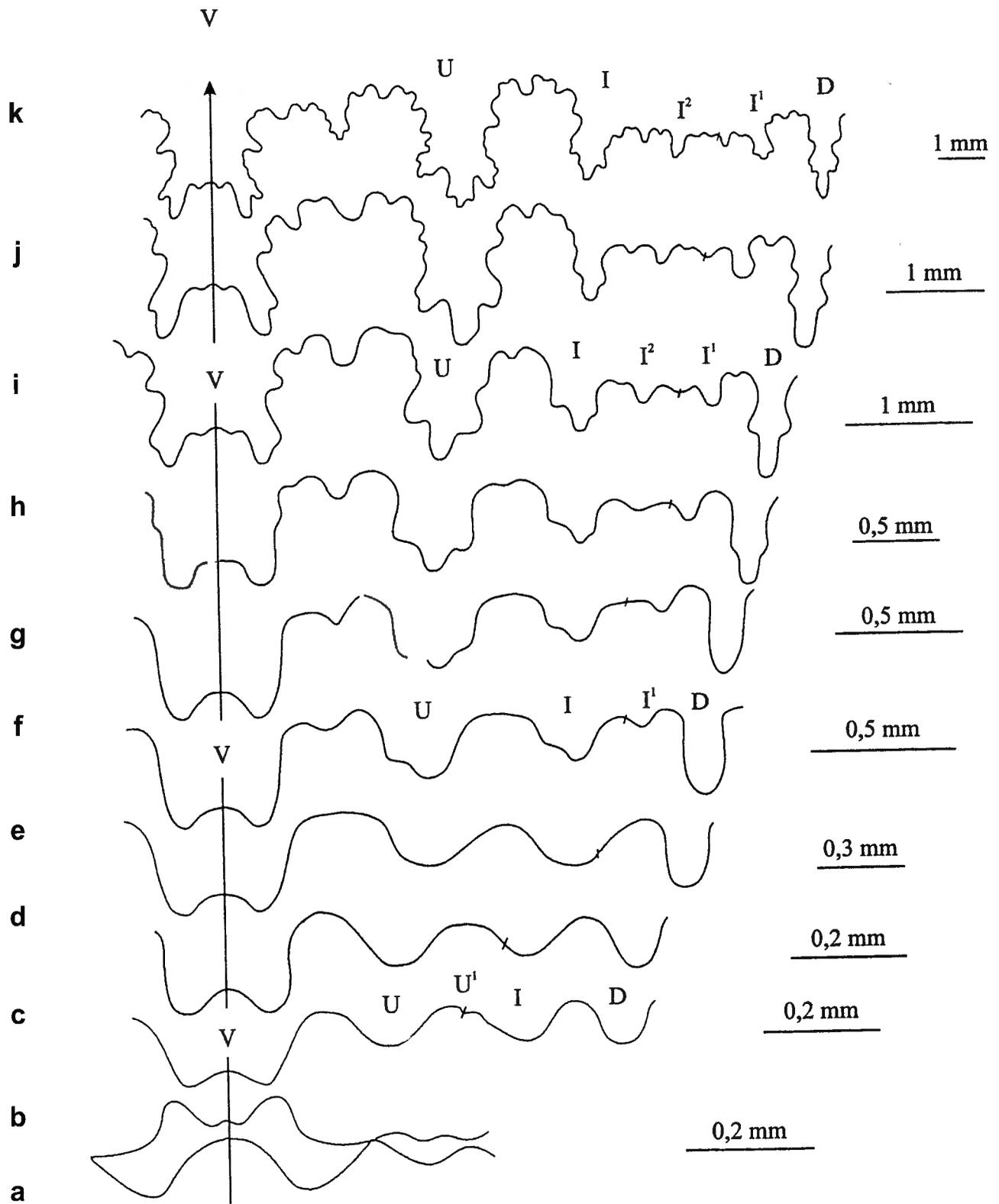


Fig. 2 — Changes in suture line during the ontogeny of shell of *Deshayesites consobrinoides* (SINZOW, 1898). a, b, c, d — 1,2,3,8 lines, e — end of second whorl, f — beginning of third whorl, g — middle of third whorl, h — end of third whorl, i — beginning of fourth whorl, j — end of fourth whorl, k — middle of fifth whorl. a, b — MSU 40/96; c-k — MSU 41/96 (MIKHAILOVA, 1976, with changes).

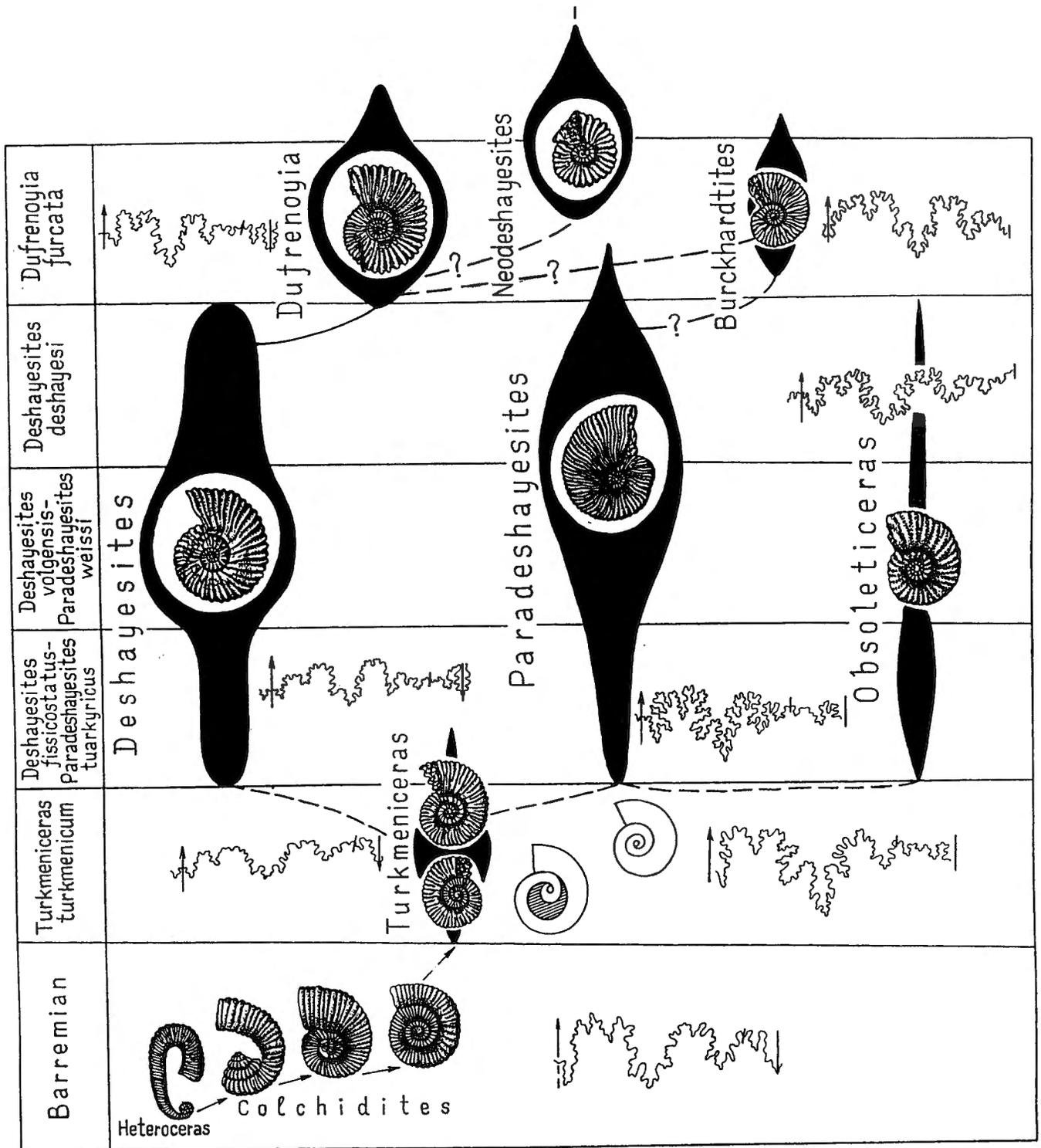


Fig. 3 — Phylogeny of the superfamily Deshayesitaceae.

frenoyia KILIAN & REBOUL, 1915; *Burckhardtites* HUMPHREY, 1949 and probably *Neodeshayesites* CASEY, 1964.

Remarks. Deshayesitidae differ from the closely related family Parahoplitidae, in:
 – new elements of the suture line emerge at the expense of the inner saddle division (I/D),

- tubercles are lacking in shell ontogenesis,
- whorls are narrower,
- an often wider umbilicus.

Deshayesitidae sometimes show a tendency towards rib smoothing in the centre of the flanks and on the venter.

These facts require an additional explanation, since the Deshayesitidae until about 1950 were often included into

the Parahoplitidae, and only the ontogenetic study of the suture line of these families revealed the fundamental difference in the way new elements appear in the area of the seam.

The necessity of distinguishing independent Deshayesitidae was based on several supplementary arguments (MIKHAILOVA, 1983).

- (1) Primasuture (the second suture line) of the family Deshayesitidae consists of four lobes: ventral, umbilical, inner lateral and dorsal (VUID). The same primasuture is present in the family Parahoplitidae.
- (2) The new lobes in the deshayesitids appear as a result of the saddle I/D division, i.e. the saddle, which originally occurred behind the seam. The lobes I¹ and I² originate in this saddle. The inner lateral lobe I in the course of ontogenesis shifts to the external side of the shell and a new lobe I¹ moves to the place of lobe I.
- (3) The new lobes in the parahoplitids emerge as a result of saddle U/I division; in these lobes U¹, U², etc. are formed. The inner lobe preserves its initial position behind the seam, near the dorsal lobe.

The morphogenesis of the suture line of the genus *Turkmeniceras* (TOVBINA, 1963), the earliest member of the family Deshayesitidae, confirms the statements above.

SCHINDEWOLF (1966) removed the difference in formulae for the suture lines of deshayesitids and parahoplitids. He noted the primasuture in parahoplitids and deshayesitids differently, assuming that parahoplitids have lobes ELU₁I, and deshayesitids ELU₂I (to explain SCHINDEWOLF's views we use his own terminology). Therefore, the next (fifth) lobe of these two groups should be noted differently: lobe U₁ appears on deshayesitids and lobe U₂ on parahoplitids. As a result, the suture line formula of the two forms at this stage becomes similar: ELU₂U₁I. SCHINDEWOLF (1966) believed that parahoplitids are characterized by orthochronous, and deshayesitids by heterochronous evolution. He also introduced this notion for Jurassic ammonites. In case of orthochronous evolution lobe U₁ is present in the primasuture, and then appears lobe U₂. The heterochronous evolution is characterized by a delay in the emergence of U₁: lobe U₂ occurs in the primasuture and lobe U₁ appears later.

Our supplementary study of the earliest morphogenetic stages of the suture line in Deshayesitidae and Parahoplitidae revealed a new important feature. It was shown that the primasuture and following two or three suture lines in all of the mentioned groups consist of five lobes rather than four (MIKHAILOVA, 1976, 1983; BOGDANOVA, MIKHAILOVA, 1999, fig. 2). This five-lobe primasuture was also found during the revision of the genus *Turkmeniceras*.

Primary changes of the two mentioned families are of the same type:

- 1 – the primasuture is five-lobed (VUU¹ID),
- 2 – on the first whorl the first umbilical lobe is reduced and the number of lobes decreases to four (VUID),
- 3 – this suture line is preserved until the middle of the second whorl,

4 – afterwards new elements appear in the same way as was previously assumed by the authors of the present paper.

The formula of the suture line was supplemented in the early stage.

VUU¹ID → VUID → VUII²I¹D (Deshayesitidae)

VUU¹ID → VUID → VUU¹U²ID (Parahoplitidae)

Figure 2 shows the morphogenesis of the suture line of *Deshayesites consobrinoides* (SINZOW, 1898) and it is possible to trace both the reduction of the lobe U¹ on the seam and the appearance of lobes I¹ and I². BOGDANOVA, MIKHAILOVA (1999) noted that in the revised volume "Treatise..." (WRIGHT *et al.*, 1996) the Parahoplitidae and Deshayesitidae are both integrated into the superfamily Deshayesitaceae, although questionably. In the diagnoses of both families is mentioned that new elements emerge from one saddle U/I (according to the terminology of Ruzhentsev). We consider there are no grounds for including the Parahoplitidae (even questionably) into the Deshayesitaceae. By establishing the presence of an unstable five-lobe primasuture in Parahoplitaceae, Deshayesitaceae and Douvilleicerataceae the assumption that these taxa descended from heteromorph Ancylocerataceae (Fig. 3, see also p. 195) was confirmed and that they inherited their peculiar primasuture with the reduction of a lobe (MIKHAILOVA, 1983).

Genus *Turkmeniceras* TOVBINA, 1963

* 1963 – *Turkmeniceras*: TOVBINA, p. 100.

1999 – *Turkmeniceras*: BOGDANOVA, MIKHAILOVA, p. 51 (with detailed synonymy).

Type species: *T. turkmenicum* TOVBINA, 1962; turkmenicum Zone; Turkmenistan.

Description. Shell evolute with loosely coiled or contacting second whorl (Pl. 1, Fig. 3). Cross-section subrectangular to rectangular-oval (Fig. 4A). Whorls slowly expanding. Umbilicus wide. Ribbing closely or densely spaced. One or two intermediate ribs occur between two main ribs; rib intercalation is regular. Ribs weakly S-bent. Umbilical nodes absent.

Suture formula: (V₁V₁)UI:I¹D. Inner lateral lobe (I) is on the outside of the whorl, and lobe I¹ at the time of initiation in saddle I/D is near the seam, and later occurs behind the seam on the inner side of the whorl (Fig. 4B).

Species composition: Seven species: *T. turkmenicum* TOVBINA, 1962, *T. geokderense* TOVBINA, 1962, *T. multicoatum* TOVBINA, 1963, *T. rarecostatum* BOGDANOVA, 1971, *T. tovbinae* sp. nov., turkmenicum Zone of Turkmenistan; *T. catulloi* PARONA, 1897, Barremian (?) of Italy; *T. tumidum* BOGDANOVA, 1971, turkmenicum and taurkyricus Zones of Turkmenistan.

Remarks: In 1962 TOVBINA (p. 84) described two new *Turkmeniceras* species but gave no diagnosis for the genus *Turkmeniceras*. This genus was validly established

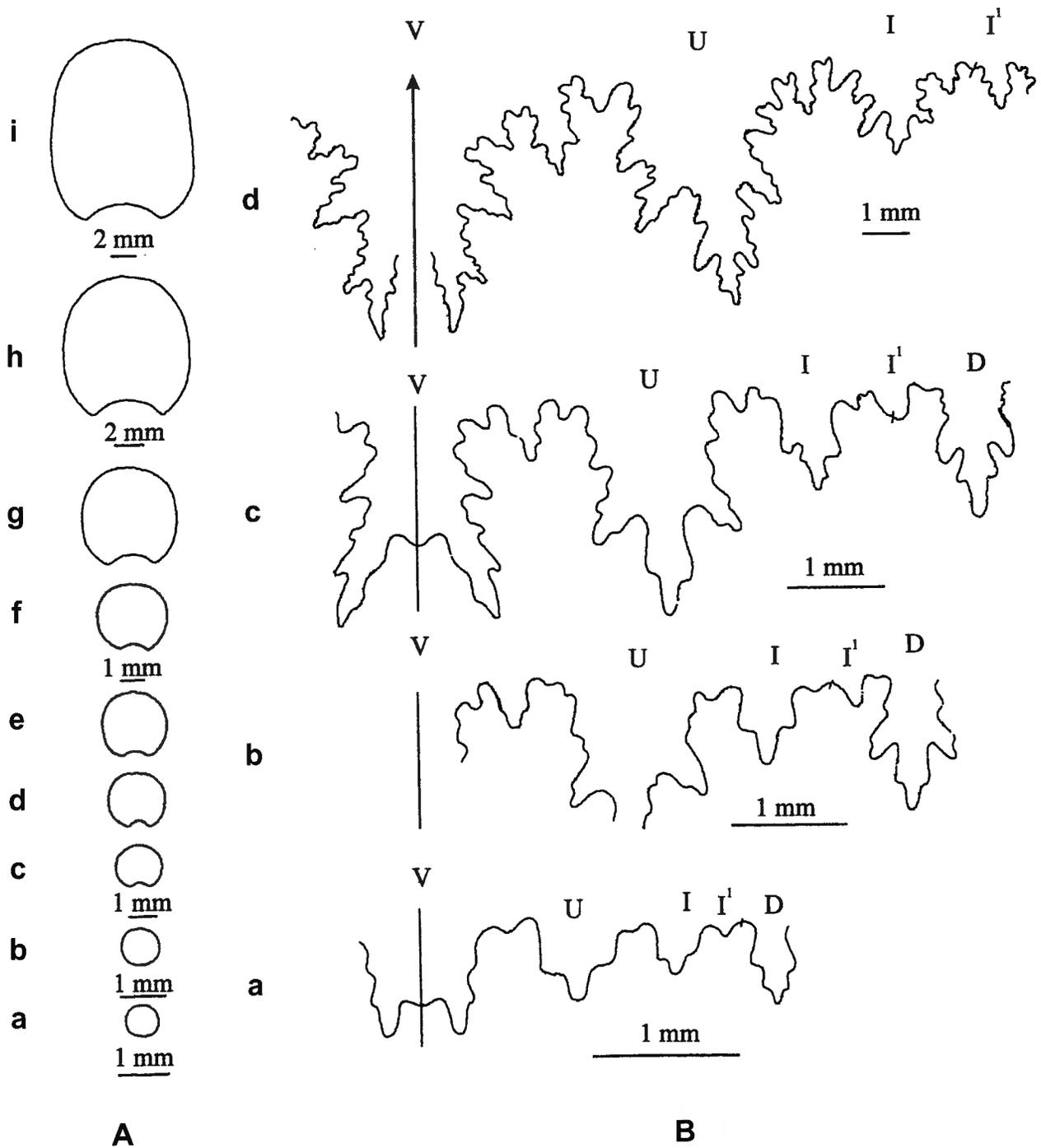


Fig. 4 — A — Changes of whorl section in ontogeny of shell of *Turkeniceras rarecostatum* BOGDANOVA, 1971. Holotype CNIGR Museum 3/10096: a — H = 0.6 mm, W = 0.65 mm, b — H = 0.9 mm, W = 1.1 mm (a, b — second whorl); c — H = 1.3 mm, W = 1.4 mm, d — H = 1.6 mm, W = 1.6 mm, e — H = 2.0 mm, W = 2.1 mm (c-e — third whorl); f — H = 2.6 mm, W = 2.7 mm, g — H = 4.6 mm, W = 4.6 mm (f, g — fourth whorl); h — H = 8.3 mm, W = 7.6 mm (middle of fifth whorl); i — H = 13.0 mm, W = 11.5 mm (middle of sixth whorl). B — Changes in the suture during ontogeny of shell of *Turkeniceras turkmenicum* TOVBINA, 1962. CNIGR Museum 14/10367: a — H = 1.45 mm, W = 1.6 mm, b — H = 2.9 mm, W = 3.1 mm, c — H = 3.6 mm, W = 3.5 mm, d — H = 13.1 mm, W = 8.5 mm.

in 1963. The earliest genus of the family Deshayesitidae differs from the possible ancestral genus *Colchidites* in the absence of the helicoidal stage in ontogenesis, more incised inner and umbilical saddles. The inner lobe of *Turkmeniceras* is more shifted to the outside, inasmuch as in *Colchidites* this lobe is near the seam.

Turkmeniceras turkmenicum TOVBINA, 1962

Pl. 1, Figs. 1, 2; Text-fig. 4

*1962 – *Turkmeniceras turkmenicum*: TOVBINA, p. 84, pl. 44, fig. 1.

1963 – *Turkmeniceras turkmenicum*: TOVBINA, p. 103, pl. 1, figs. 1-3, text-fig. 4.

1999 – *Turkmeniceras turkmenicum*: BOGDANOVA, PROZOROVSKY, pl. 1, figs. a-c, f,g.

Holotype: CNIGR Museum 1/8293, *Turkmeniceras turkmenicum* Zone, Sekizjab, Kopet-Dag, Turkmenistan.

Description: Shells are medium-sized (D up to 65-70 mm), flattened ($W/D = 0.27$). The first whorl embraces the initial chamber, the second whorl is unfolded (initiation and extent of divergence vary in different specimens of the species), the third whorl adjoins the second, subsequent whorls embrace one another for 1/4 or 1/3; whorls high ($H/D = 0.36-0.40$), moderately increasing. Flanks are flattened, slightly converging towards the venter (also flattened). Umbilicus wide ($Du/D = 0.33-0.37$) with low steep walls. Ribs sharp, moderately dense; main ribs, beginning from fifth whorl, engird the whorl. In the middle of the flank or somewhat higher some of the main ribs branch, and intermediate ribs appear at the same height.

Suture line (see Fig. 4B): with narrow and high elements $VUI:I^1D$. Umbilical lobe (U) is asymmetric, slightly longer than ventral (V). First umbilical lobe (I^1) is situated on the umbilical bend.

Remarks: *Turkmeniceras turkmenicum* differs from *T. cattuloi* (PARONA, 1897, p. 141, pl. 17, fig. 5) in narrower umbilicus and sharper and less numerous ribs on earlier whorls without bundles at the umbilical shoulder.

Distribution: *Turkmeniceras turkmenicum* Zone; Tuarkyr, Kopet-Dag, Bolshoi and Malyi Balkhan, Turkmenistan.

Turkmeniceras geokderense TOVBINA, 1962

Pl. 1, Figs. 5, 6; Text-fig. 5

*1962 – *Turkmeniceras geokderense*: TOVBINA, p. 84, pl. 44, fig. 2 a-b.

1963 – *Turkmeniceras geokderense*: TOVBINA, p. 105, pl. 2, figs. 1, 2, text-fig. 5.

1999 – *Turkmeniceras geokderense*: BOGDANOVA, PROZOROVSKY, pl. 1, figs. j-l.

Holotype: CNIGR Museum 7/8293, *Turkmeniceras turkmenicum* Zone; Geokdere, Tuarkyr, Turkmenistan.

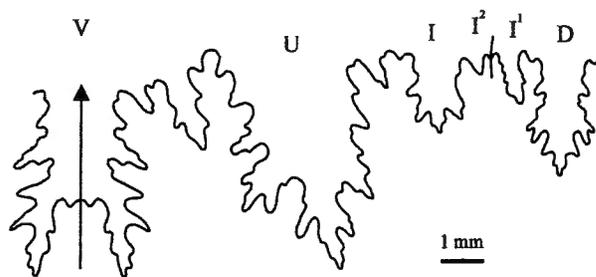


Fig. 5 — Suture line of *Turkmeniceras geokderense* TOVBINA, 1962. CNIGR Museum 19/10367: H = 7.3 mm, W = 5.0 mm.

Description: Large (D up to 140 mm), flattened ($W/D = 0.27$) shells. Whorls high ($H/D = 0.36-0.40$), moderately increasing, the first whorl embraces the initial chamber, the second adjoins the first whorl, then embracing evolves and later whorls overlap for 1/3. Flanks flat, venter wide, flat. Umbilicus moderately wide ($Du/D = 0.31-0.33$), umbilical walls from low, gently sloping to high steep. Whorl section high, rectangular-oval. Main ribs are single, more rarely biplicate, starting at the seam. Intermediate ribs (double or more rarely single) between main ribs appear in the centre of flanks. All ribs are slightly curved, on the venter they form a wide gently sloping arch forwards. On earlier whorls they are not weakened.

Suture line (Fig. 5): $VUI:I^1D$ with wide slightly asymmetric umbilical lobe equal to the ventral. The inner lobe (I) gradually transfers from the umbilical bend to the flank.

Remarks: *Turkmeniceras geokderense* differs from *T. turkmenicum* in the lack of the unfolded stage in ontogenesis, narrower umbilicus, and more intermediate ribs.

Distribution: *Turkmeniceras turkmenicum* Zone; Tuarkyr, Kopet-Dag, Bolshoi and Malyi Balkhan, Turkmenistan.

Turkmeniceras rarecostatum BOGDANOVA, 1971

Pl. 1, Fig. 4; Text-figs. 4, 6

*1971 – *Turkmeniceras rarecostatum*: BOGDANOVA, p. 66, pl. 6, figs. 3, 4, text-figs. 5, 6.

1999 – *Turkmeniceras rarecostatum*: BOGDANOVA, PROZOROVSKY, pl. 2, figs. c, d.

Holotype: CNIGR Museum 3/10096, *Turkmeniceras turkmenicum* Zone; Tekedzhik, Tuarkyr, Turkmenistan.

Description: Shells of medium size (D up to 45.5 mm), flattened or of medium width ($W/D = 0.24-0.33$). Whorls are moderately increasing, overlapping for more than 1/5. Flanks flat, venter wide, flat. Umbilicus wide ($Du/D = 0.36-0.37$) with low steep walls. Whorl section is shown

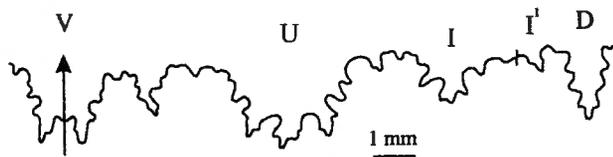


Fig. 6 — Suture line of *Turkmeniceras rarecostatum* BOGDANOVA, 1971. Holotype CNIGR Museum 3/10096: H = 13 mm.

in Fig. 4A. There are few thin and strong ribs, slightly S-shaped and straightening on the last whorl. Main ribs emerge at the seam and almost regularly alternate with short intermediate ribs. Some of the main ribs bifurcate. The ribs cross the venter with slight wide bend towards the aperture.

Suture line (Fig. 6): VUI:I'D is characterized by wide, weakly divided elements. Umbilical lobe is slightly asymmetric, as long as ventral lobe. Inner lobe (I) is situated on the umbilical wall.

Remarks: *Turkmeniceras rarecostatum* differs from *T. turkmenicum* and *T. geokderense* in greater width of the whorls (almost square in cross section), fewer almost regularly alternating main and intermediate ribs and weak division of seam saddle of the suture line.

Distribution: *Turkmeniceras turkmenicum* Zone; Tuarkyr, Turkmenistan.

***Turkmeniceras tumidum* BOGDANOVA, 1971**

Pl. 1, Fig. 8; Text-fig. 7

- * 1971 — *Turkmeniceras tumidum*: BOGDANOVA, p. 69, pl. 6, fig. 5, text-fig. 7.
- 1979 — *Deshayesites antiquus*: BOGDANOVA, p. 161, pl. 1, fig. 4, text-fig. 5a.
- 1983 — *Deshayesites antiquus*: BOGDANOVA, p. 138, pl. 2, figs. 5, 6; pl. 3, fig. 8, text-fig. 7.
- ? 1999b — *Deshayesites antiquus*: CECCA *et al.*, p. 270.
- 1999 — *Turkmeniceras tumidum*: BOGDANOVA, PROZOROVSKY, pl. 2, figs. a, b.
- 1999 — *Deshayesites antiquus*: BOGDANOVA, PROZOROVSKY, pl. 2, fig. e.

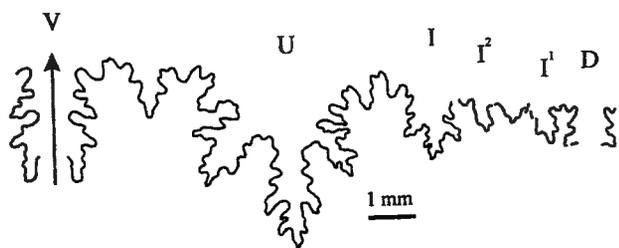


Fig. 7 — Suture line of *Turkmeniceras tumidum* BOGDANOVA, 1971. CNIGR Museum 6/10096: H = 25 mm.

(1998) 2000 — *Deshayesites antiquus*: GONNET *et al.*, p. 129, pl. 3, figs. 2-4.

Holotype: CNIGR Museum 5/10096, *Turkmeniceras turkmenicum* Zone; Gobekadzhi, Tuarkyr, Turkmenistan.

Description: Shells large (D up to 80-82 mm), medium thick ($W/D = 0.34-0.35$). Whorls are moderately increasing ($H/D = 0.40-0.42$), overlapping for $1/5$. Flanks are flat, venter wide and flat. Umbilicus moderately wide ($Du/D = 0.30-0.31$) with low, rather steep walls. Whorl section is low and trapezoidal. Main ribs appear at the seam and almost all of them bifurcate on whorls < 60 mm in diameter at umbilical bend, on larger whorls — in the middle of flank or higher. At the same growth stage, length and number of ribs decreases from 3 to 1 or to complete extinction in some intervals. All ribs become coarser with growth, very weakly S-shaped or almost straight.

Suture line (Fig. 7): VUII':I'D has a symmetric umbilical lobe, an inner lobe I, situated on the flank, and seam saddle complicated by two well-developed teeth (prolobes). In representatives of the species from the *P. tuarkyricus* Zone one of the suture teeth evolves into rather distinct lobe I², lobe I being shifted to the flank.

Remarks: *Turkmeniceras tumidum* differs from *T. rarecostatum* by its larger dimensions, more numerous coarse ribs and a more dissected suture saddle.

Distribution: *Turkmeniceras turkmenicum* Zone, Tuarkyr, Malyi Balkhan, *Turkmeniceras turkmenicum* and *Paradeshayesites tuarkyricus* zones, Tuarkyr, Turkmenistan; *Paradeshayesites tuarkyricus* Zone, La Bédoule (Bouches-du-Rhône, France).

***Turkmeniceras tovbinae* sp. nov.**

Pl. 1, Fig. 7; Pl. 11, Fig. 1; Text-fig. 8

1963 — *Turkmeniceras* sp. indet: TOVBINA, p. 106, pl. 2, fig. 3.

Derivation of name: Named after the Russian palaeontologist S. Z. Tovbina.

Holotype: CNIGR Museum 9/8293, *Turkmeniceras turkmenicum* Zone; Gobekadzhi, Tuarkyr, Turkmenistan.

Paratypes: CNIGR Museum 236/10367, *Turkmeniceras turkmenicum* Zone, Gobekadzhi; 237/10367, *Turkmeniceras turkmenicum* Zone, Geokdere; Tuarkyr, Turkmenistan.

Material: eight shell and mould fragments of various sizes. Earlier whorls are not preserved. Suture line is distinctly visible.

Description: Large flattened shells with trapezoidal whorl section. Umbilical walls low, rather steep. Ribbing dense, consist of main and intermediate ribs. Main ribs are

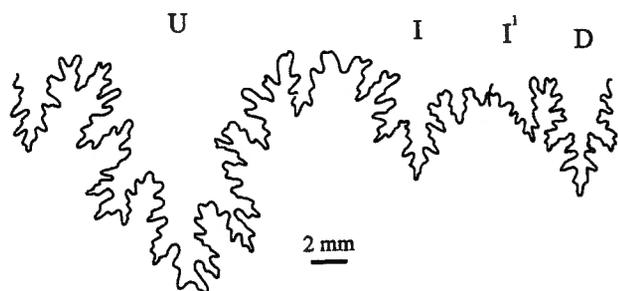


Fig. 8 — Suture line of *Turkmeniceras tovbinae* sp. nov. Holotype CNIGR Museum 9/8293: H = 21.8 mm, W = 15.8 mm.

mostly branching; double branching forming bundles is not infrequent. Main ribs appear at the seam, on the umbilical wall they are thin, in the transition to the flank these ribs become thicker to form high crests on the umbilical bend. Intermediate ribs (2 or 3 between main ribs) appear at various height of the whorl, some of them sometimes with recurring branching. All ribs of the flank are radial, weakly S-shaped, on the venter they form a very weak wide bend towards the aperture. In the middle of flanks ribbing is slightly smoothed.

Suture line (Fig. 8). Umbilical lobe wide, asymmetric, situated below ventral lobe; lateral saddle wide, bifid, occurs at the same level as outer saddle; lobe I occurs on umbilical bend, with the growth of the shell it moves to the flank; saddle I/I¹ is divided by two teeth on the umbilical bend; dorsal lobe shorter than umbilical lobe.

Measurements:

No	D	H	W	Du	H/D	W/D	Du/D
237/10367	66.7	26.5	19.4	26.2	0.40	0.29	0.39

Remarks: *Turkmeniceras tovbinae* differs from well-known species of the genus *Turkmeniceras* in its dense, irregular nodular ribbing and more divided saddle I/I¹. The rather densely ribbed *T. geokderense* is characterized by fewer intermediate ribs and absence of bundles. Features of the new species mentioned above allow it to be considered as the youngest member of the genus *Turkmeniceras* along with a similarly “advanced” species as *T. tumidum*.

Distribution: *Turkmeniceras turkmenicum* Zone; Gobe-kadzhi, Tekedzhik, Geokdere, Tuarkyr, Turkmenistan.

Genus *Deshayesites* KAZANSKY, 1914

- 1875 — *Hoplites*: NEUMAYR, p. 29 pars.
 1914 — *Hoplites (Deshayesites)*: KAZANSKY, p. 99.
 1922 — *Parahoplitoides*: SPATH, p. 111.
 1926 — *Deshayesites*: RENNGARTEN, p. 30.
 1964 — *Deshayesites*: CASEY, p. 291.
 1999 — *Deshayesites*: BOGDANOVA, MIKHAILOVA, p. 51.

Type species. *Ammonites deshayesi* D'ORBIGNY, 1841; Lower Aptian; Northern France.

Diagnosis. Shell small, medium-sized or large. Whorls rectangular-oval, moderately rapidly or rapidly increasing. Ribs widely to closely spaced. Rib intercalation regular or irregular. One to two intercalating ribs present. In coarsely ribbed species umbilical nodes are present. In juveniles ribbing interrupts at venter.

Suture line morphogenesis of the genus *Deshayesites* is the most complete (see above, p. 00, Fig. 2). Primasuture is five-lobed (VUU¹ID), early reduction of lobe U¹ and later appearance of new lobes (I¹, I²) as a result of saddle division I/D. Formula of the suture line at the adult stage is (V₁V₁) UII²:I¹D.

Composition: In addition to the type species, about forty species are assigned to this genus. Besides the species mentioned earlier (BOGDANOVA, MIKHAILOVA, 1999, p. 525), are: *D. boegvadi* (ROSENKRANTZ in BØGVAD & ROSENKRANTZ, 1934) (Lower Aptian, fissicostatus Zone of NE Greenland); *D. flexuosus* CHIRIAC, 1981 (Lower Aptian, deshayesi Zone of Romania); *D. bedouliensis* CECCA *et al.*, 1999b (Lower Aptian, tuarkyricus Zone of SE France); *D. bogdanovae* AVRAM, 1999 (Lower Aptian of Romania).

Comparison: The genus *Deshayesites* differs from the genus *Turkmeniceras* in its non-perforated early whorls (first and second whorls) and in more involute succeeding whorls, in crescent ribbing, irregular intercalation of secondary ribs, in the presence of umbilical nodes in some species, in larger number of inner lobes [the inner saddle (I/D) more strongly incised] and in lobes I and I² present on the flanks.

Distribution. Lower Aptian, Western and Eastern Europe, Central Asia.

Deshayesites consobrinus (D'ORBIGNY, 1841)

Pl. 4, Figs. 1-3

- * 1841 — *Ammonites consobrinus*: D'ORBIGNY, p. 147, pl. 47, figs. 1-3.
 1964 — *Deshayesites consobrinus*: CASEY, p. 350, text-figs. 123 a-c, 124 a, b.
 non 1979 — *Deshayesites consobrinus*: BOGDANOVA, p. 159, pl. 2, figs. 3,4 (= *D. kemperi* sp. nov.).
 non 1999 — *Deshayesites consobrinus*: BOGDANOVA, PROZOROVSKY, pl. 3, figs. g-i (= *D. kemperi* sp. nov.).
 (1998) 2000 — *Deshayesites consobrinus*: ROPOLLO *et al.*, p. 163, figs. 3 – 1-2,4.

Lectotype (selected by CASEY, 1964): 5579a, d'Orbigny Coll., Laboratoire de Paléontologie, Muséum National d'Histoire naturelle, Paris, Lower Aptian, La Bédoule (Bouches-du-Rhône, France).

Description: Shell medium-sized to large (D = 40-150 mm), flattened and of medium thickness (W/D = 0.25-

0.36). Whorls are overlapping for $\frac{1}{4}$, slowly increasing. Flanks are flat or slightly convex, venter is narrow, convex, sometimes rather wide, flattened. Umbilicus wide ($D_u/D = 0.35-0.38$) with low, gently sloping walls. Whorl section rectangular-oval. Ribs thin, sharp, high, distinctly S-shaped and slightly inclined forwards from the radius. Main ribs appear on the umbilical wall, single or bifid. Intermediate ribs, one for each interval, short, single ribs are lacking on adult whorls. On whorls of $D = 10-12$ mm venter ribs are essentially weakened, on later whorls they cross the venter to form a steep arch towards the aperture. Suture line pattern is characteristic of the genus.

Remarks: *Deshayesites consobrinus* (D'ORBIGNY, 1841) differs from *D. deshayesi* (D'ORBIGNY, 1840) in having a larger shell, narrower and less overlapping whorls. CASEY (1964, p. 350) selected a lectotype from the d'Orbigny collection (5579a; CASEY, 1964, text-fig. 124b). ROPOLO *et al.*, 1998 (2000a) revised newly collected specimens of *D. consobrinus* from its stratotype area (Cassis – La Bédoule) and agreed with CASEY's choice of a lectotype.

Distribution: *Prodeshayesites weissi* Zone, Southern France; for *D. cf. consobrinus* in CASEY (1964, p. 353) *Deshayesites forbesi* Zone, *D. fittoni* Subzone, Southern England; *D. dechyi* Zone, Daghestan, Russia; *Paradeshayesites weissi* and ? *Deshayesites deshayesi* Zones, Tuarkyr, Kubadag, Bolshoi Balkhan, Turkmenistan.

***Deshayesites dechyi* (PAPP, 1907)**

Pl. 3, Figs. 6-8; Text-fig. 9

- *1907 – *Parahoplites dechyi*: PAPP, p. 171, pl. 9, figs. 3-5 (only), not figs. 1, 2.
- 1914 – *Hoplites (Deshayesites) deshayesi*: KAZANSKY, p. 100, pl. 7, fig. 100.
- 1926 – *Deshayesites dechyi*: RENNGARTEN, p. 30, pl. 2, figs. 11-12, pl. 9, fig. 6.

- 1952 – *Deshayesites dechyi*: LUPPOV, p. 204, pl. 7, figs. 2-4.
- 1961 – *Deshayesites dechyi*: ERISTAVI, p. 50, pl. 1, fig. 12.
- 1977 – *Deshayesites dechyi*: BOGDANOVA, p. 50, pl. 2, fig. 1-5.
- 1979 – *Deshayesites dechyi*: BOGDANOVA *et al.*, p. 5, pl. 1, figs. 4,5; pl 2, figs. 1-3.
- 1999 – *Deshayesites dechyi*: BOGDANOVA, PROZOROVSKY, pl. 4, figs. d-f.

Lectotype: K.7593 Geological Museum of the Geological Institute of Hungary (MAFI), Budapest. [PAPP, 1907, p. 171, pl. 9, fig. 3, (Fig. 9a), Lower Aptian, Lavaschi, Daghestan]

Description: Flattened medium-sized shells (D from 25 to 55 mm, rarely larger) with moderately high overlapping and slowly growing whorls ($H/D = 0.40-0.43$). Whorl section rectangular-oval. Venter wide, mostly flattened. Transition of the venter to flanks is gradual, indistinct. Flanks, as a rule, flat, but sometimes weakly convex and diverging towards umbilicus. Umbilical bend smooth, umbilical wall gently sloping. Umbilicus moderately wide ($D_u/D =$ from 0.27 to 0.33).

Sculpture appears at the end of the third whorl, and at the beginning of the fourth whorl it looks like lateral swellings, first rounded, then radially elongated. True ribs can be traced from the centre of the fourth whorl. At this stage all ribs cross the venter without interruptions and weakening.

Sculpture of adult shells is represented by irregularly alternating main and intermediate ribs, up to 50 in medium-sized shells. Main ribs appear on the umbilical wall, at different height from the seam. On the umbilical bend they sometimes take the form of narrow high crests, and are rather strongly pointed forwards in the lower part of the flank. In the middle of the flank they are variously bent backwards, and on the venter they form a rather steep arch forwards.

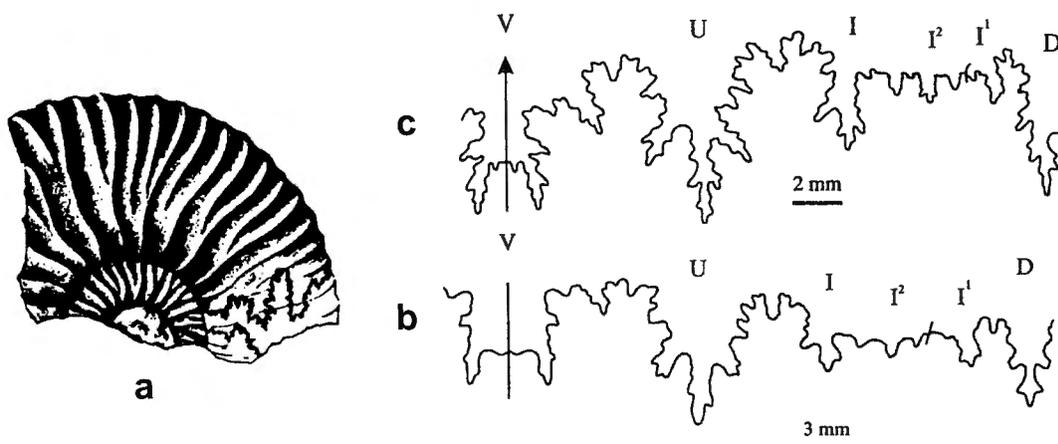


Fig. 9 — *Deshayesites dechyi* (PAPP, 1907). a – lectotype (PAPP, 1907, pl. 9, fig. 3), lateral side, Lower Aptian, Lavaschi, Daghestan; b – c – suture line: b – MSU 17/99: $H = 13.5$ mm, c – CNIGR Museum 13/10685: $H = 15.7$ mm.

Intermediate ribs (one or two per interval in earlier whorls and one in later whorls), being frontal or rear branches of main ribs, intercalate more rarely. Intercalating ribs appear on the centre of flanks. As a rule, branching ribs appear lower than intercalating ribs, most frequently in the lower third, more rarely in the lower half of flanks. When there are two intermediate ribs, the frontal rib is commonly longer than the rear.

All the ribs sharp, narrow. S-shaped rib curve typical of the species can differ widely both between different specimen or on one and the same specimen. This peculiarity combined with irregular intercalation of main and intermediate ribs imparts a chaotic, irregular character to the ribbing. On later whorls, particularly on the body chamber, intermediate ribs are often lacking and all ribs are inclined forwards. Main ribs appear on the umbilical wall, rapidly strengthen and with crescent outlines on the flanks.

Suture line (Fig. 9): ventral lobe (V) short, wide, bifid. Umbilical lobe (U) longer than ventral, slightly asymmetric, with more evolved outer branch. Inner lobe (I) is weakly evolved. One-end dorsal lobe (D) is almost of the same depth as umbilical lobe. Lobe I² is situated on umbilical wall and separated from lobe I by wide saddle. Outer and inner saddles are wide; umbilical saddle narrow, slightly lower than outer saddle.

Remarks: *Deshayesites dechyi* is one of the most widespread species of the genus. Essentially different specimens integrated into the species *Parahoplites dechyi* were depicted in PAPP (1907, pl. 9). The small specimens (figs. 1, 2) differ from large ones in ribbing and overlapping, i.e. specific features. After studying the RENN-GARTEN (1926, coll. 334) and LUPPOV (1952, coll. 6136) collections from the Caucasus in the CNIGR Museum we came to the conclusion that *Deshayesites dechyi* sensu Renngarten and sensu Luppov is similar to PAPP (1907, figs. 3-5) (large specimens).

RENNGARTEN, (1951, p. 55) thought that the Caucasus species *D. dechyi* most probably was a vicarious species often replacing *D. deshayesi* (LEYMERIE) eastwards of France.

Slight embracing, irregular ribbing and whorl section bring *D. dechyi* close to *D. bodei* VON KOENEN (1902, p. 221, pl. 9, figs. 1a-c, see Pl. 2, Fig. 1), but ribbing of the former is denser and its whorls are relatively wider.

Adult specimens of *D. dechyi* resemble *D. germanicus* (CASEY, 1964, p. 560, text-fig. 127g) in rib density, intercalation of main and intermediate ribs, the outlines of the ribs and a wide umbilicus. This is particularly true of forms with dense ribbing and those with rapidly increasing whorls. The basic difference consists in the shape of suture line elements. A specific difference is the rectangular-oval whorl section of the described species in contrast to the oval shape of *D. germanicus*.

Distribution: *Deshayesites dechyi* – *D. deshayesi* Zones, Daghestan, the Northern Caucasus and Georgia; *Parade-*

shayesites weissi and *Deshayesites deshayesi* Zones, Turkmenistan.

***Deshayesites lavaschensis* KAZANSKY, 1914**

Pl. 8, Figs. 3-5

*1914 – *Hoplites (Deshayesites) lavaschensis*: KAZANSKY, p. 105, pl. 6, fig. 86.

(non pl. 6, fig. 87 = *Paradeshayesites weissi* (NEUMAYR & UHLIG, 1881).

1999 – *Deshayesites lavaschensis*: BOGDANOVA, pl. 1, figs. 4-7.

Lectotype: KAZANSKY, 1914, pl. 6, fig. 86, Lower Aptian, Lavashi, Daghestan (initially the Kazansky collection was kept at Tomsk, but now its location is unknown). KAZANSKY figured two specimens and only one of them really belongs to his new species.

Description: Shells are small (D from 23 to 40 mm, rarely larger), semi-involute, with high whorls ($H/D = 0.37-0.43$), embracing one another slightly less than half the height. The cross section of the whorl is ellipsoidal ($W/D = 0.28-0.31$) with a narrow, rounded venter and slightly convex flanks. Umbilical wall low, gently sloping; umbilicus rather wide ($Du/D = 0.29-0.35$).

Shell is covered with thin, slightly curved dense ribs, ranging from 55 to 58 on the last whorl. Main ribs begin on the umbilical wall, gradually become stronger and with strong incline cross the lower part of the flank; in the upper part of the flank main ribs bend backwards and with slight incline forwards cross the venter. Intermediate ribs, mainly intercalating, begin above the middle of the flank, gradually become stronger and when passing to the venter, they do not differ from main ribs; rarely intermediate ribs are branches of main ribs. Sometimes ribs converge near the body chamber.

Suture line: ventral lobe (V) shallow, wide; deeper umbilical lobe (U) trifid, relatively symmetric. Outer saddle (V/U) wide, bifid with inner branch higher than outer branch.

Remarks: *Deshayesites lavaschensis* differs from *D. dechyi* in denser and almost always intercalating ribs, whereas intermediate ribs in *D. dechyi* are fairly often branches of main ribs.

Distribution: *Deshayesites dechyi* Zone, Daghestan, Northern Caucasus, Russia; Lower Aptian "plate", Mangyshlak, Kazakhstan.

***Deshayesites robustocostatus* MIKHAILOVA, 1958**

Pl. 6, Figs. 7, 8; Text-fig. 10

*1958 – *Deshayesites robustocostatus*: MIKHAILOVA, p. 25, pl. 1, fig. 6.

1999 – *Deshayesites robustocostatus*: BOGDANOVA, p. 44.

Holotype: MSU 5/99, *Deshayesites dechyi* Zone; Tsudakhar, Daghestan, Russia.

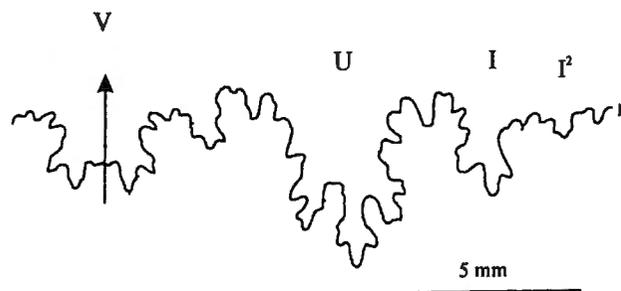


Fig. 10 — Suture line of *Deshayesites robustocostatus* MIKHAILOVA, 1958. Holotype MSU 5/99: H = 10.2 mm, W = 7.2 mm.

Description: Shells small to medium-sized (D from 15 to 45 mm), semi-evolute with high whorls, overlapping one another for no more than 1/3 of the height. Whorl section low, wide, ellipsoidal to rounded-square, then rounded-rectangular; venter rounded, flanks slightly convex, umbilical wall steep; umbilicus rather wide. When diameter is less than 15 mm, height of the whorl notably decreases and its width increases.

Thin, dense ribs represent sculpture. Main ribs begin on umbilical wall; soon they become stronger and cross the flank, at first bending slightly forwards and then (on the upper part of flank) backwards. All ribs interrupt on the venter. Intermediate ribs (one or two between neighbouring main ribs) intercalate in the middle of the flank, but sometimes they are branches of main ribs. When the whorl diameter exceeds 40 mm, ribs become stronger, widen slightly and cross the venter without weakening.

Suture line (Fig. 10): wide ventral lobe is half as long as umbilical (U) and almost equals the narrow inner lobe

(I) in depth. Trifid umbilical lobe is the deepest and is almost symmetrical. Second inner lobe (I²) occurs near the seam. Low and wide outer saddle (V/U) is bifid, with branches of different height.

Remarks: *Deshayesites robustocostatus*, when its diameter exceeds 35 mm, differs from other species in the sudden transition from sculpture with dense ribbing to sparser ribbing. Such changes in the character of the ribbing are also typical of *D. kudrjavzevi* MIKHAILOVA, 1958 (see below) but in the latter ribs become gradually less pronounced later on the shell, and there are differences in the shape of the shell

Distribution: *Deshayesites dechyi* Zone, Daghestan, Russia; Lower Aptian "plate", Mangyshlak, Kazakhstan.

***Deshayesites kudrjavzevi* MIKHAILOVA, 1958**

Pl. 5, Figs. 4-6; Text-fig. 11

*1958 — *Deshayesites kudrjavzevi*: MIKHAILOVA, p. 26, pl. 1, fig. 6.

1999 — *Deshayesites kudrjavzevi*: BOGDANOVA, p. 44.

1999 — *Deshayesites kudrjavzevi*: BOGDANOVA, PROZOROVSKY, pl. 7, fig. a.

Holotype: MSU 1/99 (= MIKHAILOVA, 1958, pl. 1, fig. 6, N 2102/1), *Deshayesites dechyi* Zone; Kuma River, Northern Caucasus, Russia.

Description: Flattened (W/D = 0.27-0.30) large shells (D from 60 to 107.5 mm) with high whorls (H/D = 0.39-0.46); in specimens of more than 75 mm in diameter embracing one another for about 1/3 of their height.

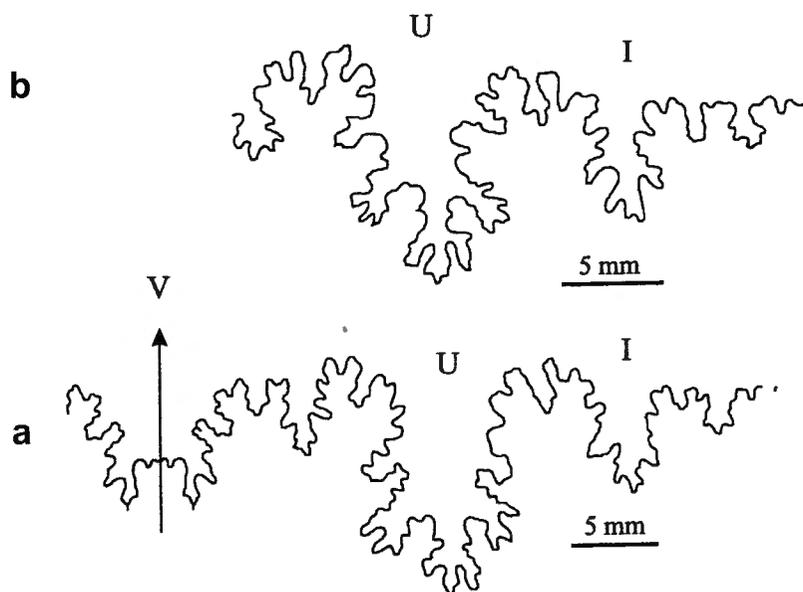


Fig. 11 — Suture line of *Deshayesites kudrjavzevi* MIKHAILOVA, 1958. a — MSU 13/97: H = 25.8 mm, b — Holotype MSU 1/99: H = 27.0 mm.

Whorl section is high-oval. Venter wide, moderately convex, gradually transforms into weakly and uniformly convex flanks; middle part of the whorl is the widest, umbilical wall low and gently sloping. Umbilicus moderately wide ($D_u/D = 0.24-0.32$).

Ribbing rather dense and irregular. On the last whorl of 110.5 mm in diameter there are 50 ribs: 27 ribs on one half of the whorl and 23 on the other. The main ribs appear in the upper part of the umbilical wall; they are similar in height and width along the flank, weakly S-shaped. Intermediate ribs on the first half of the described last whorl (commonly two intermediate ribs between neighbouring main ribs) appear in the middle of the flank; they are often branches of main ribs, and in the upper third of the flank intermediate ribs do not differ from the main ribs. On the second half of this whorl intermediate ribs almost exclusively intercalate and, as a rule, there is one intermediate rib between two neighbouring main ribs. On the flank all the ribs are distinctly inclined forwards from the radius, on the venter they do not weaken and form a wide arch forwards. On the body chamber ribs occur more rarely and lose S-shaped bend on sides. There is regular intercalation of main and intermediate (intercalating) single ribs which emerge in the upper part of flanks.

Suture line (Fig. 11): large, relatively symmetric umbilical lobe (U) is much larger than neighbouring lobes (V and I). Wide outer saddle is bifid, with branches of different height, characteristic of the genus *Deshayesites*.

Remarks: *Deshayesites kudrjavzevi* resembles *D. caseyi* sp. nov. (see below) and *D. evolvens* LUPPOV (1952, pl. 8, fig. 1) in shape and character of sculpture. Sculpture of *D. evolvens* is coarser, and when the whorl is more than 40 mm in diameter, there is a sharp bent of the ribs in the middle of the flank, whereas *D. kudrjavzevi* is characterized by general weakening of sculpture at this stage. *D. kudrjavzevi* differs from representatives of *D. dechy* with dense ribbing in large size of the shell and changes in ribbing on large whorls.

Distribution: *Deshayesites dechy* Zone, Northern Caucasus, Russia; *Paradeshayesites weissii* and *Deshayesites deshayesi* Zones, Turkmenistan; Lower Aptian "plate", Mangyshlak, Kazakhstan.

***Deshayesites volgensis* SAZONOVA, 1958**
Pl. 3, Figs. 3, 4; Text-fig. 12

*1958 – *Deshayesites volgensis*: SAZONOVA, p. 119, pl. 1, figs. 1, 2, 4; pl. 5, fig. 3.

2002 – *Deshayesites volgensis*: BARABOSHKIN, MIKHAILOVA, pl. 3, fig. 1.

Holotype: CNIGR Museum 1/11805, *Deshayesites volgensis* Zone; Sengiley, Ulyanovsk Region, Russia.

Description: Shells small to medium-sized (D up to 35 mm), from semi-involute to semi-evolute ($D_u/D = 0.28-0.35$). Whorl section high-oval ($W/H = 0.70$) with

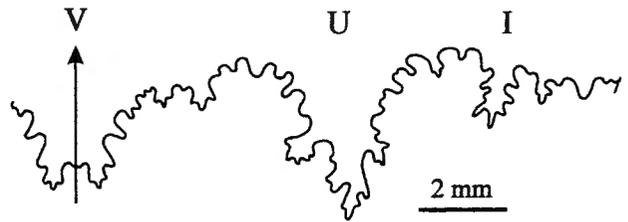


Fig. 12 — Suture line of *Deshayesites volgensis* SAZONOVA, 1958. MSU 30/96: H = 11.0 mm, W = 8.2 mm.

narrow, rounded venter and weakly convex flanks. Umbilical wall is rather low, umbilicus from rather narrow to relatively wide.

Sculpture is represented by distinct, dense ribs (40 to 42 on the last whorl) (Pl. 3, Fig. 3). Main ribs emerge on the umbilical wall, soon become stronger and with slight, if any, bend (subradially) cross the flank. Intermediate ribs are branches of main ribs, diverge from them in the middle of the flank; on older whorls they sometimes appear irrespective of main ribs. On the venter all the ribs are similar and cross it with a distinct bend forwards.

Suture line (Fig. 12): shallow bifid ventral lobe (V); deeper umbilical lobe (U) is trifid, slightly asymmetric; small inner lateral lobe (I) is half as long as umbilical lobe; wide inner saddle with branches of different height (V/U) and a slightly higher narrow lateral saddle (U/I).

Remarks: *Deshayesites volgensis* is typical for the zone of the same name from the Lower Aptian of the Volga Region, Ulyanovsk. These Lower Aptian forms from the Middle Volga were mentioned earlier as *D. deshayesi* (D'ORBIGNY, 1841), or as *D. consobrinoides* (SINZOW) (1898, pl. A, fig. 10).

D. volgensis is very close to the English species *D. forbesi* CASEY, 1961. According to CASEY, the holotype of *D. volgensis* is too small for critical analysis of the species, but two paratypes (SAZONOVA, 1958, pl. 1, figs. 2, 4) are very close to *D. forbesi*.

We consider that both taxa should be preserved. *D. forbesi* differs from *D. volgensis* in larger dimensions, lower point of rib branching and a more distinct rib bend on the flank. True, in the holotype of *D. forbesi*, this feature is traced all over the last whorl, and in the specimen from the Volga Region it is distinct only on the second half of the last whorl (compare Pl. 3, Fig. 2 with CASEY, 1961, pl. 81, fig. 2).

CASEY (1964, p. 325) when interpreting SAZONOVA (1958, p. 120) considered that *D. volgensis* occurred in the *D. deshayesi* Zone, i.e. above the level with *D. forbesi*. But in fact, they occur at the same stratigraphic level.

Distribution: *Deshayesites volgensis* Zone, Ulyanovsk Region, Russia.

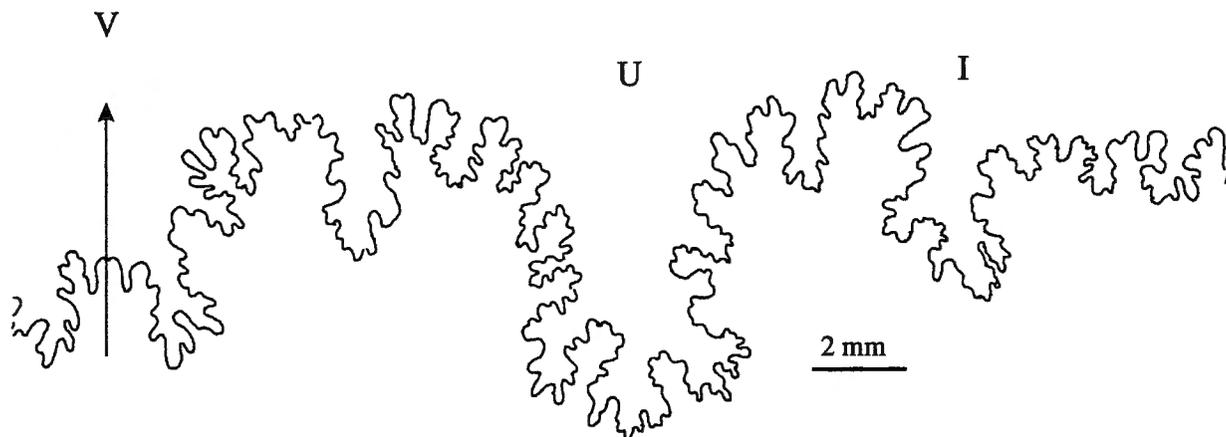


Fig. 13 — Suture line of *Deshayesites gracilis* CASEY, 1964. MSU 25/96: H = 18.5 mm, W = 14.9 mm.

***Deshayesites gracilis* CASEY, 1964**

Pl. 6, Figs. 5, 6; Text-fig. 13

- *1964 — *Deshayesites gracilis*: CASEY, p. 324, pl. 47, fig. 10.
 1999 — *Deshayesites gracilis*: AVRAM, p. 444, fig. 4C.
 2002 — *Deshayesites gracilis*: BARABOSHKIN, MIKHAILOVA, pl. 2, fig. 3.

Holotype: BM C3034, Atherfield Clay Series, Crackers, Atherfield, Isle of Wight, UK.

Description: Shell is medium-sized ($D = 40\text{--}55$ mm), semi-involute ($Du/D = 0.25\text{--}0.30$) with high rounded cross section; the whorl is the widest on the umbonal bend. Flanks flattened, venter narrow, rounded. Umbilicus is relatively narrow, umbilical wall steep.

Raised ribs, approaching 50 on the last whorl, often represent sculpture. Main ribs appear on the umbonal bend, soon become stronger, with an S-shaped bend on the flank and cross the venter with a wide bend forwards. Intermediate ribs are branches of main ribs, or appear independently of these in the middle or on the lower third of flanks. There are one or two intermediate ribs between two neighbouring main ribs.

Suture line (Fig. 13): with shallow ventral lobe (V); a deeper, slightly asymmetric umbilical lobe (U); small sharply asymmetric inner lateral lobe (I); wide outer saddle with branches of slightly unequal height (V/U) is deeply dissected by secondary lobe; narrower, but slightly higher lateral saddle (U/I).

Remarks: CASEY (1964, p. 325) discussed the resemblance of *D. gracilis* with several close taxa [*D. forbesi* CASEY, 1961, *D. forbesi* var. *koeneni* CASEY, 1964, *D. multicostatus* SWINNERTON, 1935, *D. subfissicostatus* (SINZOW, 1898)]. On the whole we agree with CASEY, but we have a few remarks for the last of these species (see above).

Distribution: *Deshayesites forbesi* Zone, Isle of Wight, UK; Romania; *D. volgensis* Zone, Ulyanovsk Region, Russia.

***Deshayesites luppovi* BOGDANOVA, 1983**

Pl. 2, Figs. 8, 9; Text-fig. 14

- 1952 — *Deshayesites* aff. *dechy*: LUPPOV, p. 203, pl. 7, fig. 1.
 * 1983 — *Deshayesites luppovi*: BOGDANOVA, p. 139, pl. 3, figs. 1-6, text-fig. 8.
 1999 — *Deshayesites luppovi*: AVRAM, p. 447, figs. 5F, G.
 1999 — *Deshayesites luppovi*: BOGDANOVA, PROZOROVSKY, pl. 3, fig. f.
 (1998) 2000 — *Deshayesites luppovi*: GONNET, ROPOLO & CONTE, p. 130, pl. 2, figs. 1,2; pl. 4, fig. 2.

Holotype: CNIGR Museum 23/9442, *Paradeshayesites weissi* Zone; Bordzhakly, Bolshoi Balkhan, Turkmenistan.

Description: Shells medium-sized (D up to 73 mm), flattened ($W/D = 0.21\text{--}0.27$). Whorls high ($H/D = 0.35\text{--}0.40$), overlapping for one third, with slow growth. Flanks and venter flattened. Umbilicus from moderately wide to wide ($Du/D = 0.30\text{--}0.36$) with low steep walls. Whorl section is rectangular-oval. Ribs dense, strongly S-shaped, strongly flattened in the upper part of the flanks and on the venter. Main ribs appear on the umbilical wall, form high longitudinal crests on the umbonal bend, often bifurcate in the lower third of the whorl height. Single intermediate ribs appear irregularly between main ribs and are lacking on the body chamber.

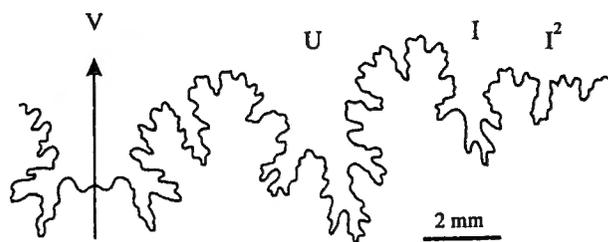


Fig. 14 — Suture line of *Deshayesites luppovi* BOGDANOVA, 1983. CNIGR Museum 27/9442: H = 17.5 mm.

Suture line (Fig. 14): outer part of the lobe line is preserved. Wide ventral lobe (V); trifid asymmetric umbilical lobe (U) is slightly deeper than ventral lobe; narrow, shallow inner lobe (I); small second inner lobe (I^2); lobe I^3 near umbonal wall.

Remarks: *Deshayesites luppovi* differs from *D. dechy* in a greater number of flat and more curved ribs on flanks and the venter, in lesser relative height of whorls and the presence of umbilical lobe I^3 .

Distribution: Lower Aptian, north-west Caucasus, Russia; *Paradeshayesites tuarkyricus* and *P. weiss* Zones, Turkmenistan; *P. tuarkyricus* Zone, Southern France; *P. weiss* Zone, Romania.

***Deshayesites pappi* BOGDANOVA, 1991**
Pl. 3, Fig. 5; Text-fig. 15

- *1991 – *Deshayesites pappi*: BOGDANOVA, p. 82, pl. 2, figs. 4–6, text-fig. 3.
- 1999 – *Deshayesites pappi*: BOGDANOVA, p. 347, pl. 1, fig. 8.
- 1999 – *Deshayesites pappi*: BOGDANOVA, PROZOROVSKY, pl. 5, fig. c-e.
- 1999a – *Deshayesites pappi*: CECCA *et al.*, pl. 1, fig. 8.

Holotype: CNIGR Museum 9/12730, *Paradeshayesites weiss* Zone; Tekedzhik, Tuarkyr, Turkmenistan.

Description: Shells small to medium-sized (D up to 30.3 mm), of medium width ($W/D = 0.30-0.37$). Whorls moderately high ($H/D = 0.34-0.38$), with moderate and slow growth, not much overlapping. Flanks weakly convex, venter wide, flattened. Umbilicus wide ($Du/D = 0.35-0.36$) with low gently sloping wall. Whorl section rectangular-rounded. Ribs dense, sharp, distinctly S-shaped, slightly curved backwards from the radius. Main ribs appear at the seam, most of them are bifurcate. Intermediate ribs rare, beginning in the middle of the flank, but are lacking on the body chamber. Ribs are strongly bent on the venter towards the aperture.

Suture line (Fig. 15): characterized by wide, moderately dissected elements. Ventral lobe (V) wide, shallow. The deepest umbilical lobe (U) is wide, symmetrical or weakly asymmetrical, with low-set and weakly developed lateral branches. Shallow narrow inner lobe (I) occurs at the umbilical bend, near it and close to the seam there is a small second inner lobe (I^2). Bifid outer saddle (V/U) with tops of various heights.

Remarks: *Deshayesites pappi* differs from *D. dechy* in lesser dimensions, greater width, less overlapping of whorls and fewer ribs directed backwards from the radius. Such features as small dimensions of the shell and distinct bifurcating ribs approach Turkmenian specimens of *D. volgensis* SAZONOVA (1958, p. 119, pl. 1, figs. 1, 2, 4). But the Turkmenian species differs from those from the Volga Region in less overlapping and irregular ribbing.

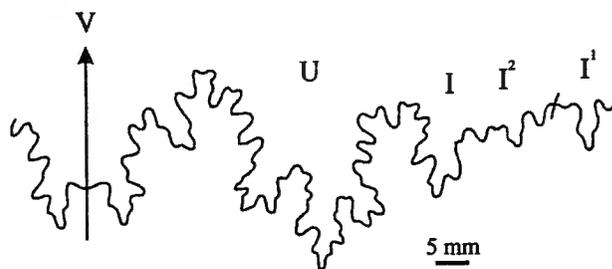


Fig. 15 — Suture line of *Deshayesites pappi* BOGDANOVA, 1991. CNIGR Museum 15/12730: H = 8.0 mm.

D. pappi differs from *D. consobrinus* in its smaller shell, the presence of dense bifurcating ribs and greater whorl inflation.

AVRAM (1999, p. 452) included the species into the synonymy of *D. pygmaeus* CASEY (1964, p. 20, pl. 50, fig. 5). But *D. pappi* differs from the latter in less overlapping, finer ribbing and higher location of rib bifurcation and in having fewer ribs. In the Bordzhakly section (Bolshoi Balkhan, Turkmenistan) a specimen of ammonite almost similar to the English species *D. pygmaeus* was found, which explicitly differs from samples included into *D. pappi*.

Distribution: *Paradeshayesites weiss* Zone; Tuarkyr, Bolshoi Balkhan, Kubadag, Turkmenistan; *Deshayesites dechy* Zone, Dagestan, Russia.

***Deshayesites caseyi* sp. nov.**
Pl. 5, Figs. 1, 2

Derivation of name: in honour of Raymond Casey – English palaeontologist and stratigrapher.

Holotype: MSU 6/99, *Deshayesites dechy* Zone, Kuban, Northern Caucasus, Russia.

Paratypes: MSU 7/99, 8/99, 9/99, *Deshayesites dechy* Zone, Kuban, Northern Caucasus, Russia.

Material: About 40 poorly preserved specimens (shells are incomplete), initial whorls are ferruginous and often destroyed.

Description: Semi-evolute shell with high ($H/D = 0.38-0.41$) and narrow ($W/D = 0.23-0.24$) whorls, overlapping preceding whorl less than a half of height. Whorl section is rather high than wide, with slightly rounded venter and flattened flanks, slightly diverging towards umbilicus. Umbilicus moderately wide ($Du/D = 0.30-0.32$) with low and gently sloping walls.

Shell is smooth up to 2.7 mm of whorl height. Ribs appear at 2.7 mm of the whorl height (specimen n° 6/99): main ribs are distinct on flanks and hardly visible on venter.

Intermediate ribs are not distinct. Later main and intermediate ribs are similar. Main ribs originate at umbilical wall; intermediate ribs are slightly lower than mid-flanks, equal to those on venter with slight bend towards the aperture.

When the whorl reaches 35-40 mm in diameter, ribs become coarser and less numerous. Rib intercalation is irregular, sometimes intermediate ribs are lacking; sometimes one or two are present between a pair of main ribs.

There are about 22 ribs on half of the last whorl at a diameter of 41 mm, and 18 coarse ribs on half the last whorl at a diameter of about 85 mm. Ribs bent slightly forwards and are less sinusoid than earlier ribs. Rib intercalation is regular and bifurcation occurs very rarely.

Suture line is not visible.

Measurements:

No	D	H	W	Du	H/D	W/D	Du/D
8/99	41.3	17.0	—	13.2	0.41	—	0.32
9/99	45.5	17.8	—	13.9	0.39	—	0.31
7/99	66.7	25.5?	16.1	20.0?	0.38	0.24	0.30
6/99	85.0	33.0	19.7	25.5	0.39	0.23	0.30

Remarks: *Deshayesites caseyi* up to 40 mm in diameter is very similar to *D. consobrinoides* (SINZOW) in whorl-section and type of sculpture, but its umbilicus is wider. Shells of *D. caseyi* of larger diameter are characterized by coarser and more spaced ribs, and differ from *D. consobrinoides* in greater whorl thickness and in having fewer ribs. The described species differs from *D. kudrjavzevi* (see above) in coarser ribs and narrower whorl-section. *D. caseyi* is rather similar to *D. evolvens* LUPPOV (1952, pl. 8, fig. 1). Main differences of whorls of more than 40 mm in diameter are:

1. dense, somewhat sigmoid ribs with indistinct shape of *D. caseyi*,
2. two or three intermediate ribs between a pair of main ribs of uncertain origin in *D. evolvens*.

Distribution: *Deshayesites dechyi* Zone; Kuban, Northern Caucasus, Russia.

Deshayesites kemperi sp. nov.

Pl. 4, Figs. 4, 5; Pl. 10, Figs. 4-6; Text-fig. 16

1979 — *Deshayesites consobrinus* D'ORBIGNY: BOGDANOVA, 1979, p. 159, pl. 2, fig. 3, 4.

1999 — *Deshayesites consobrinus*: BOGDANOVA, PROZOROVSKY, pl. 3, figs. g-i.

Derivation of name: in honour of Edwin Kemper, German palaeontologist and stratigrapher.

Holotype: CNIGR Museum 31/10367, *Paradeshayesites weissi* Zone, Bordzhakly, Bolshoi Balkhan, Turkmenistan.

Paratypes: CNIGR Museum 32/10367, 35/10367, *Paradeshayesites weissi* Zone, Bordzhakly; 257/10367, *P. weissi* Zone, Utuludzha; Bolshoi Balkhan, Turkmenistan.

Material: Ten ammonite shells of various preservations. Suture line well defined.

Description: Shells medium-sized, with whorls of medium width, slowly increasing and weakly overlapping. Whorls section trapezoidal to rectangular-oval. Flanks flat or slightly convex, venter slightly convex, rounded. Umbilicus from wide ($Du/D = 0.35-0.43$) to very wide, shallow. Umbilical walls from gently sloping to rather steep.

Ribs fine, high, sharp, distinctly S-shaped on the flank. Intercalation of one intermediate rib between two main ribs is predominant. Sometimes intermediate ribs are absent. Intermediate ribs are either single or branching off main ribs. Main ribs appear in the middle of the umbilical wall, and on umbilical bend they form just noticeable crests. Intermediate ribs emerge in the upper half of flanks. Main and intermediate rib sometimes converge low. Ribbing density changes with growth: from denser and fine on phragmacone to infrequent and coarse on body chamber. All ribs cross the venter as a steep arch forwardly, somewhat strengthened and thickened.

Suture-line (Fig. 16): characterized by rather wide elements. There are two inner lobes on the outside of the whorl: lobe I occurs near umbilical bend and lobe I² on umbilical wall.

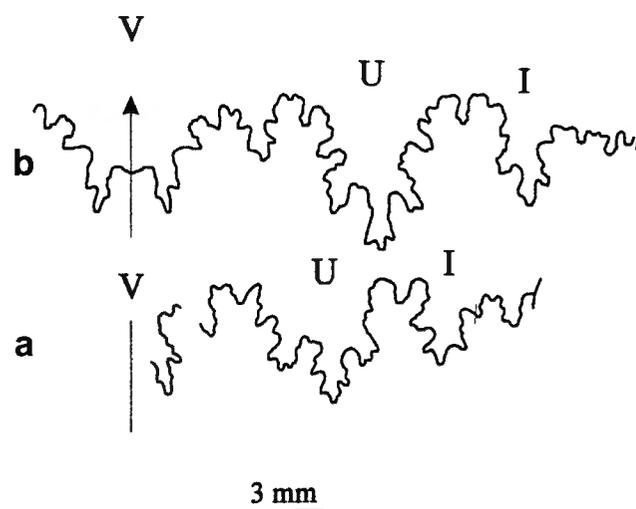


Fig. 16 — Suture line of *Deshayesites kemperi* sp. nov. a — MSU 12/99: H = 11.0 mm, W = 9.0 mm, b — CNIGR Museum 258/10367: H = 12.0 mm.

Measurements:

No	D	H	W	Du	H/D	W/D	Du/D
34/10367	38.7	14.3	10.7	13.8	0.37	0.36	0.36
259/10367	42.5	14.7	9.6	18.1	0.34	0.23	0.43
67/10367	43.5	16.2	9.7	16.3	0.35	0.22	0.35
32/10367	45.0	15.5	12.7	17.2	0.37	0.35	0.38
258/10367	49.3	17.4	14.0	20.3	0.35	0.30	0.40
31/10367	51.7	17.8	11.7	18.7	0.34	0.23	0.36

Remarks: BOGDANOVA (1979, pl. 2, figs. 3, 4) described some Turkmenian specimens as *D. consobrinus*. Later, KEMPER (1995) and AVRAM (1999) reassigned these specimens. KEMPER (1995, p. 179, 188, pl. 3, figs. 4, 5) assigned them to *D. bodei* (VON KOENEN) to which they undoubtedly belong (Pl. 2, Fig. 1). KEMPER (1967, 1995) considered that *D. bodei* is restricted to the lowest Aptian zone: in Germany this is the *Deshayesites tenuicostatus* Zone, *D. bodei* Subzone and in Turkmenistan the *Paradeshayesites tuarkyricus* Zone (probably its lower part). Some features are common between our Turkmenian specimens and the German *D. bodei*. Yet, the Turkmenian specimens differ from *D. bodei* in having shorter sub radial or backwards bending intermediate ribs (in *D. bodei* ribs are distinctly bending forwards off the radius). Therefore we assigned the Turkmenian specimens of "*D. consobrinus*" to *D. kemperi* nov.spec. *D. kemperi* sp. nov. belongs to the *D. bodei* group but is stratigraphically more widespread (see "Distribution"). The establishment of *D. kemperi* known not only from Turkmenistan, but also from Daghestan, eliminates the contradictions that CECCA et al., (1999b, p. 284) mentioned.

AVRAM (1999) established a new species *D. bogdanovae* and assigned specimens named *D. consobrinus* by BOGDANOVA and Romanian specimens to this species (AVRAM, 1999, p. 452, figs. 8A-C). In our opinion, the Romanian specimens of *D. bogdanovae* differ from *D. kemperi* sp. nov. in denser and coarser ribbing on adult whorls and have more bifurcating ribs and a lower point of branching. Also according to AVRAM (1999, p. 458), the Romanian species *D. bogdanovae* is distributed throughout the Lower Aptian – *fissicostatus*, *forbesi*, *deshayesi* Zones (AVRAM used the English zonation for the Lower Aptian).

D. bodei and other species of the lowermost German Aptian have not been found neither in Turkmenistan nor in the Northern Caucasus, but are present in more northern areas, such as the Volga Region.

Distribution: *Paradeshayesites tuarkyricus* and *P. weissii* zones, Tekedzhik, Gobekadzhi, Tuarkyr; Jangadzha, Kubadag; Utuludzha, Bordzhakly, Bolshoi Balkhan, Turkmenistan; *Deshayesites dechyi* Zone, Butri, Daghestan, Russia.

Genus *Paradeshayesites* KEMPER, 1967

*1967 – *Paradeshayesites*: KEMPER, p. 124.

1999 – *Paradeshayesites*: BOGDANOVA, MIKHAILOVA, p. 53.

Type species. *Hoplites laeviusculus* VON KOENEN, 1902; Lower Aptian, tenuicostatus Zone; northern Germany (see Pl. 7, Fig. 1).

Description. Shell small to large. Whorls high, compressed, strongly involute, rapidly expanding, rectangular-oval in cross section. Ribbing fine, closely spaced, forming bundles, often consisting of fine striae. Branching of ribs near the umbilical shoulder. Umbilical nodes distinct. From seven to nine intercalating ribs present. In earlier species of *Paradeshayesites* (such as *P. tuarkyricus*) ribbing is not interrupted on venter, but it is in later species (*P. terminalis* BOGDANOVA et al., 1979).

Structure of the suture line is typical for the *Deshayesitidae*. Outer saddle (V/U) with branches of different height, but narrower than in the genus *Deshayesites*. Umbilical lobe (U) from asymmetric to almost symmetric. Inner lobe (I) is situated far from the seam, in saddle I/D up to three additional lobes (I¹, I² and I³) originate during ontogenetic development. Suture formula (V₁V₁)UII²I³:I¹D.

Composition: The genus consists of over 20 species (the list of the species is given in BOGDANOVA, MIKHAILOVA, 1999).

Comparison: *Paradeshayesites* differs from *Deshayesites* in high, rapidly increasing whorls, in densely spaced fasciculate ribbing, with distinct umbilical nodes, and in the presence of four inner lobes (instead of three in *Deshayesites*).

Remarks: *P. tuarkyricus* and *P. oglanlensis* were figured in BOGDANOVA (1979) and described in 1983.

Distribution: Lower Aptian of: Western Europe; Middle Volga, Northern Caucasus, Russia; Turkmenistan.

Paradeshayesites topleyi (SPATH, 1930)

Pl. 7, Fig. 2; Pl. 9, Figs. 1, 2; Text-fig. 17

*1930 – *Deshayesites topleyi*: SPATH, p. 430, pl. 15, fig. 5.

1964 – *Deshayesites topleyi*: CASEY, p. 342, pl. 51, fig. 1; pl. 54, fig. 4, pl. 55, fig. 1.

?1999 – *Deshayesites* cf. *topleyi*: AVRAM, p. 451, fig. 7H.

1999 – *Deshayesites topleyi*: BOGDANOVA, PROZOROVSKY, pl. 5, fig. i.

Holotype: GSM 57688 (formerly L.F. Spath coll. 834), Atherfield Clay Series, Lower Lobster Bed, Atherfield, Isle of Wight, UK.

Description: Shells large (D up to 112 mm), flattened (W/D = 0.26-0.30). Whorls overlap for 3/5 and 2/5, moderately increasing. Flanks weakly convex, venter convex.

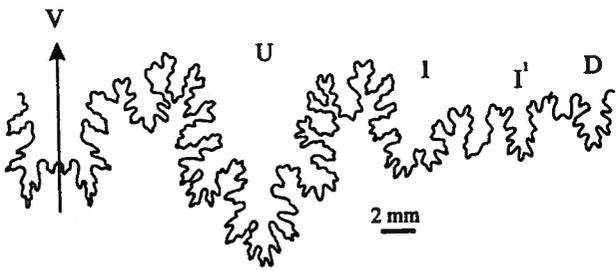


Fig. 17 — Suture line of *Paradeshayesites topleyi* (SPATH, 1930). CNIGR Museum 78/10367: H = 28.7 mm.

Umbilicus from relatively narrow to moderately wide ($D_u/D = 0.23-0.29$) with rather high and steep walls. Whorl section moderately high ($H/D = 0.40-0.46$), triangular-oval.

Ribbing dense, main ribs emerge on umbilical wall, intermediate ribs in the upper third of flanks. On whorls with D up to 20 mm, ribs distinct, one main rib intercalates with two intermediate ribs. Ribs on whorls from 20 to 50 mm in diameter are strongly smoothed in the middle of the flanks. The umbilical crests originate at the base of main ribs. On later whorls ribs strengthen again, main ribs often branch out (without bundles), with one or two intermediate ribs. All ribs are slightly weakened on the venter.

Suture line (Fig. 17): characterized by wide, strongly dissected elements $VU I^2 : I^1 D$. Umbilical lobe (U) is symmetrical, twice as long as ventral (V). Inner lobe (I) is wide, second inner lobe (I^2) is situated on the umbilical wall, and first inner lobe occurs behind the seam.

Remarks: *Paradeshayesites topleyi* belongs to an unusual group of taxa within the genus *Paradeshayesites*,

characterized by a different sculpture development during the shell growth and the presence of a stage with smoothed ribbing on the flanks. Among the described species of the genus *Paradeshayesites*, also *P. tuarkyricus* is characterized by distinct rib smoothing. However, *P. topleyi* differs sharply in having the least ribs (30 instead of 40-65 for half a whorl) and fewer intermediate ribs, wider and coarser ribs and umbonal ridges, a narrower umbilicus, higher and more overlapping whorls, and fewer inner lobes. It is unlikely that the specimen depicted by AVRAM (1999, p. 451, fig. 7H) can be assigned to *P. topleyi* because the specimen from Romania does not show the smoothed sculpture characteristic of English, Turkmenian and Volgian specimens. In fact, the bidichotomous ribs of *P. topleyi* are simply flattened and besides, triple rib division has the shape of a real bundle.

Distribution: *Deshayesites forbesi* Zone, Southern England; *D. volgensis* Zone, Middle Volga, Russia; *Paradeshayesites weissii* Zone, Tuarkyr, Kubadag, Turkmenistan; Lower Aptian (lower part), Romania.

Paradeshayesites callidiscus (CASEY, 1961)

Pl. 3, Fig. 1; Pl. 8, Figs. 1, 2; Pl. 10, Fig. 1; Text-fig. 18

*1961 — *Deshayesites callidiscus*: CASEY, p. 594, pl. 80, fig. 10.

1964 — *Deshayesites callidiscus*: CASEY, p. 327, pl. 49, fig. 3; pl. 53, fig. 2.

1968 — *Deshayesites kabanovi*: GLAZUNOVA, p. 317, pl. 74, fig. 1.

1973 — *Deshayesites kabanovi*: GLAZUNOVA, p. 127, pl. 81, fig. 2, non pl. 79, fig. 2, pl. 80, fig. 2.

1999 — *Deshayesites callidiscus*: BOGDANOVA, PROZOROVSKY, pl. 6, figs. e,f.

2002 — *Prodeshayesites callidiscus*: BARABOSHKIN, MIKHAILOVA, pl. 1, fig. 1.

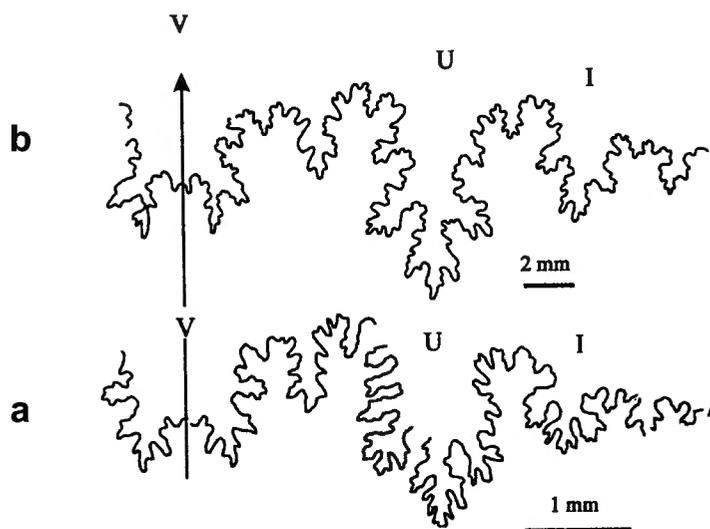


Fig. 18 — Suture line of *Paradeshayesites callidiscus* (CASEY, 1961). a — CNIGR Museum 101/10367: H = 24.1 mm, b — MSU 36/96: H = 34.0 mm, W = 20.6 mm.

Holotype: BM 48836, Atherfield Clay Series, Crackers, Atherfield, Isle of Wight, UK.

Description: Shells large (D up to 100 mm), flattened, of medium thickness ($W/D = 0.26-0.33$). Whorls high ($H/D = 0.46-0.54$), half-overlapping. Flanks are almost flat, venter wide, flattened. Umbilicus relatively narrow ($Du/D = 0.18-0.24$) with low gently sloping walls. Whorl section rectangular-oval.

Ribbing dense, ribs wide, flat, bundle-shaped. Main ribs appear on the umbilical wall, become much thicker on the umbilical bend and form crests or ridges; many of them are doubly branching on the flank. Infrequent intermediate ribs are situated between branches of main ribs. All ribs are slightly smoothed in the middle of flanks and on the venter. On whorls up to 25-30 mm in diameter ribs are interrupted on the venter.

Suture line (Fig. 18): characterized by strongly dissected elements. Umbilical lobe is wide, asymmetric, twice as long as the ventral lobe. Inner trifid lobe I is shortened and widened in its lower part. The outer saddle (V/U) has branches of different height and is much higher than the neighbouring saddle (U/I).

Remarks: *Paradeshayesites callidiscus* differs from *P. topleyi* (SPATH) in less sharp ribs weakening on the venter and flanks, distinctly developed umbilical crests or ridges on ribs and the presence of three inner lobes (I, I², I³) on the outside. Adult whorls of *P. callidiscus* of 50 mm in diameter are similar to *Obsoleticeras levigatum* (BOGDANOVA, 1991) in rib smoothing. Earlier whorls of *P. callidiscus* are characterized by much denser bundle ribbing.

Distribution: *Deshayesites forbesi* Zone, *Paradeshayesites callidiscus* Subzone, Southern England; *Deshayesites volgensis* Zone, Middle Volga, Russia; *Paradeshayesites weissi* and *Deshayesites deshayesi* Zones, Tuarkyr, Kubadag, Bolshoi Balkhan, Turkmenistan.

***Paradeshayesites tuarkyricus* (BOGDANOVA, 1983)**

Pl. 7, Fig. 7; Text-figs. 19, 20

- 1979 – *Deshayesites tuarkyricus*: BOGDANOVA, p. 153, 155, pl. 2, fig. 2.
 *1983 – *Deshayesites tuarkyricus*: BOGDANOVA, p. 132, pl. 1, figs. 1-4; pl. 2, fig. 4.
 1999 – *Deshayesites tuarkyricus*: BOGDANOVA, PROZOROVSKY, pl. 3, figs. a-c.
 1999a – *Deshayesites tuarkyricus*: CECCA *et al.*, pl. 1, fig. 2; Figs. B, C, D.

Holotype: CNIGR Museum 1/9442, *Paradeshayesites tuarkyricus* Zone, Lausan, Tuarkyr, Turkmenistan.

Description: Shells medium-sized to large (D = 40-120 mm), flattened ($W/D = 0.28-0.30$). Whorls are overlapping for half or two thirds of the height. Umbilicus is relatively narrow ($Du/D = 0.18-0.22$), step-like, fairly deep. Cross-section is high ($H/D = 0.46-0.51$), rectangular-

lar-oval (Fig. 19). Flanks are slightly convex. Venter is narrow, convex.

Ribbing is distinctly bundle-shaped: fine-channelled S-shaped ribs diverge from umbilical crests and repeatedly branch on the flank. The number of intermediate ribs increases between earlier and later whorls from 1-2 to 7-9. In the middle third of the flanks the ribbing weakens. The ribs cross the venter without weakening, with strong bending towards the aperture.

Suture line (Fig. 20): The incompletely observed suture line is characterized by strongly dissected inner lobes (I, I², I³). Inner lobe (I) is sharply asymmetric; second (I²) and third (I³) inner lobes are situated outside.

Remarks: *Paradeshayesites tuarkyricus* differs from *P. weissi* (NEUMAYR & UHLIG, 1881) in closer, fine, repeatedly branching ribs (channelled character of ribbing), distinct umbilical crests, rib smoothing in the middle of the flanks, rectangular-oval whorl section.

The Tuarkyr form closely resembles one of the species depicted in UHLIG (1883, pl. 21, fig. 1) as “*Hoplites borovae*” but the taxon named according to VAŠICEK (1973, p. 61, pl. 3, fig. 1,2) *Deshayesites beskidensis* (UHLIG, 1883). UHLIG’s species, judging from the illustrations in UHLIG (1883) and VAŠICEK (1973) has similar channelled ribs on younger whorls, rather narrow umbilicus and high flat whorls. The structure of the suture line is also similar. However, strong rib coarseness on adult whorls with appearance of distinct umbilical tubercles in rib bases, as well as gradual rib weakening in the upper part of flanks and on the venter, do not allow to assign the Tuarkyr material and UHLIG’s specimens from Hradště (Karvina, Czech Republic) to one and the same species.

Distribution: *Paradeshayesites tuarkyricus* Zone, Tuarkyr, Bolshoi and Malyi Balkhan, Turkmenistan.

***Paradeshayesites weissiformis* (BOGDANOVA, 1983)**

Pl. 7, Fig. 3; Text-fig. 21

- *1983 – *Deshayesites weissiformis*: BOGDANOVA, p. 134, pl. 2, figs. 1-3; pl. 3, fig. 7.
 ?1995 – “*Deshayesites*” *oglanlensis*: DELANOY, p. 74, pl. 2, figs. 1a, 1b.
 1999 – *Deshayesites weissiformis*: AVRAM, p. 440, figs. 3A, E.
 ?1999 – *Paradeshayesites* aff. *oglanlensis*: AVRAM, p. 441, figs. 4A.

Holotype: CNIGR Museum 7/9442, *Paradeshayesites tuarkyricus* Zone, Umokdere, Tuarkyr, Turkmenistan.

Description: Shells large (D up to 110 mm), flattened or of medium width ($W/D = 0.28-0.33$). Whorls almost half-overlapping, rapidly increasing. Flanks weakly convex, venter flattened. Umbilicus from relatively narrow to moderately wide ($Du/D = 0.22-0.26$) with low vertical walls. Whorl section is high ($H/D = 0.44-0.51$), rectangular-oval, slightly widening towards the umbilicus.

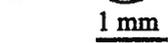
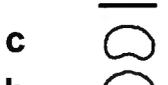
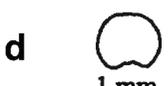
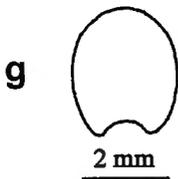
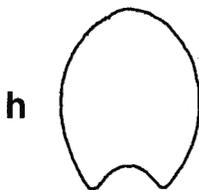
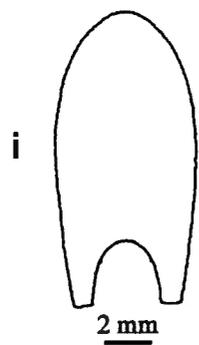


Fig. 19

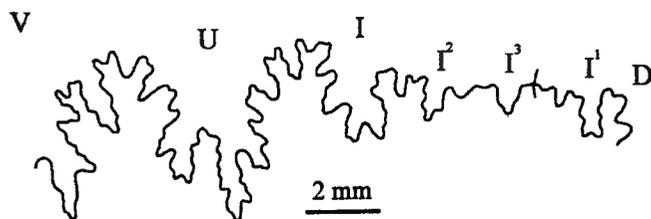


Fig. 22

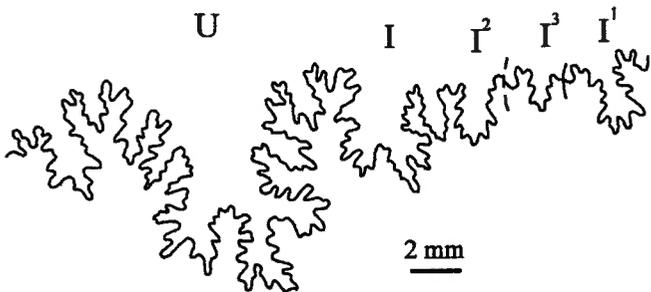


Fig. 21

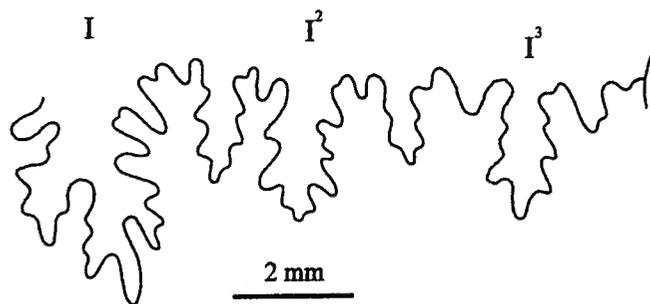


Fig. 20

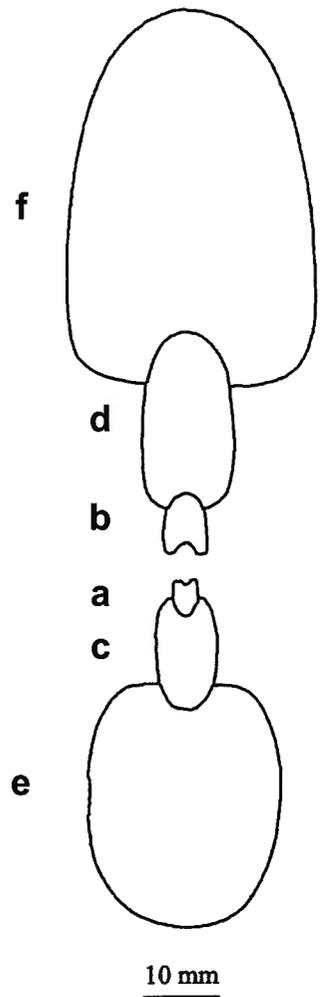


Fig. 23

Fig. 19 — Changes of the whorl section in the ontogeny of the shell of *Paradeshayesites tuarkyricus* (BOGDANOVA, 1983). CNIGR Museum 5/9442: a – H = 0.3 mm, b – H = 0.42 mm (a, b – first whorl), c – H = 0.5 mm, d – H = 0.95 mm (c, d – second whorl), e – H = 1.3 mm, f – H = 1.8 mm, g – H = 2.8 mm, h – H = 4.0 mm (e-h – third whorl), i – H = 12.0 mm.

Fig. 20 — Suture line of *Paradeshayesites tuarkyricus* (BOGDANOVA, 1983). CNIGR Museum 5/9442: H = 12.0 mm.

Fig. 21 — Suture line of *Paradeshayesites weissiformis* (BOGDANOVA, 1983). CNIGR Museum 10/9442: H = 19.5 mm.

Fig. 22 — Whorl section of *Paradeshayesites oylanlensis* (BOGDANOVA, 1983). CNIGR Museum 17/9442: a – H = 5.7 mm, b – H = 9.1 mm, c – H = 15.1 mm, d – H = 21 mm, e – H = 32 mm, f – H = 50.1 mm.

Fig. 23 — Suture line of *Paradeshayesites oylanlensis* (BOGDANOVA, 1983). CNIGR Museum 13/9442: H = 14 mm.

Ribs dense, coarse, distinctly S-shaped. Main ribs appear on umbilical wall, strengthen slightly on umbilical bend. In the lower third of the height of the whorls height all ribs bifurcate, and on half of the flank nearly every second rib shows recurring branching of main ribs. Intermediate ribs of various length appear at both levels of main rib branching. On whorls of less than 20 mm in diameter, ribs are interrupted on the venter, but on adult whorls they cross it as a wide weakly convex arc.

Suture line (Fig. 21): with sharply asymmetric umbilical lobe (U), slightly longer than the ventral (V). Four inner lobes, I, I², I³ and I¹, but only I¹ is situated behind the seam.

Remarks: *Paradeshayesites weissiformis* differs from *P. weissii* (NEUMAYR & UHLIG, 1881) in its denser ribbing because of more numerous branching ribs, especially double branching, coarser ribs, more strongly inflated whorls and wider venter. A series of transitional forms relates *P. weissiformis* and *P. tuarkyricus*. This is particularly pronounced on inner whorls of 25-30 mm in diameter. Some specimens of both species of this size are almost indistinguishable in shape, number of ribs and character of sculpture. At the same size, larger whorls of *P. tuarkyricus* are less inflated, have a narrower umbilicus, finer sculpture and more ventral ribs.

P. aff. oglanlensis in AVRAM (1999, p. 441, fig. 4A) should probably be assigned to *P. weissiformis* because close bundle-shaped ribbing characteristic for specimens from Romania is not characteristic for *P. oglanlensis* shells of the same size.

Distribution: *Paradeshayesites tuarkyricus* Zone, Tuarkyr, Bolshoi Balkhan, Turkmenistan; Lower Aptian, Romania.

***Paradeshayesites oglanlensis* (BOGDANOVA, 1983)**

Pl. 7, Fig. 4; Text-figs. 22, 23

- 1979 – *Deshayesites oglanlensis*: BOGDANOVA, p. 153, 155, pl. 2, fig. 5a – b (nomen nudum).
- * 1983 – *Deshayesites oglanlensis*: BOGDANOVA, p. 136, pl. 1, figs. 5-9.
- 1997 – *Deshayesites oglanlensis*: AGUADO *et al.*, fig. 7e.
- 1999 – *Deshayesites oglanlensis*: BOGDANOVA, PROZOROVSKY, pl. 3, figs. d,e.
- 1999b – *Deshayesites oglanlensis*: CECCA *et al.*, p. 278, pl. 1, figs. 2-4.
- (1998) 2000 – *Deshayesites oglanlensis*: GONNET *et al.* p. 129, pl. 1, figs. 1,2; pl. 2, fig. 4.
- non 1995 – “*Deshayesites*” *oglanlensis*: DELANOY, p. 74, pl. 2, figs. 1a, 1b

Holotype: CNIGR Museum 12/9442, *Paradeshayesites tuarkyricus* Zone, Oglanly, Bolshoi Balkhan, Turkmenistan.

Description: Shells medium to large (D = 38-120 mm), flattened (W/D = 0.22-0.28). Whorls overlap for 2/5 of the height, high (H/D = 0.43-0.51), rapidly increasing.

Flanks are flat, venter is flattened. Umbilicus from relatively narrow to moderately wide (Du/D = 0.21-0.28) with low steep walls. Whorl section from high-oval to almost rounded and rounded-rectangular (Fig. 22).

Ribs, on whorls up to 100 mm in diameter, are dense, fasciculate. Main ribs emerge on the umbilical bend with tubercles in the base. Lower rib branching starts from the tubercles, upper rib branching starts approximately in the middle of a flank. Single and branching intermediate ribs of various lengths appear at the same levels. Ribs on whorls over 100 mm in diameter are simple, infrequent. Ribs on the venter of the earliest whorls (D < 15 mm) are weakened or interrupted, on later whorls cross the venter with a slight bend forwards.

Suture line (Fig. 23): observed almost completely (VUII²I³:I¹D). Umbilical lobe (U) asymmetric, slightly longer than ventral (V). Three inner lobes on the outside of the whorl; one of them, I³, at the seam.

Remarks: *Paradeshayesites oglanlensis* differs from *P. tuarkyricus* in less dense ribs, umbilical tubercles on earlier whorls and coarse, rare ribs on later whorls. The latter feature makes *P. oglanlensis* similar to “*Hoplites*” *borovae* (UHLIG, 1883, pl. 21, fig. 1) which, according to VAŠICEK (1973, p. 61, pl. 3, figs. 1,2) is *Deshayesites beskidensis* (UHLIG, 1883). However, in the latter, rib coarsening and appearance of umbilical tubercles are observed at a later stage. Specimens of *Paradeshayesites oglanlensis* of 40-50 mm in diameter are similar to *P. laeviusculus* (VON KOENEN) (1902, pl. 8, fig. 4a) in rib density, but not in the following: higher branching of main ribs and short intermediate ribs of *P. laeviusculus* (VON KOENEN), more elongated section of *P. oglanlensis* with parallel lateral walls, and different outlines of elements of the suture line (in the latter they are high and narrow instead of wide and short). “*Deshayesites*” *oglanlensis* (DELANOY, 1995, pl. 2, figs. 1a, 1b) is more similar to *Paradeshayesites weissiformis*.

Distribution: *Paradeshayesites tuarkyricus* Zone, Tuarkyr, Bolshoi and Malyi Balkhan, Kubadag, Kopet-Dag, Turkmenistan; La Bédoule (Bouches-du-Rhône, France); Betic Cordillera, Southern Spain.

***Paradeshayesites planicostatus* (BOGDANOVA, 1991)**

Pl. 7, Figs. 5, 6; Text-fig. 24

- *1991 – *Deshayesites planicostatus*: BOGDANOVA, p. 80, pl. 2, figs. 1-3, text-fig. 2.
- 1999 – *Deshayesites planicostatus*: AVRAM, p. 447, fig. 6A (only), not 6 B.

Holotype: CNIGR Museum 4/12730, *Paradeshayesites tuarkyricus* Zone, Bordzhakly, Bolshoi Balkhan, Turkmenistan.

Description: Shells medium-sized (D = 34-50 mm), very flattened (W/D = 0.19-0.21). whorls high (H/D = 0.42-0.44), moderately increasing, overlapping for 2/5 of the

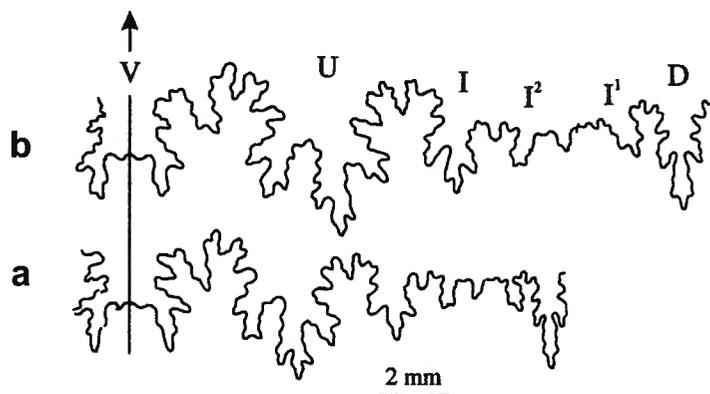


Fig. 24 — Suture line of *Paradeshayesites planicostatus* (BOGDANOVA, 1991). CNIGR Museum 5/12730: a — H = 8.9 mm, b — H = 12.0 mm.

height. Flanks are flat, venter flattened. Umbilicus moderately wide ($Du/D = 0.28$) with low vertical walls. Cross section rectangular.

Ribbing dense. Main ribs begin with inflating and tubercles on the umbonal bend; they are usually bifurcated in the lower third of the flank. Intermediate, intercalating ribs sometimes occur in the upper third of the flanks. All ribs strongly widen and flatten at the point of origin. The middle of the whorls ribs are noticeably smoothed, and on the venter strongly bent towards the aperture and appreciably weakened without interrupting.

Suture line (Fig. 24): $VU I I^2 I^3 : I^1 D$. Umbilical lobe (U) wide, sharply asymmetric, longer than the ventral one. Inner lobe (I) narrow, shallow, second and third inner lobes (I^2 è I^3) shallower; first inner lobe (I^1) and well-shaped relatively deep dorsal lobe (D) occur behind the seam.

Remarks: *Paradeshayesites planicostatus* differs from:

- *P. oylanlensis* in having fewer wide flat ribs and shorter intermediate ribs,
- *P. tuarkyricus* in wider umbilicus, essentially lesser number of wide ribs, including the intermediate ribs.
- Sculpture smoothing in the middle of the flank is a feature common with *P. tuarkyricus*.
- Rib weakening in *P. planicostatus* is similar in juveniles and in adults, and in *P. tuarkyricus* it appears only on whorls of more than 35–40 mm in diameter.
- Specimens of *P. tuarkyricus* are characterized by a greater number of intermediate ribs and narrower umbilicus.

Distribution: *Paradeshayesites weissii* and *P. tuarkyricus* Zones, Bolshoi Balkhan and Kubadag, Turkmenistan; *Paradeshayesites weissii* Zone, Romania.

***Paradeshayesites similis* (BOGDANOVA, 1991)**
Pl. 10, Figs. 2, 3; Text-fig. 25

*1991 — *Deshayesites similis*: BOGDANOVA, p. 84, pl. 1, figs. 2, 3, pl. 2, figs. 7, 8, text-fig. 4.

- 1999 — *Deshayesites cf. similis*: AVRAM, p. 440, figs. 2D, F.
- 1999 — *Deshayesites similis*: BOGDANOVA, PROZOROVSKY, pl. 5, fig. 4.
- 1999a — *Deshayesites similis*: CECCA *et al.*, pl. 1, figs. A,B.
- 2001 — *Paradeshayesites similis*: CONTE, p. 49, SVR 042, SVR 043.
- 2002 — *Paradeshayesites similis*: BARABOSHKIN, MIKHAILOVA, pl. 4, fig. 1.

Holotype: CNIGR Museum 16/12730, *Paradeshayesites weissii* Zone, Tekedzhik, Tuarkyr, Turkmenistan.

Description: Shells large (D up to 121 mm), flattened ($W/D = 0.26-0.30$). Whorls high ($H/D = 0.46-0.48$), moderately increasing, half overlapping. Flanks slightly convex, venter rather narrow, convex. Umbilicus relatively narrow ($Du/D = 0.19-0.23$) with low gently sloping walls. Whorl section trapezoidal.

Ribbing dense, ribs fine, bundle-shaped. Main ribs appear on umbilical wall, become stronger on umbilical bend and form a crest or a ridge. Most of the ribs bifurcate (= dichotomous) in the lower third of flanks, and in the middle of the flanks some of the ribs undergo a second branching (= bidichotomous). Long intermediate intercalating ribs, occurring between or inside branches of main ribs. With whorl growth the number of intermediate ribs

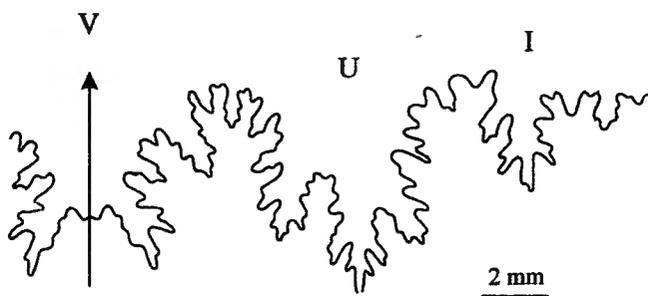


Fig. 25 — Suture line of *Paradeshayesites similis* (BOGDANOVA, 1991). CNIGR Museum 16/12730: H = 15.6 mm.

increases from 1 to 4. On the second to fourth whorls ribs are lacking on venter, on the following whorls they are weakened.

Suture line (Fig. 25): characterized by wide and high elements. Umbilical lobe (U) asymmetric, longer than ventral one (V). Inner lobe (I) occurs behind lobe U, and second inner lobe (I²) on umbonal bend.

Remarks: *Paradeshayesites similis* resembles *P. tuarkyricus* in the large rib-number and bundle-shaped ribbing. There are fewer ribs on the venter of *P. similis*, mainly because there are fewer intermediate ribs and slightly more umbonal ribs. Ribbing coefficients also differ: 3.5-4 in *P. similis* and 4.2-5 in *P. tuarkyricus*. Ribs of *P. similis* are coarser, intermediate ribs appear only in the middle of the flank, a smooth band is lacking in the middle of the whorl, whereas most of the ribs of *P. tuarkyricus* appear near the outer bend, and in the lower part of flanks the ribs are smoothed and only fine striae corresponding to the main ribs are visible. Overlapping in *P. tuarkyricus* is slightly deeper than in *P. similis*. *P. similis* has only two inner lobes on the outside of the whorl (I and I²) in contrast to the three lobes in *P. tuarkyricus*.

P. similis differs from *P. oglanlensis*, which has an equal number of bundled ribs, in more inflated and overlapping whorls, a narrower umbilicus, and crests at the base of the main ribs instead of distinct umbilical nodes.

Among *P. similis* specimens there are forms similar to representatives of *P. callidiscus* with wider and flatter ribs and an outlined band of rib smoothing in the middle of the flanks. The *P. similis* specimens, however, have more ribs (about a hundred for a whorl in typical representatives of *P. similis* in contrast to 70-74 in *P. callidiscus*).

The same feature distinguishes *P. similis* from *P. weissi* which has rarely more than two intermediate ribs.

Distribution: *Paradeshayesites weissi* Zone, Tuarkyr, Kubadag, Kopet-Dag, Bolshoi and Malyi Balkhan, Turkmenistan; *Deshayesites volgensis* Zone, Sengiley, Middle Volga Region, Russia; Lower Aptian, Southern France; *Paradeshayesites weissi* Zone, Romania.

Genus *Obsoleticeras* BOGDANOVA & MIKHAILOVA, 1999

1961 – *Prodeshayesites*: CASEY, p. 592 (pars).

1964 – *Prodeshayesites*: CASEY, p. 353 (pars).

*1999 – *Obsoleticeras*: BOGDANOVA, MIKHAILOVA, p. 53.

Type species: *Prodeshayesites obsoletus* CASEY, 1964; Lower Aptian, fissicostatus Zone, obsoletum Subzone; SE England.

Description. Shell with high, rapidly expanding whorls, oval in cross-section. Early whorls with more or less widely spaced ribbing, later in ontogenesis ribbing disappears. Umbilical nodes absent. Suture line with slightly asymmetric umbilical lobe. Outer saddle (V/U) very

wide, with almost equal tops. In saddle I/D there are two (I¹, I²), sometimes three (I³) additional lobes.

Composition: Five species: *Obsoleticeras falcatum* (CASEY, 1964), Lower Aptian of England; *O. jacksoni* (CASEY, 1964), forbesi Zone (fittoni Subzone) of England; *O. lestrangei* (CASEY, 1964), tenuicostatus Zone of NW Germany; fissicostatus Zone (bodei Subzone) of England; *O. levigatum* (BOGDANOVA, 1991), weissi and deshayesi zones of Turkmenistan; Lower Aptian of Mangyshlak; *O. obsoletum* (CASEY, 1961), fissicostatus Zone (obsoletum Subzone) of England; tenuicostatus Zone in NW Germany (according to KEMPER, 1967).

CASEY (1980, p. 656) considered: “The *obsoletus* horizon has not yet been recognized outside southern England. Because of the stratigraphical implications of the record, it is important to point out that the “*Paradeshayesites obsoletus*” of KEMPER (1967, p. 126, pl. 12, figs. 3a,b) from the Aptian of Alstätte, Germany, is not conspecific with the British form”.

Remarks: *Obsoleticeras* differs from *Deshayesites* in high, rapidly expanding whorls and almost smooth shell in adults. It differs from the genus *Paradeshayesites* in the absence of fasciculate ribbing and umbilical nodes, fewer ribs in the early whorls and in the disappearance of ribbing in adults, whereas in *Paradeshayesites* the smoothing of the ribbing is observed only in the middle stage of shell growth.

Distribution: Lower Aptian of England, NW Germany, Turkmenistan, Mangyshlak, Kazakhstan and the Middle Volga region, Russia.

Obsoleticeras levigatum (BOGDANOVA, 1991)

Pl. 11, Figs. 2, 3; Text-fig. 26

*1991 – *Deshayesites levigatus*: BOGDANOVA, pl. 3, fig. 4, text-fig. 5.

1999 – *Deshayesites levigatus*: BOGDANOVA, PROZOROVSKY, pl. 6, figs. g,h.

2002 – *Obsoleticeras levigatum*: BARABOSHKIN, MIKHAILOVA, pl. 2, fig. 1.

Holotype: CNIGR Museum 24/12730, *Paradeshayesites weissi* Zone, Utuludzha, Bolshoi Balkhan, Turkmenistan.

Description: Shells large (D up to 150 mm), flattened (W/D = 0.26). Whorls high (H/D = 0.46-0.47), moderately increasing, overlapping half of the whorl. Flanks flat, somewhat diverging from the periphery; venter rather narrow, weakly convex. Umbilicus relatively narrow (Du/D = 0.21), with high gently sloping walls. Whorl section rectangular-oval. Whorls up to D=50-60 mm are covered with distinct fine ribs crossing the venter with a strong bend forwards. On later whorls ribs soon become smoothed on most of the flanks and on the venter. They become wide, flat, ribbon-shaped, slightly S-shaped. On whorls more than 100 mm in diameter, ribbing disappears completely on the flank.

Suture line (Fig. 26): characterized by wide and low

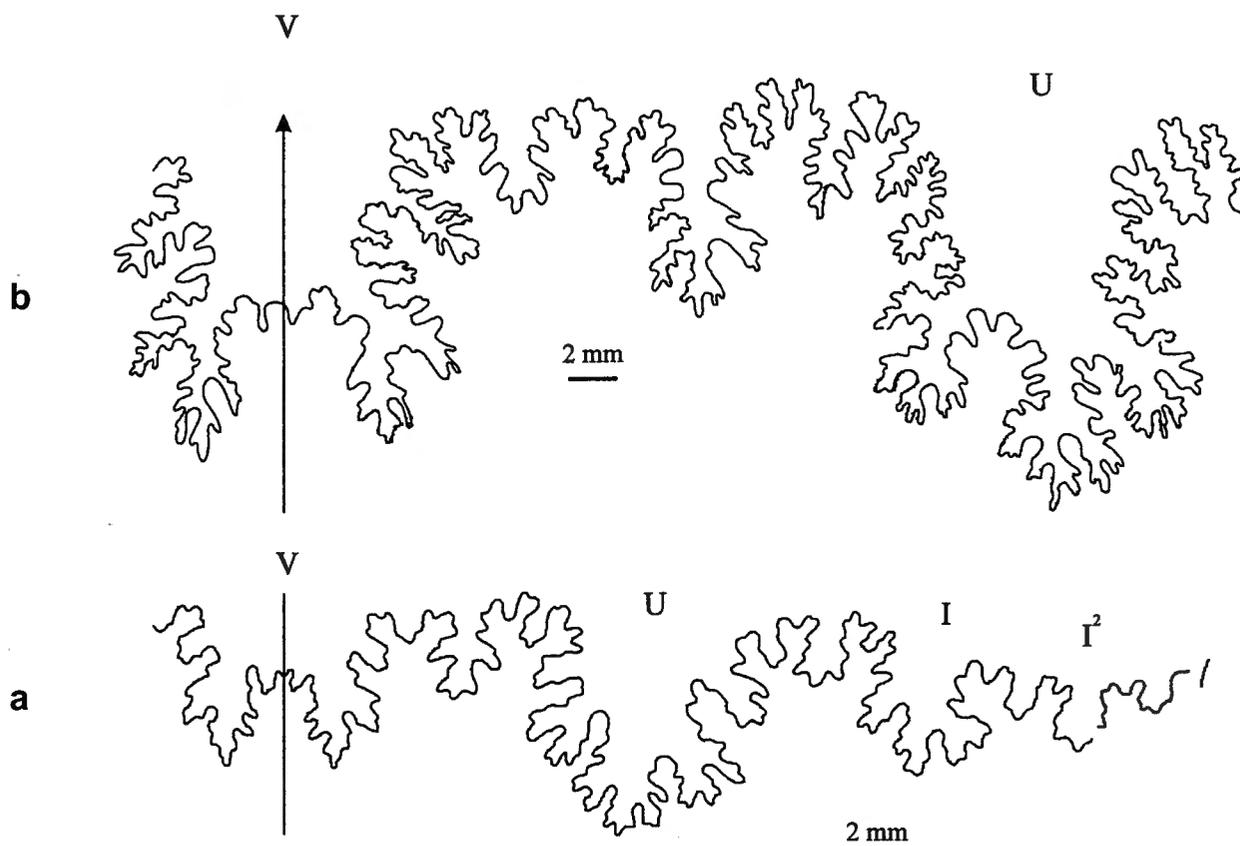


Fig. 26 — Suture line of *Obsoleticeras levigatum* (BOGDANOVA, 1991). a — CNIGR Museum 27/12730: H = 33.8 mm, b — MSU 20/96: H = 40.0 mm, W = 30.5 mm.

elements. Umbilical lobe wide, asymmetric, slightly longer than ventral. Inner lobes (I and I²) gradually decrease towards the seam, and lobe I¹ occurs behind the seam. Outer saddle (V/U) very wide, bifid with tops of slightly different height.

Remarks: *Obsoleticeras levigatum* resembles *Paradeshayesites topleyi* (SPATH, 1930, p. 430, pl. 15, fig. 5) in sculpture smoothing, but sharp differences exist between them: in *O. levigatum* smoothing is preserved on last whorls, whereas in *P. topleyi* with shell growth coarse dull ribbing evolves after the “smoothed” stage; on large whorls of *O. levigatum* there are traces of coarse ribs, but on the whole, ribbing of this species is finer than in *P. topleyi*. Besides, specimens of *O. levigatum* have a narrower umbilicus, higher overlapping and a more elongated whorl section than in *P. topleyi*.

Earlier whorls of *O. levigatum* with sharp pointed ribs resemble earlier whorls of *Paradeshayesites callidiscus* and *P. grandis* (SPATH, 1930, p. 427, pl. 17, fig. 2a, b), but on the whole, shells of *O. levigatum* differ from them in prolonged stage of smoothed whorls, and from *P. callidiscus* also in flatter whorls.

Distribution: *Paradeshayesites weissii* and *Deshayesites deshayesi* Zones, Tuarkyr, Kubadag, Bolshoi Balkhan,

Turkmenistan; *D. volgensis* Zone, Middle Volga Region, Russia.

Genus *Dufrenoyia* KILIAN & REBOUL, 1915

- *1915 — *Parahoplites* (*Dufrenoyia*): KILIAN & REBOUL, p. 34.
- 1922 — *Stenhoplites*: SPATH, p. 110.
- 1923 — *Dufrenoyia*: SPATH, p. 147.
- 1925 — *Dufrenoyia*: BURCKHARDT, p. 15.
- 1949 — *Dufrenoyia*: HUMPHREY, p. 119.
- 1964 — *Dufrenoyia*: CASEY, p. 373.
- 1999 — *Dufrenoyia*: BOGDANOVA, MIKHAILOVA, p. 53.

Type species. *Ammonites furcatus* J. de C. SOWERBY in FITTON, 1836; Hythe Beds, Hythe, Kent, England.

Description. Shell medium-sized, rarely large. Cross-section rounded-trapezoidal, with flattened and narrow venter. Umbilicus relatively wide. In adults one intermediate rib intercalates between two main ribs, weakening and disappearing on venter and forming nodes on ventrolateral shoulder.

Suture line is traced approximately from the end of the second whorl (Fig. 27). Up to the beginning of the third whorl the suture line consists of four lobes: a bifid ventral lobe (V), an entire umbilical (U), inner lateral (I), and dorsal (D) lobes. The fifth lobe emerges from subdivision

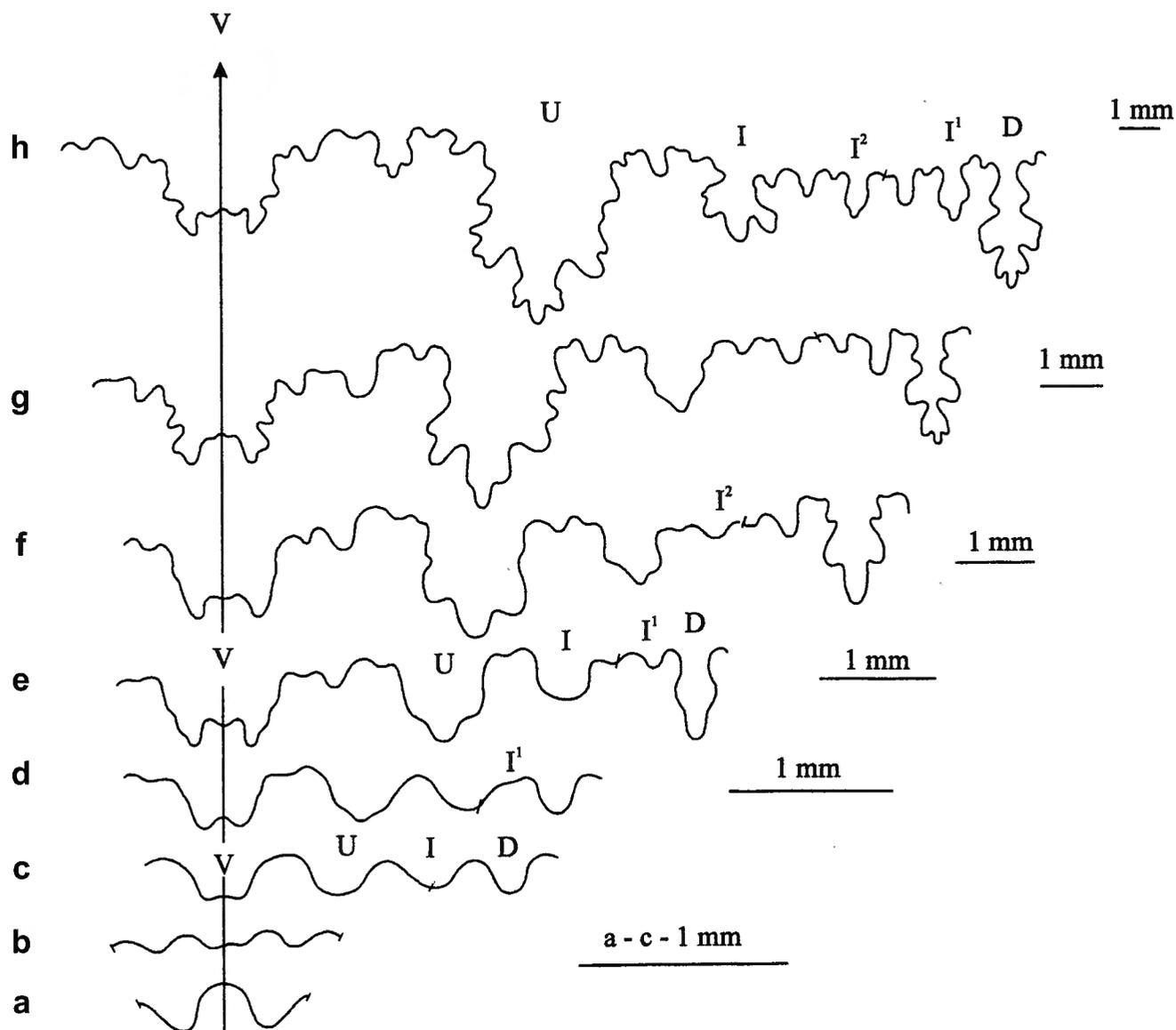


Fig. 27 — Changes in the suture line during the ontogeny of the shell of *Dufrenoyia subfurcata* (KAZANSKY, 1914). MSU 8/99: a, b — first, second lines, c — the middle of second whorl, d — middle of third whorl, e — beginning of fourth whorl, f — end of fourth whorl, g — middle of fifth whorl, h — end of fifth whorl.

of the inner saddle (I/D) of the third whorl. The external saddle first has branches of unequal height, but at the end of fifth to beginning of sixth whorl, the height of these branches becomes equal.

Sutural formula: $(V_1V_1)(U_2 U_1 U_2) I:I^1D$.

Composition. The genus consists of over 30 species (for an extensive list see BOGDANOVA, MIKHAILOVA, 1999, p. 527).

Remarks: *Dufrenoyia* differs from other genera of the family Deshayesitidae in its flat venter often with weakened ribs, sometimes with ventro-lateral tubercles.

There are two problems with the genus *Dufrenoyia*.

1. The first concerns the spelling of the generic name: *Dufrenoyia* or *Dufrenoyia*;
2. The second is about the type species of *Dufrenoyia*: *Ammonites furcatus* J. de C. SOWERBY, 1836 or *Ammonites dufrenoyi* D'ORBIGNY, 1841.

These problems were frequently discussed, and in great detail by HUMPHREY (1949, p. 119) and CASEY (1964, p. 373). Following the rule of priority, the authors accept the spelling of the name *Dufrenoyia*, as given by KILIAN & REBOUL (1915, p. 34).

Concerning the selection of the type species: HUMPHREY (1949) thought that it is *Ammonites dufrenoyi* D'ORBIGNY, 1841, whereas CASEY (1964) thought it is *Ammonites furcatus* J. de C. SOWERBY. We agree with

CASEY's arguments, though we do not consider this problem as definitely solved.

Distribution. Lower Aptian – Upper Aptian (Gargasian), Europe, Turkmenistan; Upper Aptian, Texas (USA), Mexico, North America; Colombia, Venezuela, South America.

Dufrenoyia furcata (J. de C. SOWERBY, 1836)
Pl. 12, Figs. 1-3; Text-fig. 28

- * 1836 – *Ammonites furcatus*: J. de C. SOWERBY, p. 339, pl. 14, fig. 17.
non 1907-1913 – *Hoplites (Neocomites) furcatus*: KILIAN, p. 280, pl. 8, fig. 3, 4.
1964 – *Dufrenoyia furcata*: CASEY, p. 378, pl. 62, figs. 2, 3; pl. 63, fig. 1; text-fig. 106 a-c.
1999 – *Dufrenoyia furcata*: BOGDANOVA, PROZOROVSKY, pl. 8, figs. d,e.

Holotype: GSM. Geol.Soc.Coll. 2290, Hythe Beds, Hythe, Kent, UK.

Description: Shells medium-sized (D up to 30 mm), inflated ($W/D = 0.42-0.43$). Whorls low ($H/D = 0.32-0.34$), growing slowly, overlapping for 1/3 of the height. Flanks convex, venter wide, flat. Umbilicus moderately wide ($Du/D = 0.27-0.34$) with low almost vertical walls.

Ribs sparse and coarse, wide and flat in upper half of the flanks. Almost regular intercalation of main and intermediate ribs is occasionally interrupted when the intermediate ribs are lacking. On the ventro-lateral bend the ribs terminate sharply in acute tubercles elevated over the venter and elongated along the spiral. On whorls of $D = 25$ mm, the tubercles situated opposite each other are connected across the venter by wide flat straight ribs.

Suture line (Fig. 28): characterized by narrow, somewhat asymmetrical lobes U, I, I², I¹, narrow one-end dorsal lobe (D) and shallow bifid ventral lobe (V). Outer saddle (V/U) wide, asymmetrically bifid.

Remarks: Flat, frequently ribbed forms, more closely resembling *Dufrenoyia dufrenoyi* (D'ORBIGNY, 1841, pl. 33, figs. 4, 6) were taken by many authors for *D. furcata*. KILIAN, who reproduced the figure of *Ammonites dufrenoyi*, but named it *Hoplites (Neocomites) furcatus* (see above), made the same mistake. *D. furcata* differs distinctly from *D. dufrenoyi* in its lower and weakly increasing and less overlapping whorls, in its fewer, coarse ribs, that widen sharply towards the venter. These features make *D. furcata* similar to a form depicted by D'ORBIGNY (1841, pl. 33a, figs. 3-6) and named also *Ammonites dufrenoyi*, but essentially differing from our "lectotype" of *D. dufrenoyi* (see below).

Species close to *D. furcata* are *D. lurensis* (KILIAN, 1888) and *D. notha* (CASEY, 1964). *D. furcata* differs from *D. lurensis* (KILIAN, 1888, pl. 20, fig. 2) in less inflated whorls, narrower ribs and the presence of intermediate ribs. From *D. notha* CASEY (1964, p. 386, pl. 63,

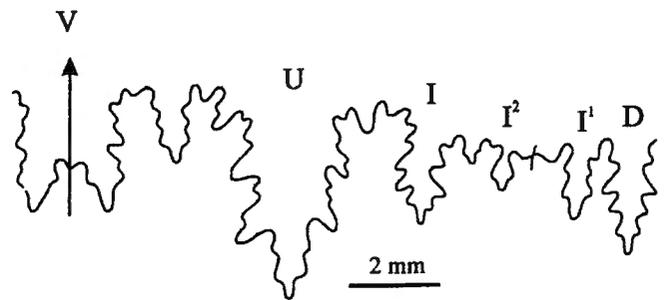


Fig. 28 — Suture line of *Dufrenoyia furcata* (J. de C. SOWERBY, 1836). CNIGR Museum 136/10367: H = 8.8 mm, W = 6.9 mm.

fig. 8a, b; pl. 64, fig. 5a, b) it differs in ribs, which strongly widen toward the venter.

D. furcata differs from the coarse-ribbed Mexican form *D. justinae* HILL (1893, pl. 21, fig. 6) in later appearance of true ribs on the venter.

Distribution: *Dufrenoyia furcata* Zone, Northern Caucasus, Russia; Tuarkyr, Kubadag, Bolshoi Balkhan, Turkmenistan; *Tropaeum bowerbanki* Zone, England; Southern France.

Dufrenoyia dufrenoyi (D'ORBIGNY, 1841)
Pl. 12, Figs. 7-9

- *1841 – *Ammonites Dufrenoyi*: D'ORBIGNY, p. 200, pl. 33, figs. 4-6, pl. 33a, figs. 3-6.
1925 – *Dufrenoyia aff. dufrenoyi*: BURCKHARDT, p. 18, pl. 10, figs. 1-4, 7-9.
1949 – *Dufrenoyia dufrenoyi*: HUMPHREY, p. 123, pl. 8, figs. 1-6.
1999 – *Dufrenoyia dufrenoyi*: BOGDANOVA, PROZOROVSKY, pl. 8, fig. a-c.

Lectotype (designated here): D'ORBIGNY, 1841, pl. 33, figs. 4-6, Gargasian, Gargas, France.

Description: Shells mainly small (D up to 26 mm), medium wide ($W/D = 0.28-0.36$). Whorls high ($H/D = 0.40-0.46$), moderately increasing, overlapping for 3/5 of the height. Flanks moderately convex. Venter weakly convex, becomes flattened with shell growth. Umbilicus shallow, relatively narrow or moderately wide ($Du/D = 0.23-0.28$). Whorl section trapezoidal.

Ribbing rather dense, with almost regular alternation of main and intermediate ribs. Main ribs emerge on umbilical wall, intermediate, in the lower third of the flanks. The ribs flatten in the middle of the flanks; then on the outer bend they sharply terminate to form acute "tubercles", slightly elevated above the venter. Up to $D = 30$ mm, venter smooth, then weak cross ribs appear, connecting the "tubercles".

Suture line: with wide symmetrical umbilical lobe (U) twice as long as the ventral lobe (V).

Remarks: *Dufrenoyia dufrenoyi* differs from *D. furcata* (J. de C. SOWERBY) in higher and flatter whorls, denser and less coarse ribs, more overlapping of whorls.

After the publication of the second edition of the cephalopod "Treatise" (WRIGHT *et al.*, 1996) a problem arose: fig. 212, 2c, d, figures an unusual figure of D'ORBIGNY's *Ammonites dufrenoyi* (1841). By checking the four copies of the Atlas of D'ORBIGNY's monograph (1840-1842) present in the All-Russian Geological Library (St. Petersburg, VSEGEI), we established the following: in three copies Plate 33 shows a traditional *A. dufrenoyi*, but in one of the copies there is second Plate 33 (let us conditionally name it 33 a) wherein the "unusual" version used in WRIGHT *et al.* (1996) is depicted. We thought it necessary to show both versions in our Plate 12: Fig. 8 – usual and Fig. 7 – unusual. In the description of *D. dufrenoyi* we selected the usual depicted specimen as the lectotype of *Ammonites dufrenoyi*.

Distribution: Lower Aptian, SE France, Mexico; Lower Aptian, *Dufrenoyia furcata* Zone, Tuarkyr, Kubadag, Kopet-Dag, Bolshoi and Malyi Balkhan, Turkmenistan.

***Dufrenoyia scalata* CASEY, 1964**

Pl. 12, Fig. 5

*1964 – *Dufrenoyia scalata*: CASEY, p. 386, pl. 63, fig. 1.

Holotype: GSM 108195, Ferruginous Sands, mouth of Whale Chine, Atherfield, Isle of Wight, U.K.

Description: Shells large ($D = 28.8-103$ mm), medium thick ($W/D = 0.29-0.35$). Whorls moderately high ($H/D = 0.41-0.45$), moderately increasing, overlapping at half-height. Venter flat, flanks flattened at the top and convex at the bottom. Umbilicus moderately wide ($Du/D = 0.28-0.35$), with low steep walls. Whorl section trapezoidal.

Ribs rather dense, coarse, wide and high. Main ribs emerge on umbilical bend, intermediate, in the lower third or in the middle of flanks (occur irregularly). On the outer bend ribs form "tubercles", elongated along the spiral, which on whorls of > 20 mm in diameter are connected on the venter by wide straight ribs.

Suture line: with wide low ventral lobe (V). Umbilical lobe (U) narrow, asymmetric, somewhat longer than the ventral lobe. Inner lateral lobe (I) also narrow, asymmetric, occurs on umbilical bend, lobe I^2 , on umbilical wall.

Remarks: *Dufrenoyia scalata* differs from *D. furcata* in less wide shells and in ribs bending backwards, and in the earlier appearance of ribs on the venter.

Distribution: *Tropaeum bowerbanki* Zone, *Cheloniceras meyndorfi* Subzone, Southern England; *Dufrenoyia furcata* Zone, Bolshoi Balkhan, Kubadag, Tuarkyr, Turkmenistan.

***Dufrenoyia fursovae* BOGDANOVA, 1991**

Pl. 12, Fig. 10; Text-fig. 29

*1991 – *Dufrenoyia fursovae*: BOGDANOVA, p. 88, pl. 2, figs. 9-11, text-fig. 6.

1999 – *Dufrenoyia fursovae*: BOGDANOVA, pl. 2, fig. 10.

1999 – *Dufrenoyia fursovae*: BOGDANOVA, PROZOROVSKY, pl. 8, fig. g.

Holotype: CNIGR Museum 28/12730, *Dufrenoyia furcata* Zone, Oglanly, Bolshoi Balkhan, Turkmenistan.

Description: Shells medium-sized, flattened ($W/D = 28-38$), with moderately increasing whorls, overlapping at a little more than half-height. The venter flat, flanks regularly convex, the whorl is widest almost in the middle of the height or slightly shifted towards the umbilicus. Whorl section rectangular-oval. Umbilicus moderately narrow ($Du/D=23-24$), shallow, stepwise. Umbilical walls low, rather steeply inclined. Umbilical bend gently sloping.

Dense ribbing is represented by clearly S-shaped main and one or two intermediate ribs. Main ribs emerge on umbilical wall and cross the umbilical bend as narrow crests. Intermediate ribs of various lengths. Sometimes, one of intermediate ribs branches off a main rib. Long ribs appear in the lower quarter of flanks, short ribs usually appear in the middle. All ribs narrow and fine in the lower half of the flanks, slightly flattened towards the periphery. They end sharply on the outer bend to form slightly elevated "tubercles". The venter is smooth to the whorl height of 12-15 mm; on later whorls it is crossed first by a little elevated thickening, and then sharp, straight radial ribs, connecting adjacent radial rib ends.

Suture line (Fig. 29): $VU I I^2: I^1 D$. On large whorls a supplementary lobe can form in saddle I^2/I^1 , first on the umbilical seam, then shifting onto the whorl outside. Sometimes, this lobe has been regarded as an independent lobe I^3 (BOGDANOVA, 1991, p. 89, text-fig. 6b).

Remarks: *Dufrenoyia fursovae* differs from *D. discoidalis* CASEY, 1964, which also has more than one intermediate rib, in narrower and more abundant ribs. From *D. sinzovi* LUPPOV in LUPPOV *et al.*, 1949, characterized by early appearance of radial ribs on the outside similar to *D. fursovae*, the latter differs in flatter ribs and more

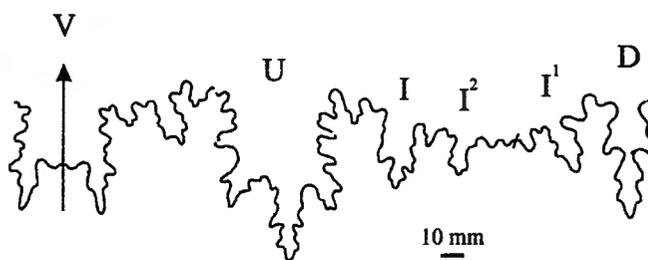


Fig. 29 — Suture line of *Dufrenoyia fursovae* BOGDANOVA, 1991. CNIGR Museum 33/12730: H = 17.6 mm.

frequent appearance of two intermediate ribs between adjacent main ribs, and narrower umbilicus.

Distribution: *Dufrenoyia furcata* Zone, Tuarkyr, Bolshoi Balkhan, Kubadag, Kopet-Dag, Turkmenistan; Lower Aptian, Mangyshlak, Kazakhstan.

Genus *Burckhardtites* HUMPHREY, 1949

- *1925 – *Neocomites*: BURCKHARDT, p. 14 (pars).
 1939 – *Neocomites*: SCOTT, p. 974 (pars).
 1949 – *Burckhardtites*: HUMPHREY, p. 130.

Type species: *Neocomites nazasensis* BURCKHARDT, 1925, Upper Aptian (Gargasian), Mexico.

Description: Shells medium to large, semi-involute, flattened, whorl section rectangular-oval, whorls from moderately to rapidly increasing, venter flat.

Ribbing of phragmocone is rather dense, alternation of main and intermediate ribs is usually regular, but sometimes second intermediate rib appears. On the body chamber ribbing sharply becomes very dense: intermediate ribs of various length appear, repeated branching of main ribs at various heights with generating obscure bundles is common. All ribs have weak crests on the umbilical bend; they form an angular bend on the ventro-lateral bend and cross the venter straight.

Suture line: characterized by a peculiar ventral lobe (V), trifid deep umbilical lobe (U) and narrow deep inner lobe (I), shifted onto the outside of the whorl. This is characteristic of the family Deshayesitidae. Inner lateral lobe I² is situated on the umbilical wall.

Composition: Five species: *Burckhardtites nazasensis* (BURCKHARDT, 1925), Upper Aptian (Gargasian) of Mexico, *B. kellumi* HUMPHREY, 1949, *B. palumbes* HUMPHREY, 1949, *B. imlayi* HUMPHREY, 1949, *B. gregoriensis* HUMPHREY, 1949, Upper Aptian (Gargasian) of Mexico, Lower Aptian (*Dufrenoyia furcata* Zone) of Turkmenistan.

Remarks: *Burckhardtites* is most likely derived from *Paradeshayesites* and its ancestor species is apparently *P. terminalis* BOGDANOVA, 1979 (BOGDANOVA *et al.*, 1979, pl. 2, fig. 9). *Burckhardtites* differs from *Dufrenoyia* in the lack of clear tubercles on the ventrolateral bend, sharp double S-shaped ribs on the flank, sharp rib thickening on the body chamber and the unusual shape of the ventral lobe: it has a wide base and a narrow top.

Distribution: Lower Aptian, *Dufrenoyia furcata* Zone, Kopet-Dag, Tuarkyr, Turkmenistan;
 Upper Aptian (Gargasian), Mexico.

Burckhardtites palumbes HUMPHREY, 1949
 Pl. 12, Fig. 11; Text-fig. 30

- *1949 – *Burckhardtites palumbes*: HUMPHREY, p. 135, pl. 11, figs. 1, 9; pl. 12, figs. 1-3.

Holotype: Museum PUM 22686, Upper Aptian (Peña Formation), Coahuila, Mexico.

Material: Three specimens of unsatisfactory preservation: CNIGR Museum 160/10367, Lower Aptian, Chalsu, Kopetdag, Turkmenistan; CNIGR Museum 440/10367, 441/10367, *Dufrenoyia furcata* Zone, Biyneu, Tuarkyr, Turkmenistan. Two last suture-lines can be observed on the specimen 160/10367.

Description: Shell is medium-sized, compressed, with whorls moderately growing in height. Venter narrow, flat; ventrolateral margin sharp; flanks slightly convex, whorls are thickest in the middle of flanks. Umbilical walls low and abrupt, umbilical rim angular. The whorl section is mainly rectangular-oval. Umbilicus moderately wide, shallow, stepped.

Shell with strong, narrow, rather regularly alternating, distinctly double sigmoid ribs. Main ribs begin near the seam. Intermediate ribs (one or two) of different length arise from the umbilical border to the middle of flanks. All the ribs become slightly wider and flatter towards venter and end near the ventrolateral margin in short radial ridges. Ribs cross venter straight with strongly raised belts. The living chamber is ornamented with dense, irregularly alternating ribs, which are finer than on the phragmocone. There are from one to five intermediate ribs of different length between adjacent main ribs. Inflexion of ribs is not equal. Radial ridge at the end of ribs disappear at the ventrolateral margin, ribs cross venter straight with slight lowering in the middle.

Suture line (Fig. 30): with three lobes on the flank (V, U, I). Ventral lobe (V) is sharply constricted in the lower part and widened in the upper part; umbilical lobe (U) wide, almost symmetric; low asymmetrically trifid inner lobe (I) and narrow second inner lobe (I²) descending toward the seam. Outer saddle (V/U) very wide, with two branches of different height.

Measurements:

No	D	H	W	Du	H/D	W/D	Du/D
160/10367	49.7	21.8	12.5	12.4	0.44	0.25	0.25

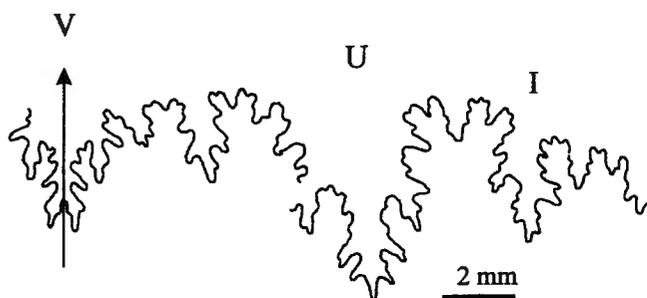


Fig. 30 — Suture line of *Burckhardtites palumbes* HUMPHREY, 1949. CNIGR Museum 160/10367: H = 15.2 mm.

Remarks: Asiatic specimens differ from the holotype in stronger ribs and in higher whorls. We consider that the latter distinction is not reliable, because HUMPHREY's Mexican specimens are deformed. *Burckhardtites palumbes* differs from *B. nazasensis* (BURCKHARDT, 1925, p. 14, pl. 3, figs. 4-7) and *B. imlayi* HUMPHREY (1949, p. 134, pl. 11, figs. 10, 11) in having fewer, more distinct ribs on the living chamber. In these features *B. palumbes* is closer to *B. kellumi* HUMPHREY (1949, p. 131, pl. 10, figs. 7, 9), but the latter has coarser and fewer ribs on its phragmocone.

Locality: *Dufrenoyia furcata* Zone, Umokdere, Tuarkyr, Chalsu, Kopet-Dag, Turkmenistan.

Distribution: Lower Aptian, *D. furcata* Zone, Tuarkyr, Kopet-Dag, Turkmenistan; Upper Aptian (Gargasian), Mexico.

***Burckhardtites gregoriensis* HUMPHREY, 1949**

Pl. 12, Fig. 12

*1949 – *Burckhardtites gregoriensis*: HUMPHREY, p. 132, pl. 11, figs. 3, 4.

Holotype: Museum PUM 24257, Upper Aptian (Peña Formation), Coahuila, Mexico.

Material: One little fragment of body chamber (*Dufrenoyia furcata* Zone, Tuarkyr, Turkmenistan).

Description: Whorls slowly growing in height, flanks evenly convex, venter wide and flat. Shell marked with dense and fine ribs. At the umbilicus border distinct elongate ridges divided into two ribs on the lower third of the flank are present. Usually between a pair of these double-ribs there is a single rib, rising a little above the umbilical border, at the level of umbilical ridges. Sometimes these ribs are also divided into two branches a little above the point of branching of main ribs. All ribs are distinctly flexuous. They cross the venter straight, forming a sharp bend at the ventrolateral margin.

Suture line invisible.

Remarks: Our specimen is almost identical with the Mexican specimen, figured by HUMPHREY (1949, pl. 11, figs. 3, 4). This species differs from other species in very dense ribbing with long and bifurcate intermediate ribs.

Locality: *Dufrenoyia furcata* Zone, Lausan (Tuarkyr, Turkmenistan).

Distribution: Lower Aptian, *Dufrenoyia furcata* Zone, Turkmenistan; Upper Aptian (Gargasian) of Mexico.

Genus *Neodeshayesites* CASEY, 1964

*1938 – *Deshayesites*: RIEDEL, p. 37.

1964 – *Neodeshayesites*: CASEY, p. 289.

1982 – *Deshayesites*: RENZ, p. 16.

1996 – *Neodeshayesites*: WRIGHT *et al.*, p. 273

Type species: *Deshayesites stutzeri* RIEDEL, 1938, Upper Aptian, Colombia.

Generic characters: Discoid shells of various size, with flanks flattened or gently convex. Ventrolateral margins well-defined, umbilical border poorly defined. Involution varies from one-third to four-fifth; at large diameters a more marked widening of the umbilical spiral is characteristic of final whorls. Sculpture consists sometimes of few, sometimes of numerous, main as well as intermediate ribs. Ribs are clearly sigmoid, often bent forwards from the radius. Main ribs usually single, but in some species they are bifurcated and doubly bifurcated. Intermediate ribs are intercalated or branch off from main ribs on different height of flanks. On early whorls all ribs are interrupted on the venter, later they cross straight over flat venter and slightly elevate on the shoulders. On later whorls ribs tend to lose elevation at ventrolateral margins and cross bending forward as a gently sloping arc.

The ontogenesis of the suture-line has not been studied so far.

Composition: *Neodeshayesites karsteni* (MARCOU, 1875), *N. columbianus* (RIEDEL, 1938), *N. nodosus* (RIEDEL, 1938), *N. stutzeri* (RIEDEL, 1938), *N. rotundus* (RIEDEL, 1938), *N. contracta* (RIEDEL, 1938), *N. albertoalvarezii* STAYO-SERNA, 1979, *N. cingulatus* ETAYO-SERNA, 1979; Colombia, Upper Aptian – Lower Albian.

Remarks: *Neodeshayesites* resembles *Dufrenoyia*. It differs from *Dufrenoyia* in the absence of real tubercles (clavi) on the ventrolateral shoulders and in the presence of umbilical ridges. *Neodeshayesites* differs from *Deshayesites* in high straight ribs on venter and angularity of shoulders. These two characters are very similar to the genus *Hypacanthoplites*. The latter has no umbilical ridges, and the lateral ribs of *Neodeshayesites* tend to be sigmoid or even biconcave, very often rursiradiate.

Distribution: Upper Aptian – Lower Albian, Colombia; Upper Aptian, Venezuela.

Conclusions – Origin and generic affinities within the family *Deshayesitidae*

The hypothesis that monomorph ammonites descended from heteromorph taxa was first suggested on the basis of ontophylogenetic studies on Jurassic-Cretaceous ammonites. Pioneering research was done by SCHINDEWOLF [1961, 1962, (1963) 1964, 1965, 1966a, b, 1968] and WIEDMANN (1966a, 1966b, 1969). Simultaneously, intensive studies on Aptian ammonites were undertaken in the ex-USSR. Based on rich and well-preserved material collected in Daghestan, Northern Caucasus and Turkmenistan, detailed studies on shell morphogenesis, sculpture

and suture line of the Deshayesitidae were undertaken (MIKHAILOVA 1957, 1958, 1976; TOVBINA, 1963, 1965; BOGDANOVA, 1971, 1979). TOVBINA (1965, p. 46) was the first to suggest that monomorph Deshayesitidae could possibly have originated from the heteromorph *Colchidites* Djanélidzé as a result of shell recoiling. In 1963 TOVBINA published the description of the genus *Turkmeniceras*: she compared its suture line morphogenesis with that of *Deshayesites* ex gr. *deshayesi* (Leymerie) (TOVBINA, 1963, text-fig. 2, 3) and because of their similarity she assigned *Turkmeniceras* to the Deshayesitidae (with a question mark). Later she also studied suture morphogeneses in *Colchidites* aff. *shaoriensis* Djanélidzé and *Turkmeniceras turkmenicum* (TOVBINA, 1965, text-fig. 2, 4), confirming the hypothesis that the family Deshayesitidae had descended from the genus *Colchidites* and demonstrating the evolutionary lineage *Colchidites* → *Turkmeniceras* → *Deshayesites* → *Dufrenoyia*. This interpretation was wholly or partially supported by WIEDMANN (1969), MIKHAILOVA (1969, 1970), BOGDANOVA (1971), KAKABADZE (1971). These authors accepted that the transition from heteromorph to monomorph ammonites is possible. This was new because until then heteromorphs had been considered to be the last members of branches that were going extinct and thus, *a priori* had been thought to be descendants of monomorphs.

The phylogenetic lineage *Heteroceras* → *Colchidites* → *Turkmeniceras* → *Deshayesites* means radical changes in the shell shape (see Fig. 3). The presence of helix and hook is characteristic of the last heteroceratids (*Heteroceras* d'Orbigny), when the hook changes into a spiral, and gradual size reduction of the helix and simultaneous increasing of whorl number in plane spiral occurs (*Colchidites*). Helix reduction and retention of umbilical perforation in early and its closing in late *Turkmeniceras* (rudiment of heteromorphs) is observed. The planospiral genus *Turkmeniceras* inherited a similar type of sculpture from *Colchidites*. *Turkmeniceras* differs from the ancestral genus *Colchidites*, in the absence of the helicoidal stage in ontogenesis, in having more incised internal (I/D) and umbilical (U/I) saddles, and in shifting of the internal lobe (I) from the seam to the umbilical rim. *Turkmeniceras* undoubtedly belongs to the family Deshayesitidae because it and the type genus *Deshayesites* unquestionably have similar shell shape and sculpture and, what is more important, the same type of suture line morphogenesis.

WIEDMANN (1969) demonstrated the probable origin of *Turkmeniceras* not only from *Colchidites* but also from *Hemihoplites*. This problem was reconsidered by SCHARIKADZE *et al.*, 1989. When they studied the ontogenesis of *Hemihoplites* (*Matheronites*) *ridzewskyi* Karakasch they noticed the similarity of the internal lobe (I) of this species with that of some *Colchidites* taxa. However, they stated that shell shape and sculpture in *Hemihoplites* (*Matheronites*) differ sharply from these of *Turkmeniceras*, and that there is no inheritance of features between *Hemihoplites* and *Turkmeniceras* as observed in *Colchidites* and *Turkmeniceras*. Therefore we herein consider

that only the transition *Colchidites* → *Turkmeniceras* is real.

In connection with the possible heteromorph origin of monomorph Deshayesitidae, unusual deshayesitids found in Ulyanovsk area, Middle Volga region (DOGUZHAIEVA *et al.*, 1990) should be mentioned. The body chamber and several preceding camerae are bent from the plane of symmetry in four *Deshayesites* specimens, and resulted in a helicoid terminal part of the shell. Asymmetrical shells in *Deshayesites* could be interpreted from several points of view, but we prefer to think that they reveal ancestral features.

Thus, *Turkmeniceras* is an ancestral genus for the family Deshayesitidae. The most likely developmental trend in *Turkmeniceras* is indicated in the species *T. tovbinae* and *T. tumidum*, which could have led to the appearance of two main genera within the family Deshayesitidae: *T. tumidum* → *Deshayesites*, *T. tovbinae* → *Paradeshayesites*.

The early taxa of the genus *Deshayesites* (apart from the absence of umbilical perforation) are characterised by (1) increasing of the overlapping of succeeding whorls, (2) appearance of strong S-shaped ribs, (3) development of crests on umbonal bends in some species, (4) irregular alternation of main and intermediate ribs, (5) a greater number of internal lobes (I, I¹, I²), (6) by position of I and I² on the flank.

The branch *Turkmeniceras* → *Paradeshayesites*, unlike that of *Turkmeniceras* → *Deshayesites*, was characterized by a faster increasing in whorl height, by the appearance of densely spaced fasciculate ribbing and by the development of four internal lobes (I, I¹, I², I³). Separation of *Obsoleticeras* from *Turkmeniceras* was accompanied not only by faster increasing of whorl height (as in the lineage *Turkmeniceras* → *Paradeshayesites*) but, mainly, by the almost complete smoothing of sculpture (in *Paradeshayesites* the ribbing becomes smooth only in the middle stage of the shell growth).

Thus, the study of evolutionary links in the family Deshayesitidae from the interval of three Lower Aptian zones revealed three main branches inheriting characteristic generic features: *Deshayesites* KAZANSKY, 1914, *Paradeshayesites* KEMPER, 1967 and *Obsoleticeras* BOGDANOVA & MIKHAILOVA, 1999. *Prodeshayesites* CASEY, 1961 could be heterogeneous. This was already shown in MOGDANOVA, MIKHAILOVA, 1999 when discussing the specific compositions of *Deshayesites*, *Paradeshayesites* and *Obsoleticeras*. This is why we reject *Prodeshayesites* CASEY, 1961.

Dufrenoyia was separated from *Deshayesites* as a result of flattening of the venter, weakening or interruption of ribs in its middle part, appearance of nodes (clavi) on ventro-lateral shoulders.

Data on the origin of *Neodeshayesites* are controversial (RENZ, 1982; ETAYO-SERNA, 1979). Evidently *Neodeshayesites* originated from *Dufrenoyia*, since both genera have similar features (p. 00).

Also the origin of *Burckhardtites* is unclear: most likely it was a descendant of densely ribbed *Parade-*

shayesites; but a relation to *Neodeshayesites* cannot totally be excluded. The stratigraphical distribution of *Dufrenoyia* and *Burckhardtites* in the European and Asian sections shows that they arose during the Early Aptian. According to HUMPHREY (1949), RIEDEL (1938), ETAYO-SERNA (1979) and RENZ (1982) *Dufrenoyia* and *Burckhardtites* continued to exist during the Late Aptian. The stratigraphical distribution of *Neodeshayesites* is uncertain. According to ETAYO-SERNA (1979) it existed during the Late Aptian and Early Albian.

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Explanation of Plates

All photographs are given in natural size, except where marked otherwise.

PLATE 1

All the specimens are from the *Turkmeniceras turkmenicum* Zone, in Turkmenistan.

- Figs. 1, 2 — *Turkmeniceras turkmenicum* TOVBINA, 1962. 1 – Holotype CNIGR Museum 1/8293. Lateral side. Sekizjab (Kopet-Dag); 2 – CNIGR Museum 15/10367. a, b – lateral side, c – front. Gobekadzhi (Tuarkyr).
- Fig. 3 — *Turkmeniceras ex gr. turkmenicum* TOVBINA, 1962. CNIGR Museum 17/10367. a – lateral side, b – lateral side, initial whorls (x20). Tekedzhik (Tuarkyr).
- Fig. 4 — *Turkmeniceras rarecostatum* BOGDANOVA, 1971. Holotype CNIGR Museum 3/10096. a – lateral side, b – front. Tekedzhik (Tuarkyr).
- Figs. 5, 6 — *Turkmeniceras geokderense* TOVBINA, 1962. 5 – Holotype CNIGR Museum 7/8293. a – lateral side, b – front. Geokdere (Tuarkyr). 6 – CNIGR Museum 19/10367. a – lateral side, b – front, c – lateral side, initial whorls (x20). Gobekadzhi (Tuarkyr).
- Fig. 7 — *Turkmeniceras tovbinae* sp. nov. Holotype CNIGR Museum 9/8293. a – lateral side, b – front, c – venter. Gobekadzhi (Tuarkyr).
- Fig. 8 — *Turkmeniceras tumidum* BOGDANOVA, 1971. Holotype CNIGR Museum 5/10096. a – lateral side, b – front, c – venter. Gobekadzhi (Tuarkyr).
- Fig. 9 — *Turkmeniceras multicostatum* TOVBINA, 1963. Holotype CNIGR Museum 5/8293. a – lateral side, b – front, c – venter. Oglanly (Bolshoi Balkhan).

PLATE 2

- Fig. 1 — *Deshayesites bodei* (VON KOENEN, 1902). Neotype RGM 61665. (KEMPER, 1967, pl. 12, fig. 6). Lateral side. Alstätte (NW Germany); Lower Aptian.
- Fig. 2 — *Deshayesites* aff. *bodei* (VON KOENEN, 1902). MSU 21/96. a – lateral side, b – front. Sokolova Gora, Saratov (Volga Region, Russia); *Deshayesites tenuicostatus* Zone.
- Fig. 3 — *Ammonites deshayesi* Leymerie. (TRAUTSCHOLD, 1865, pl. 3, fig. 16a,b). a – lateral side, b – front. Simbirsk (Volga Region, Russia); Lower Aptian.
- Figs. 4-6 — *Deshayesites consobrinoides* (SINZOW, 1898). 4 – CNIGR Museum 8/11063. (SINZOW, 1898, pl. A, fig. 8). Lateral side. Ulyanovsk (Volga Region, Russia); Lower Aptian. 5 – Lateral side. (CASEY, 1964, p. 300, text-fig. 106n, Bailly-aux-Forges (Haute-Marne, France); Lower Aptian (*Deshayesi* Zone “argiles à *Plicatula*”). 6 – Lectotype CNIGR Museum 10/11063 (SINZOW, 1898, pl. A, fig. 10). a – lateral side, b – venter (the venter view is photographed for the first time). Saratov (Volga Region, Russia); Lower Aptian.
- Fig. 7 — *Deshayesites tenuicostatus* (VON KOENEN, 1902). MSU 22/96. a – lateral side, b – venter. Sokolova Gora, Saratov (Volga Region, Russia); *Deshayesites tenuicostatus* Zone.

- Figs. 8, 9 — *Deshayesites luppovi* BOGDANOVA, 1983. 8 — Holotype CNIGR Museum 23/9442. a — front, b — lateral side. Bordzhakly (Bolshoi Balkhan, Turkmenistan); Lower Aptian, *Paradeshayesites weissi* Zone. 9 — CNIGR Museum 25/9442. a — lateral side, b — venter, c — front. Kubadag (Turkmenistan); age as on Fig. 8.
- Fig. 10 — *Deshayesites subfissicostatus* (SINZOW, 1898). CNIGR Museum 24/10910. a — venter, b — lateral side. Saratov (Volga Region, Russia); Lower Aptian.

PLATE 3

- Fig. 1 — *Paradeshayesites callidiscus* (CASEY, 1961). CNIGR Museum 10/8573. a — lateral side, b — venter. Atherfield (Isle of Wight, UK); Lower Aptian.
- Fig. 2 — *Deshayesites forbesi* CASEY, 1961. PIM 2291/3390. a — lateral side, b — front. Shilovka (Volga Region, Russia); *Deshayesites volgensis* Zone.
- Figs. 3, 4 — *Deshayesites volgensis* SAZONOVA, 1958. 3 — MSU 30/96. a — lateral side, b — venter, c — front. Shilovka (Volga Region, Russia); *Deshayesites volgensis* Zone. 4 — Holotype CNIGR Museum 1/11805. (SAZONOVA, 1958, pl. 1, fig. 1). a — venter, b — lateral side, c — front. Sengiley (Volga Region, Russia); Lower Aptian.
- Fig. 5 — *Deshayesites pappi* BOGDANOVA, 1991. Holotype CNIGR Museum 9/12730. a — venter, b — lateral side, c — front. Umokdere (Tuarkyr, Turkmenistan); *Paradeshayesites weissi* Zone.
- Figs. 6-8 — *Deshayesites dechyi* (PAPP, 1907). 6 — CNIGR Museum 8/10685. a — front, b — lateral side. Mirisinky (Tuarkyr, Turkmenistan); Lower Aptian. 7 — MSU 2/99. a — venter, b — lateral side, c — front. Verkhnie Mulebki (Daghestan, Russia); *Deshayesites deshayesi-D. dechyi* Zone. 8 — MSU 9/99. a — venter, b — lateral side. Vanashimakhi (Daghestan, Russia); age as on Fig. 7.

PLATE 4

- Figs. 1-3 — *Deshayesites consobrinus* (D'ORBIGNY, 1841). 1 — Holotype. (D'ORBIGNY, 1841, pl. 47, figs. 1, 2). a — front, b — lateral side. La Bédoule (Bouches-du-Rhône, France); Lower Aptian. 2 — CNIGR Museum 33/10367. a — lateral side, b — front. Babashi (Tuarkyr, Turkmenistan); *Paradeshayesites weissi* Zone. 3 — MSU 11/99. a — lateral side, b — front. Butri (Daghestan, Russia); Lower Aptian.
- Figs. 4, 5 — *Deshayesites kemperi* sp. nov. 4 — MSU 12/99. a — venter, b — lateral side, c — front. Butri (Daghestan, Russia); Lower Aptian. 5 — Holotype CNIGR Museum 31/10367. a — venter, b — lateral side, c — front. Bordzhakly (Bolshoi Balkhan, Turkmenistan); *Paradeshayesites weissi* Zone.
- Figs. 6, 7 — *Deshayesites deshayesi* (D'ORBIGNY, 1841). 6 — (LEYMERIE, 1842, pl. 17, fig. 17 a, b). a — lateral side, b — front. 7 — Holotype. (D'ORBIGNY, 1841, pl. 85, fig. 1, 2). a — lateral side, b — front. Villeneuve-au-Chemin (Aube, France); Lower Aptian.

PLATE 5

- Figs. 1, 2 — *Deshayesites caseyi* sp. nov. 1 — MSU 7/99. a — lateral side, b — venter. Kuban (Northern Caucasus, Russia); *Deshayesites dechyi* Zone. 2 — Holotype MSU 6/99. a — lateral side, b — venter. Occurrence and age as on Fig. 1.
- Fig. 3 — *Neodeshayesites columbianus* (RIEDEL, 1938). MSU 18/99. a — venter, b — lateral side. Colombia; ?Upper Aptian. (precise locality unknown).
- Figs. 4-6 — *Deshayesites kudrjavzevi* MIKHAILOVA, 1958. 4 — Holotype MSU 1/99. a — lateral side, b — venter. Kuma (Northern Caucasus, Russia); *Deshayesites dechyi* Zone. 5 — MSU 13/99. Front. Occurrence and age as on Fig. 4. 6 — CNIGR Museum 109/10367. Lateral side. Tekedzhik (Tuarkyr, Turkmenistan); *Deshayesites deshayesi* Zone.

PLATE 6

- Figs. 1, 2 — *Paradeshayesites imitator* (GLAZUNOVA, 1968). 1 — MSU 32/96. a — front, b — lateral side. Shilovka (Volga Region, Russia); Lower Aptian. 2 — MSU 29/96. a — lateral side, b — front. Occurrence and age as on Fig. 1.
- Fig. 3 — *Deshayesites aff. vectensis* SPATH, 1930. MSU 26/96. a — lateral side, b — venter. Shilovka (Volga Region, Russia); Lower Aptian.
- Fig. 4 — *Deshayesites saxbyi* CASEY, 1964. PIM A/3390. a — lateral side, b — venter. Shilovka (Volga Region, Russia); *Deshayesites volgensis* Zone.
- Figs. 5, 6 — *Deshayesites gracilis* CASEY, 1964. 5 — MSU 39/96. a — venter, b — lateral side. Shilovka (Volga Region, Russia); *Deshayesites volgensis* Zone. 6 — MSU 25/96. a — venter, b — lateral side. Occurrence and age as on Fig. 5.
- Figs. 7, 8 — *Deshayesites robustocostatus* MIKHAILOVA, 1958. 7 — Holotype MSU 5/99. a — lateral side, b — front. Tsudakhar (Daghestan, Russia); Lower Aptian. 8 — MSU 16/99. a — venter, b — lateral side. Occurrence and age as on Fig. 7.

PLATE 7

- Fig. 1 — *Paradeshayesites laeviusculus* (VON KOENEN, 1902). Lectotype GIG 457-1. (VON KOENEN, 1902, pl. 8, fig. 4). a, b — lateral side. Braunschweig (Germany); *Deshayesites bodei* Zone.
- Fig. 2 — *Paradeshayesites topleyi* (SPATH, 1930). CNIGR Museum 82/10367. Lateral side. Tekedzhik (Tuarkyr, Turkmenistan); *Paradeshayesites weissii* Zone.
- Fig. 3 — *Paradeshayesites weissiformis* (BOGDANOVA, 1983). Holotype CNIGR Museum 7/9442. a — lateral side, b — front, c — lateral side, inner whorls. Umokdere (Tuarkyr, Turkmenistan); *Paradeshayesites tuarkyricus* Zone.
- Fig. 4 — *Paradeshayesites oglanlensis* (BOGDANOVA, 1983). Holotype CNIGR Museum 12/9442. a — lateral side, b — front. Oglanly (Bolshoi Balkhan, Turkmenistan); *Paradeshayesites tuarkyricus* Zone.
- Figs. 5, 6 — *Paradeshayesites planicostatus* (BOGDANOVA, 1991). 5 — Holotype CNIGR Museum 4/12730. Lateral side. Bordzhakly (Bolshoi Balkhan, Turkmenistan); *Paradeshayesites tuarkyricus* Zone. 6 — CNIGR Museum 5/12730. a — lateral side, b — front. Jangadzha (Kubadag, Turkmenistan); *Paradeshayesites weissii* Zone.
- Fig. 7 — *Paradeshayesites tuarkyricus* (BOGDANOVA, 1983). Holotype CNIGR Museum 1/9442. a — venter, b — lateral side, c — front. Lausan (Tuarkyr, Turkmenistan); *Paradeshayesites tuarkyricus* Zone.

PLATE 8

- Figs. 1, 2 — *Paradeshayesites callidiscus* (CASEY, 1961). 1 — MSU 36/96. a — front, b — lateral side, c — venter. Shilovka (Volga Region, Russia); Lower Aptian. 2 — MSU 24/96. a — lateral side, b — front. Occurrence and age as on Fig. 1.
- Figs. 3-5 — *Deshayesites lavaschensis* KAZANSKY, 1914. 3 — MSU 3/99. a — lateral side, b — venter. Tsudakhar (Daghestan, Russia); Lower Aptian. 4 — MSU 4/99. a — lateral side, b — venter. Occurrence and age as on Fig. 3. 5 — CNIGR Museum 10/12927. Lateral side. Chirchili (Mangyshlak, Kazakhstan); Lower Aptian.

PLATE 9

- Figs. 1, 2 — *Paradeshayesites topleyi* (SPATH, 1930). 1 — CNIGR Museum 80/10367. a — venter, b — lateral side. Jangadzha (Kubadag, Turkmenistan); *Paradeshayesites weissii* Zone. 2 — MSU 35/96. a — lateral side (x 0,8), b — front. Shilovka (Volga Region, Russia); Lower Aptian.

PLATE 10

- Fig. 1 — *Paradeshayesites callidiscus* (CASEY, 1961). CNIGR Museum 99/10367. a — lateral side, b — venter. Tekedzhik (Tuarkyr, Turkmenistan); *Paradeshayesites weissii* Zone.
- Figs. 2, 3 — *Paradeshayesites similis* (BOGDANOVA, 1991). 2 — CNIGR Museum 17/12730. Lateral side. Tekedzhik (Tuarkyr, Turkmenistan); *Paradeshayesites weissii* Zone. 3 — MSU 23/96. a — venter, b — lateral side, c — front. Sengiley (Volga Region, Russia); Lower Aptian.
- Figs. 4-6 — *Deshayesites kemperi* sp. nov. 4 — CNIGR Museum 32/10367. a — venter, b — lateral side. Bordzhakly (Bolshoi Balkhan, Turkmenistan); *Paradeshayesites weissii* Zone. 5 — CNIGR Museum 35/10367. Lateral side. Occurrence and age as on Fig. 4. 6 — CNIGR Museum 34/10367. a — lateral side, b — front. Jangadzha (Kubadag, Turkmenistan); age as on Fig. 4.

PLATE 11

- Fig. 1 — *Turkmeniceras tovbinae* sp. nov. CNIGR Museum 235/10367. a — lateral side, b — venter. Gobekadzhi (Tuarkyr, Turkmenistan); *Turkmeniceras turkmenicum* Zone.
- Figs. 2, 3 — *Obsoleticeras levigatum* (BOGDANOVA, 1991). 2 — Holotype CNIGR Museum 24/12730. a — lateral side, b — venter. Utuludzha (Bolshoi Balkhan, Turkmenistan); *Paradeshayesites weissii* Zone. 3 — MSU 20/96. a — lateral side, b — venter. Kriushi (Volga Region, Russia); *Deshayesites volgensis* Zone.

PLATE 12

- Figs. 1-3 — *Dufrenoyia furcata* (J. de C. SOWERBY, 1836). 1 — Holotype GSM, Geol.Soc.Coll.2290. (CASEY, 1964, pl. 62, fig. 2a, b). a — venter, b — lateral side. Hythe (Kent, England); Hythe Beds. 2 — CNIGR Museum 24/12927. a — lateral side, b — venter. Shair (Mangyshlak, Kazakhstan); Lower Aptian. 3 — MSU 14/99. a — lateral side, b — venter. Belaya Rechka (Northern Caucasus, Russia); Lower Aptian.
- Fig. 4 — *Dufrenoyia lurensis* (KILIAN, 1888). Holotype (KILIAN, 1888, pl. 20, fig. 2 a, b). a — front, b — lateral side. Carniol (Alpes-de-Haute-Provence, France); Upper Aptian.
- Fig. 5 — *Dufrenoyia scalata* CASEY, 1964. MSU 15/99. a — venter, b — lateral side. Tekedzhik (Tuarkyr, Turkmenistan); Lower Aptian.
- Fig. 6 — *Dufrenoyia subfurcata* (KAZANSKY, 1914). MSU 10/99. a — front, b — lateral side, c — venter. Murada (Daghestan, Russia); Lower Aptian.
- Figs. 7-9 — *Dufrenoyia dufrenoyi* (D'ORBIGNY, 1841). 7 — (D'ORBIGNY, 1841, pl. 33a, figs. 3, 4). a — front, b — lateral side. Gargas (Vaucluse, France); Upper Aptian. 8 — (D'ORBIGNY, 1841, pl. 33, figs. 4, 5). a — front, b — lateral side. Occurrence and age as on Fig. 7. 9 — CNIGR Museum 27/12927. a — lateral side, b — venter. Shair (Mangyshlak, Kazakhstan); Lower Aptian.
- Fig. 10 — *Dufrenoyia fursovae* BOGDANOVA, 1991. CNIGR Museum 28/12927. a — lateral side, b — venter. Karashimrau (Mangyshlak, Kazakhstan); Lower Aptian.
- Fig. 11 — *Burckhardtites palumbes* HUMPHREY, 1949. CNIGR Museum 160/10367. a — lateral side, b — venter. Chalsu (Kopet-Dag, Turkmenistan); *Dufrenoyia furcata* Zone.
- Fig. 12 — *Burckhardtites gregoriensis* HUMPHREY, 1949. a — lateral side, b — venter. Lausan (Tuarkyr, Turkmenistan); *Dufrenoyia furcata* Zone.



PLATE 1

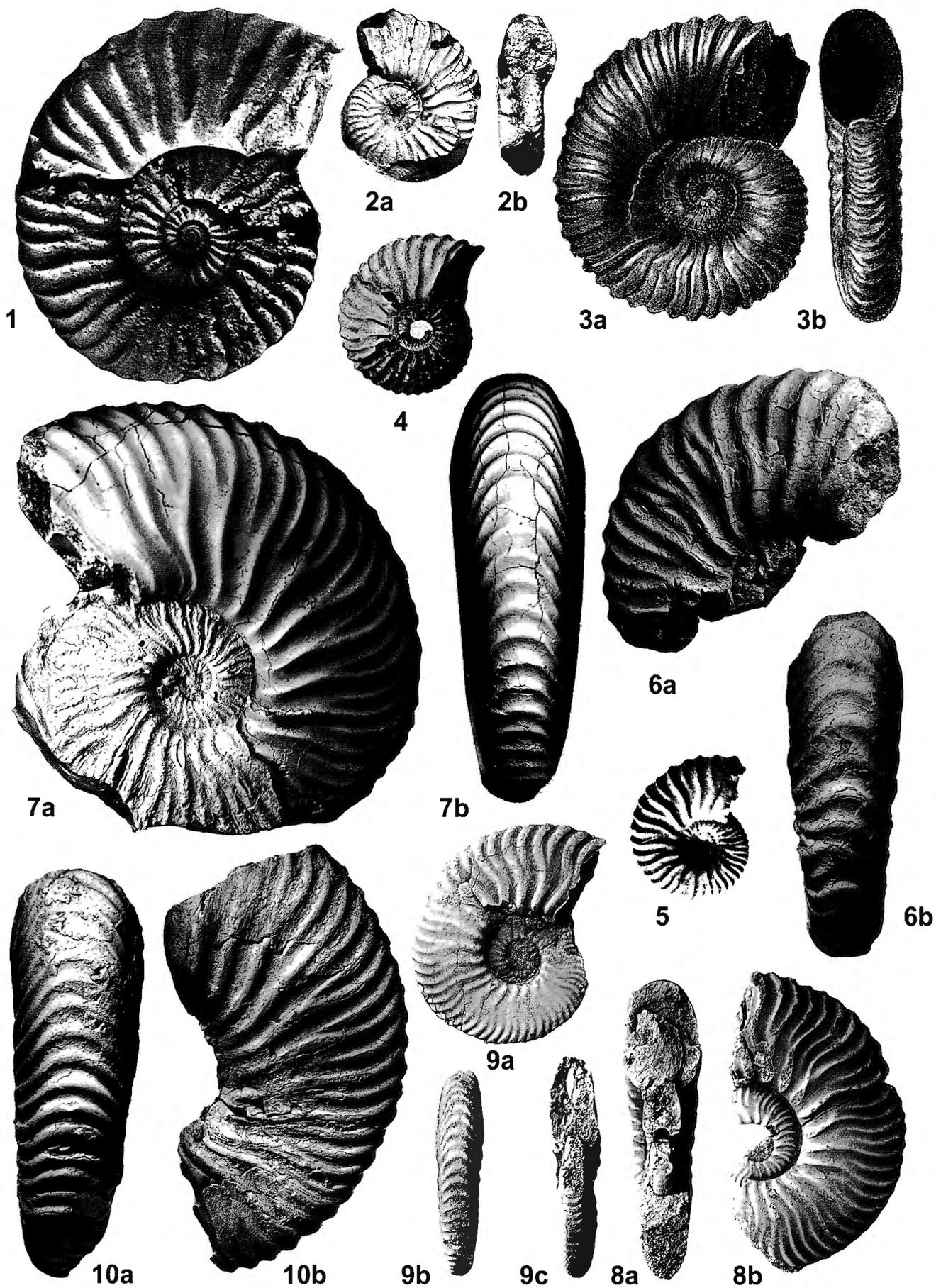


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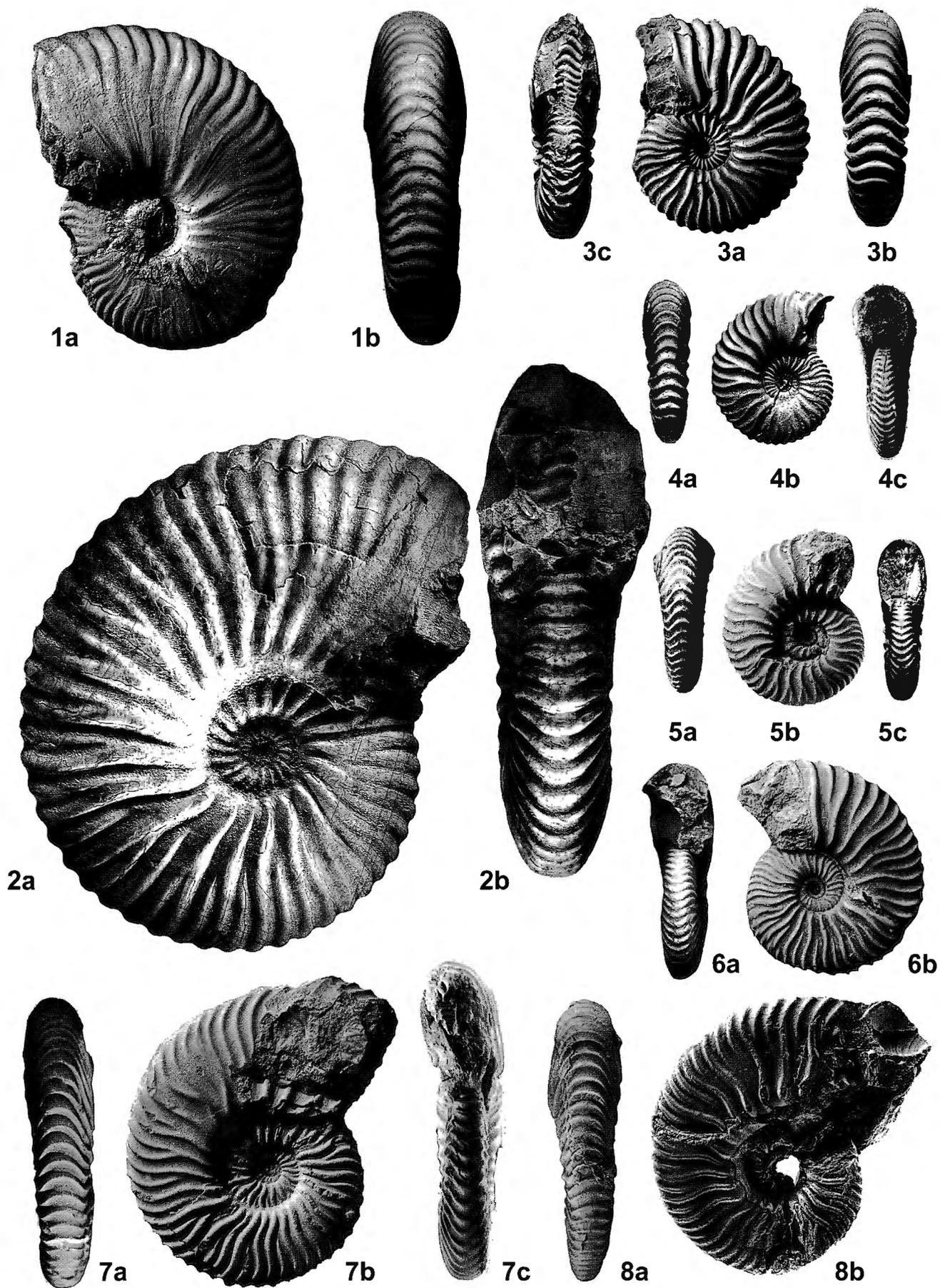


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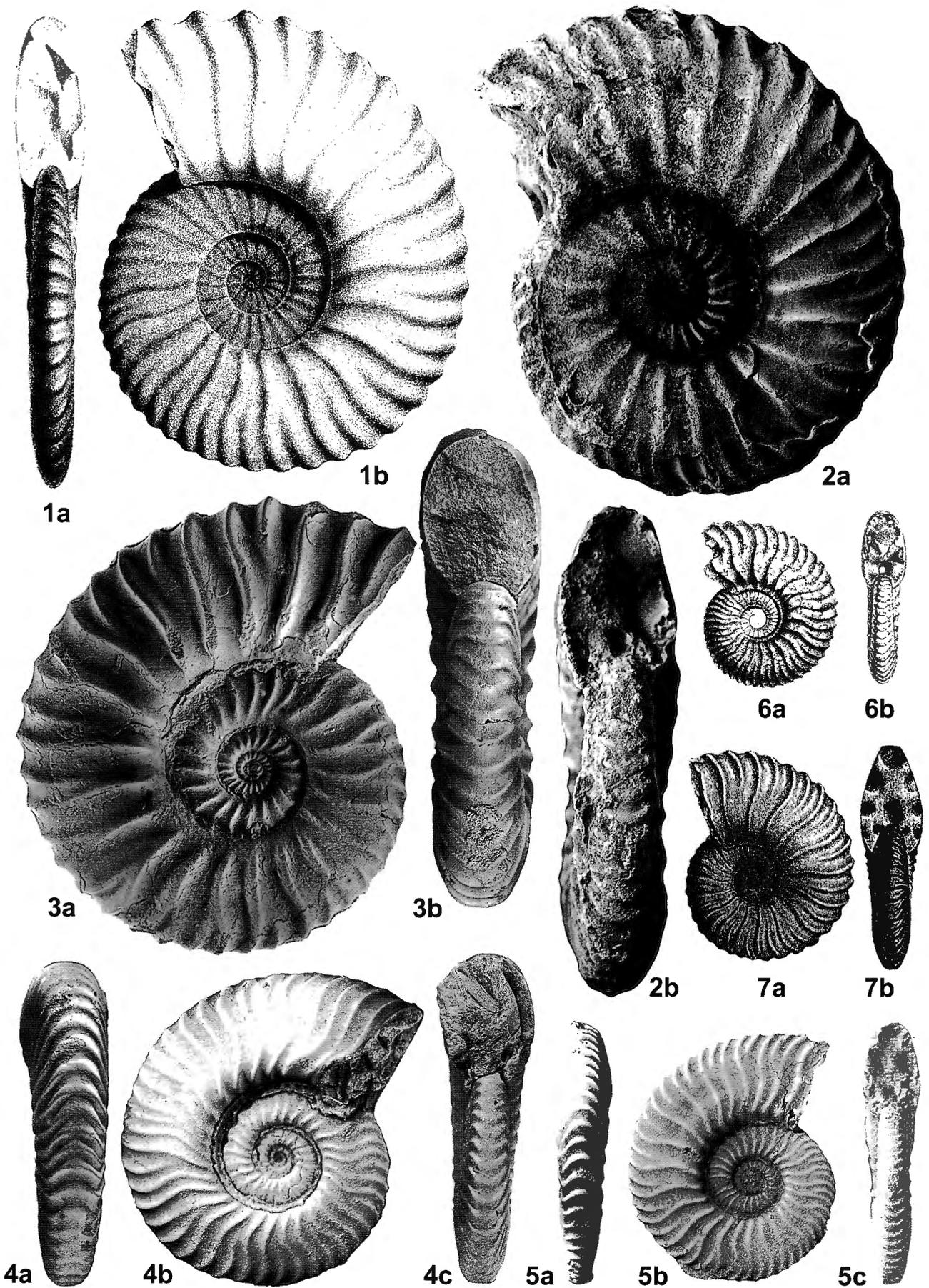


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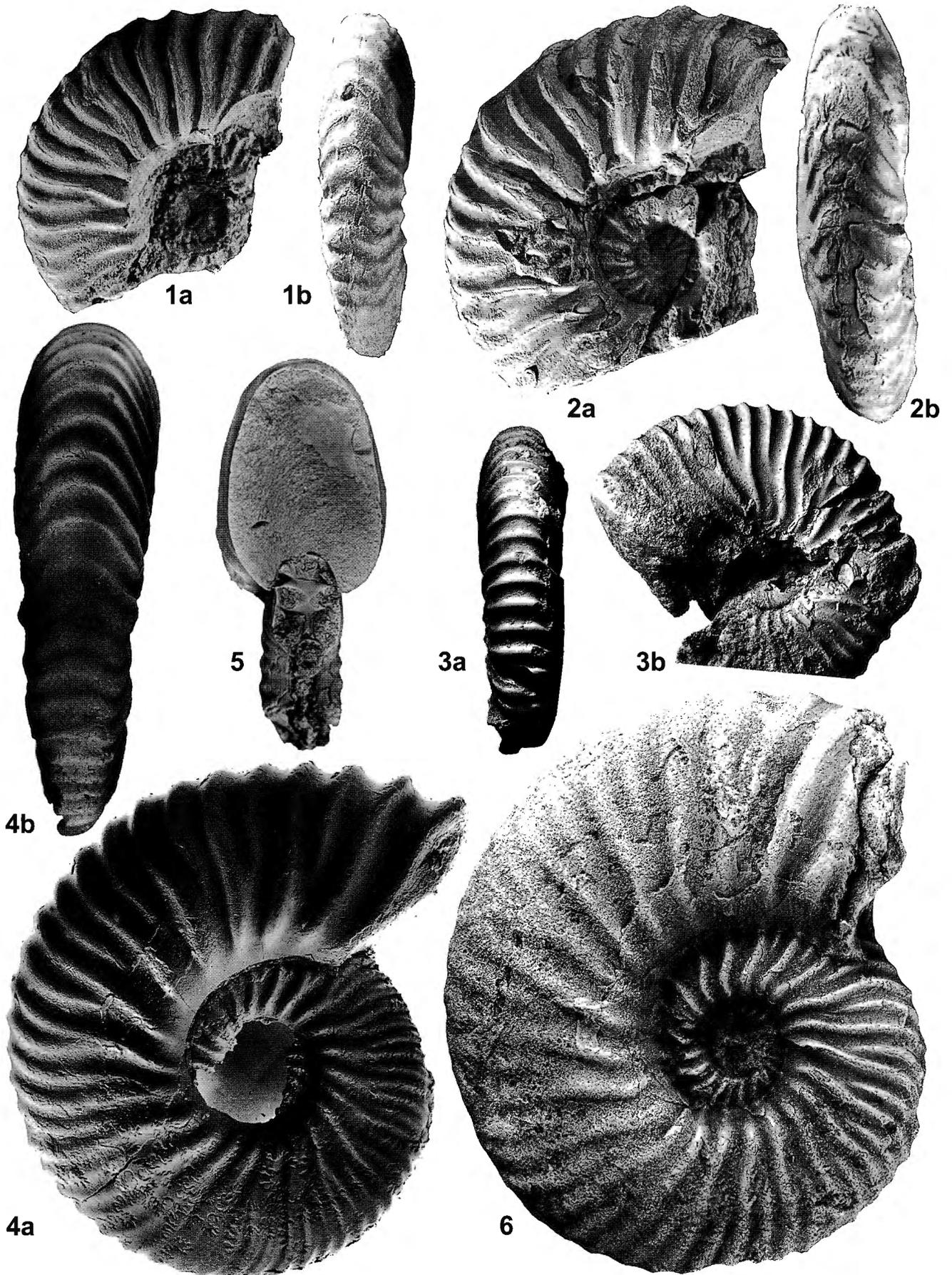


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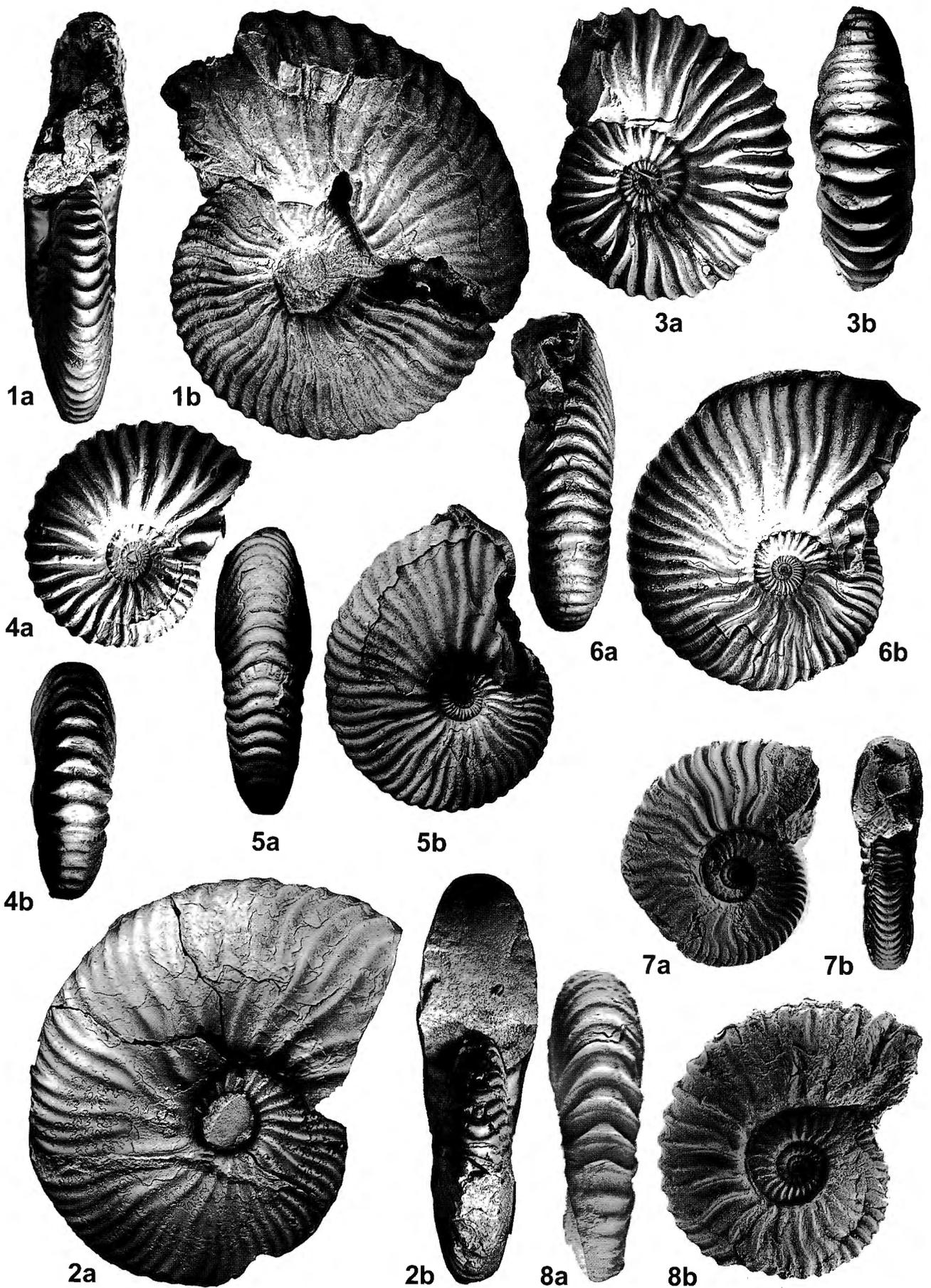
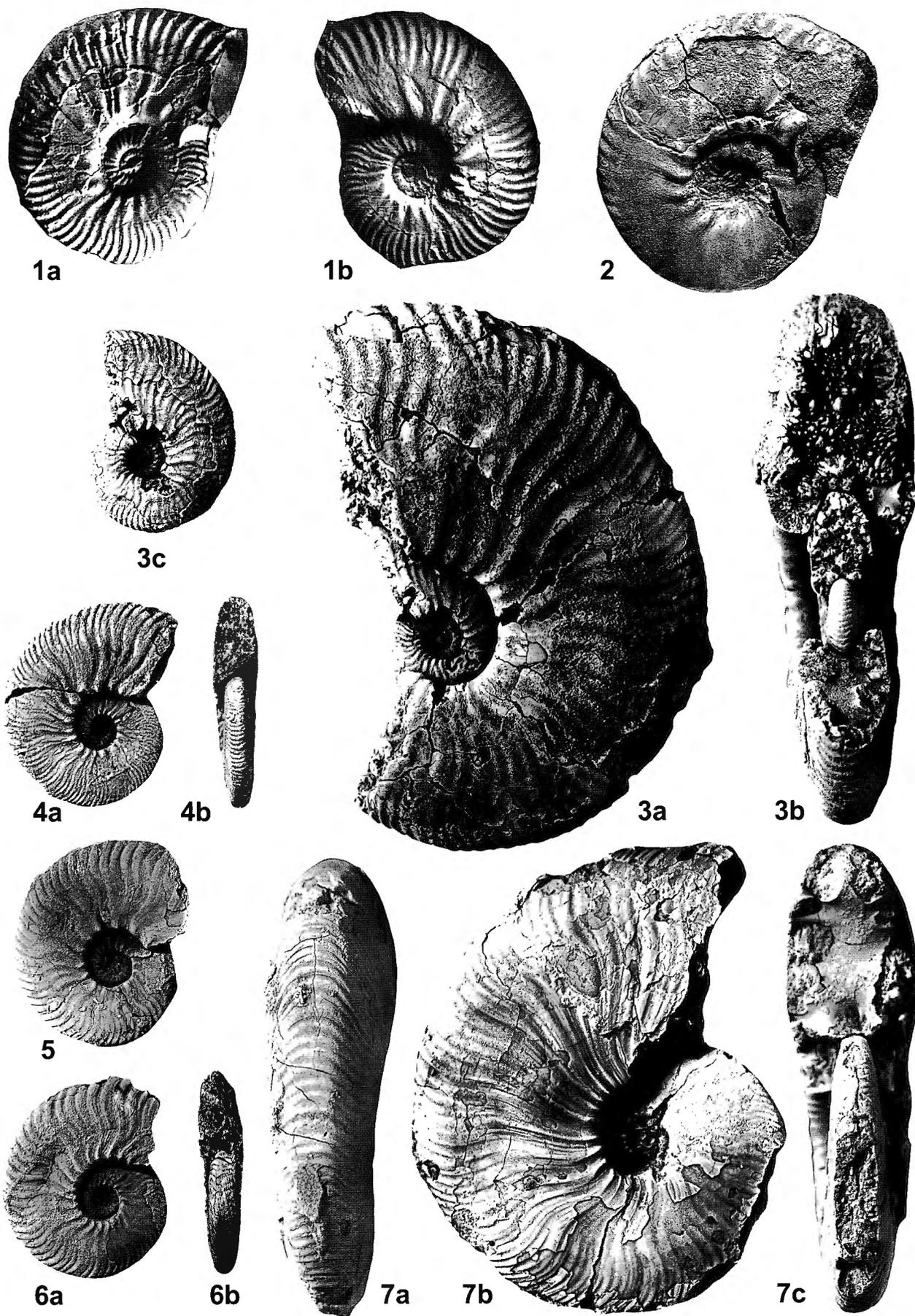


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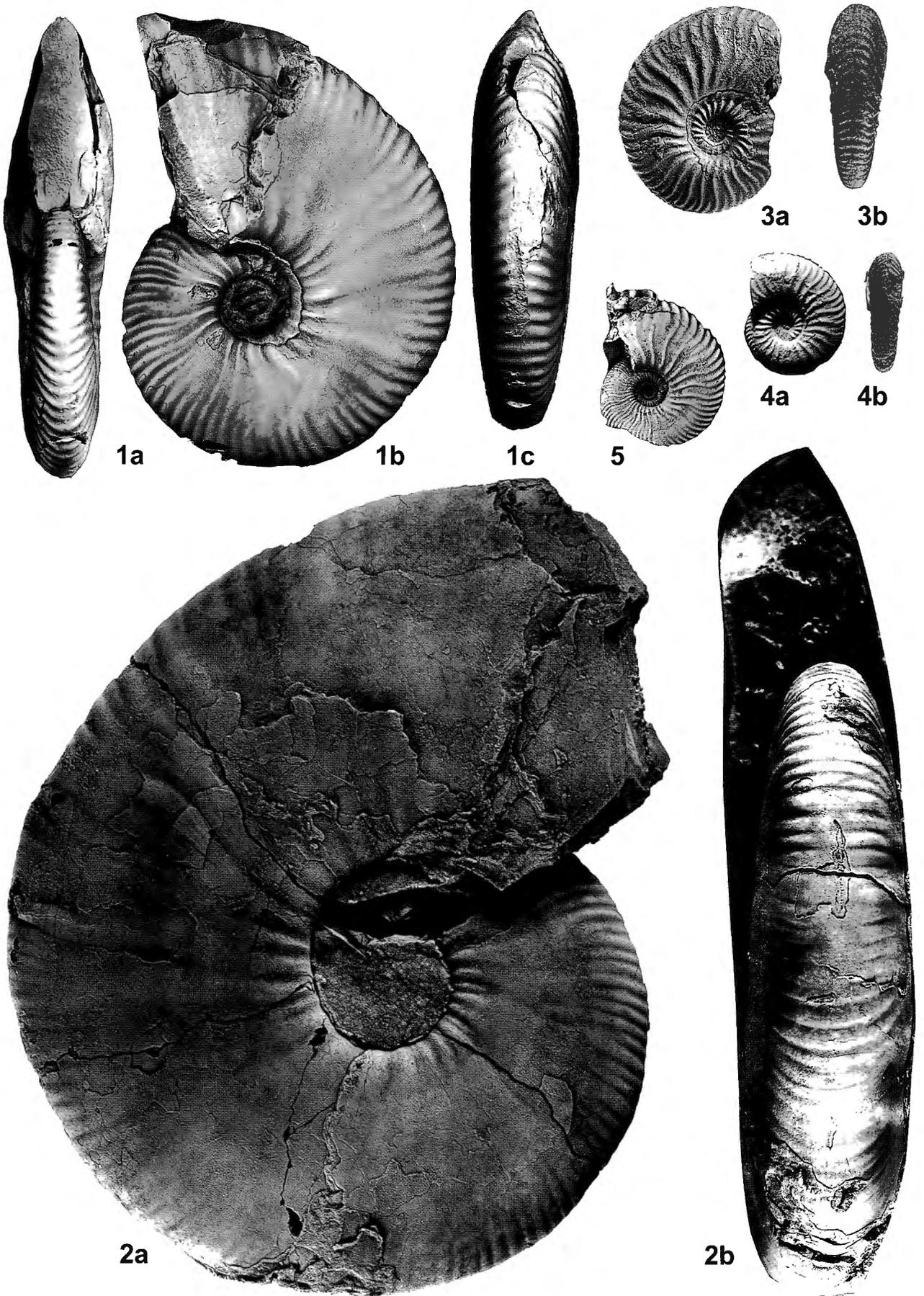


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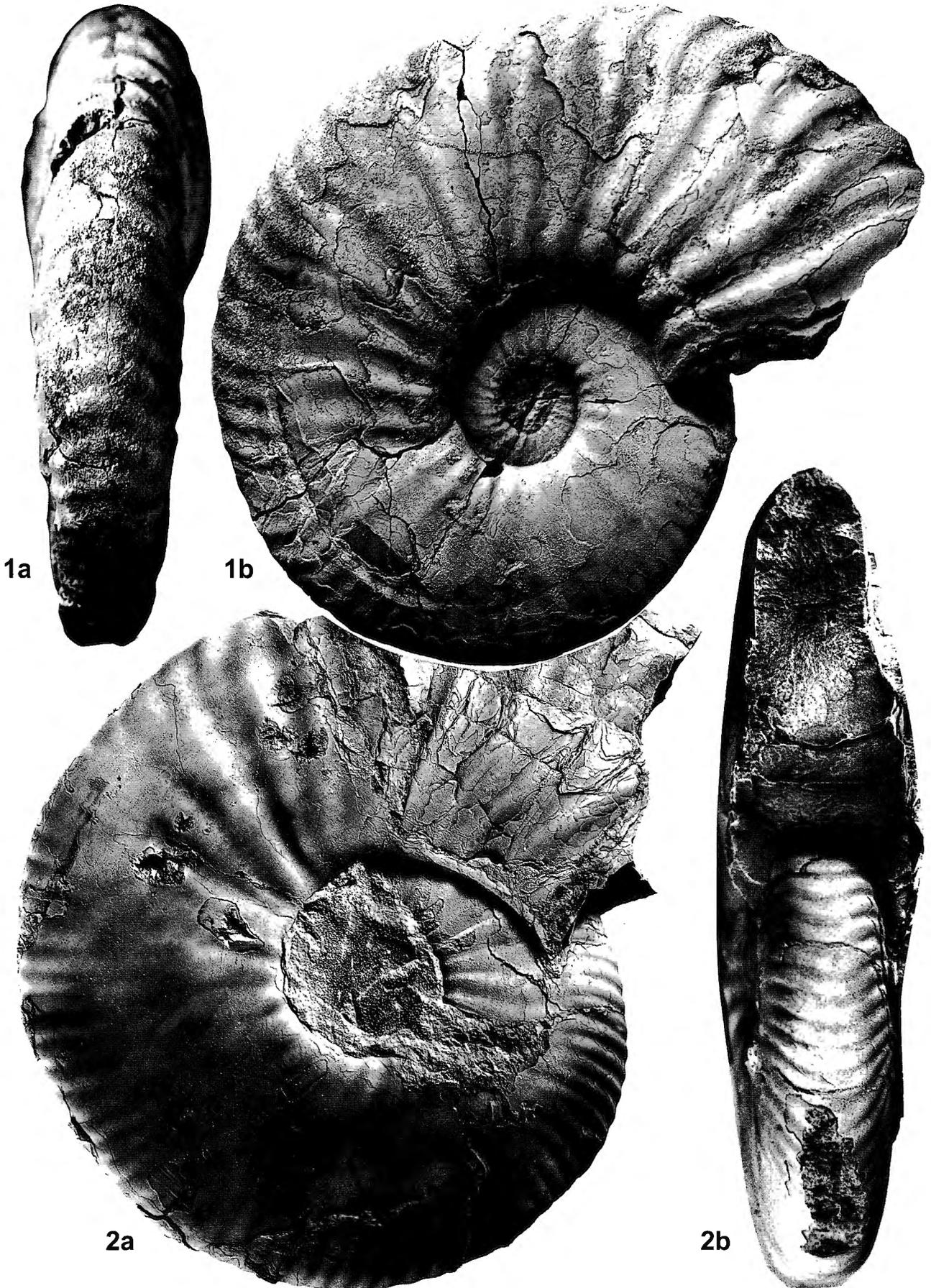


PLATE 9

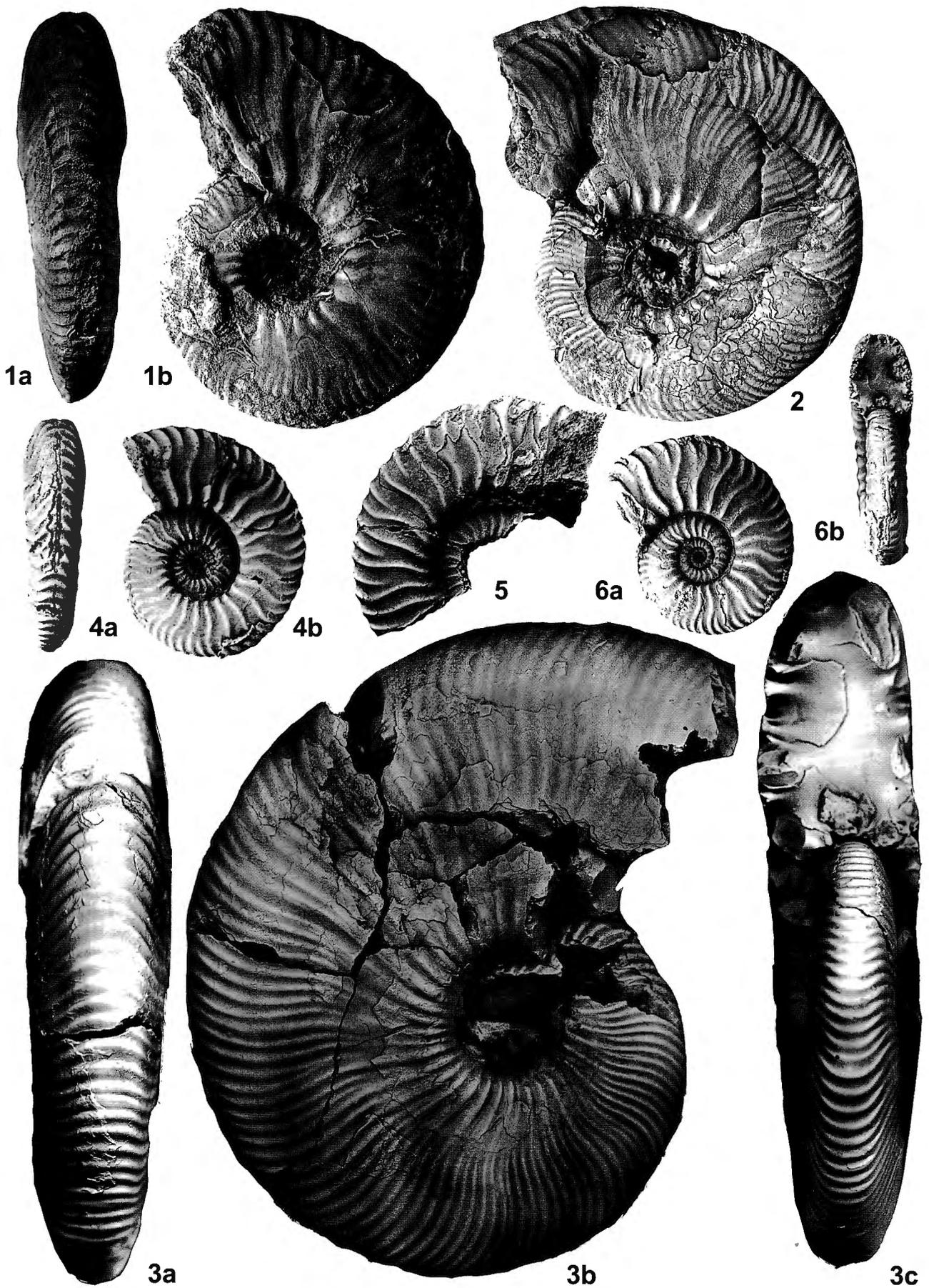


PLATE 10

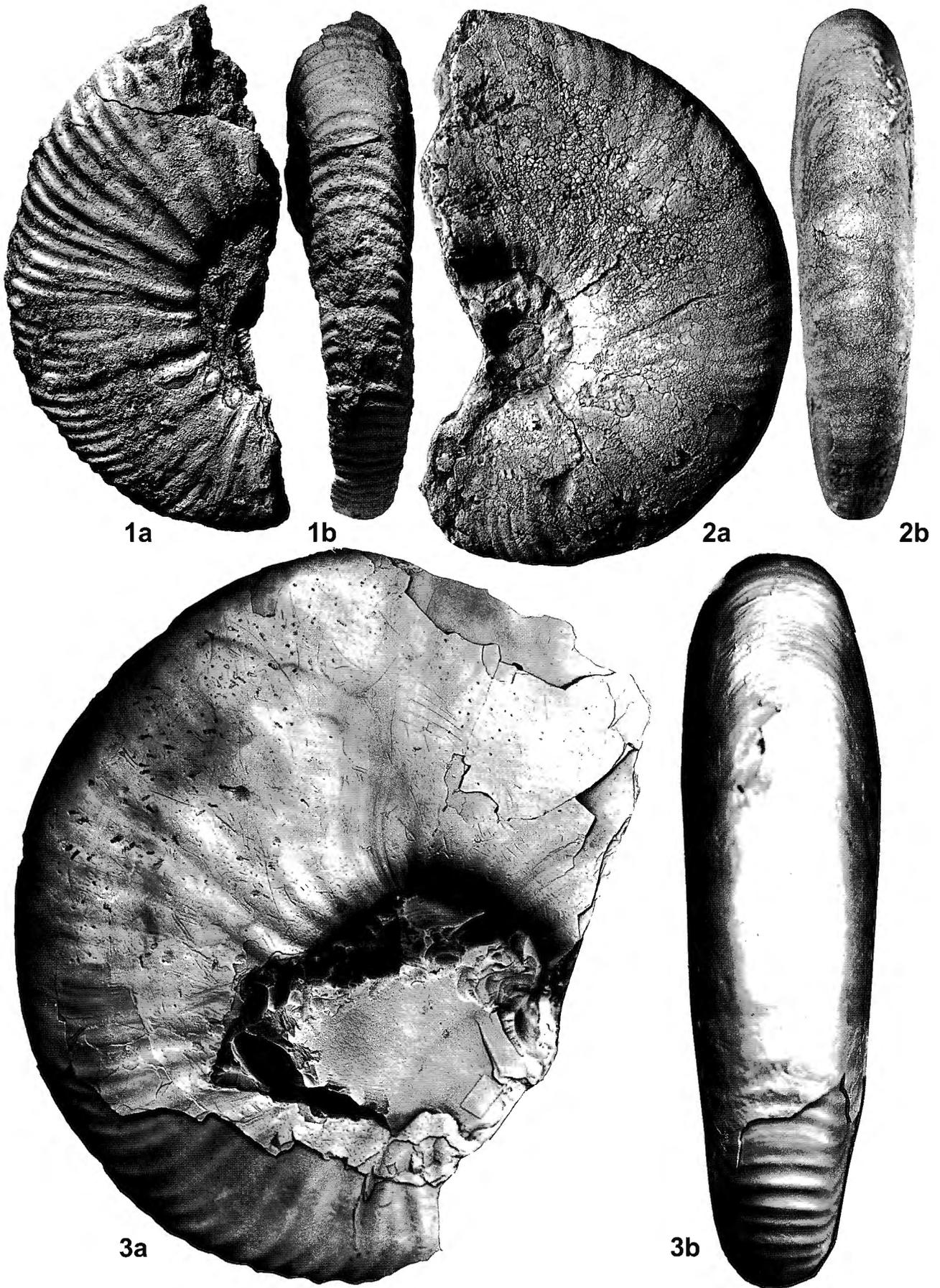


PLATE 11

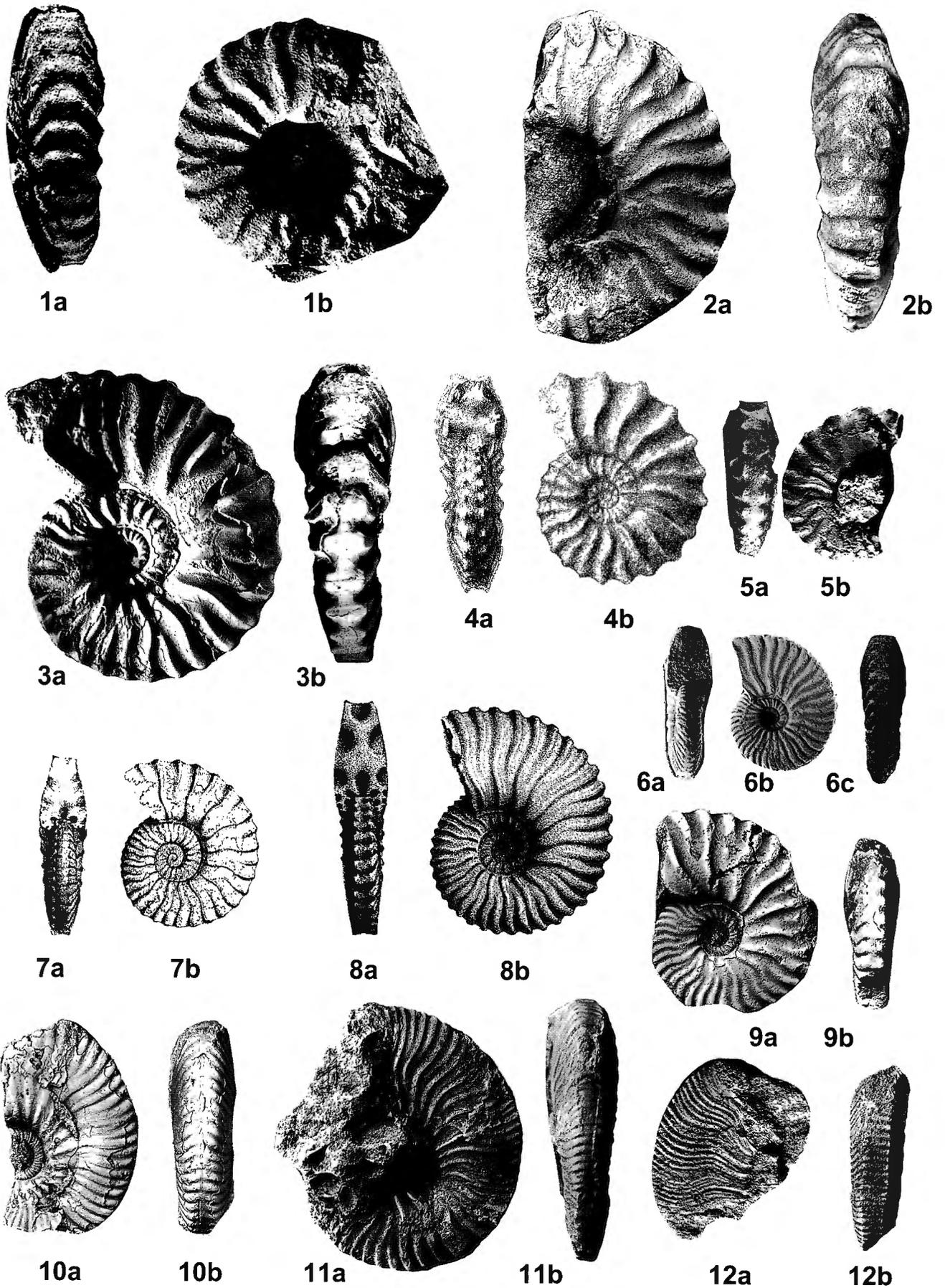


PLATE 12

