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## Monograph

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# Late Permian nautiloids from Baghuk Mountain (Central Iran)

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**Abstract.** The Wuchiapingian to Changhsingian (Late Permian) Hambast Formation of sections at Baghuk Mountain and Shahreza (Central Iran) has yielded diverse nautiloid assemblages from the early Wuchiapingian *Araxoceras* beds (nine species), the early Wuchiapingian *Protoceras* beds (one species), the late Wuchiapingian *Vedioceras* beds (twelve species) and the late Changhsingian *Paratirolites* beds (two species). These species belong to 14 genera, six of which are new: *Lutonautilus* gen. nov., *Epitainoceras* gen. nov., *Ocunautilus* gen. nov. in *Ocunautilidae* fam. nov., *Aifinautilus* gen. nov., *Baghuknautilus* gen. nov. and *Shahrezanautilus* gen. nov. A total of 24 species are described, all of which are new: *Serometacoceras pentagonum* sp. nov., *Lutonautilus cratus* gen. et sp. nov., *Lutonautilus elachus* gen. et sp. nov., *Lutonautilus cymus* gen. et sp. nov., *Tainoceras hystatum* sp. nov., *Epitainoceras lutense* gen. et sp. nov., *Foordiceras eicosacanthum* sp. nov., *Foordiceras decacanthum* sp. nov., *Foordiceras ascetum* sp. nov., *Tardunautilus aperimos* sp. nov., *Domatoceras myloide* sp. nov., *Domatoceras canonium* sp. nov., *Domatoceras ocomphalum* sp. nov., *Ocunautilus diplodocus* gen. et sp. nov., *Ocunautilus coelodesmus* gen. et sp. nov., *Ocunautilus tachytrepus* gen. et sp. nov., *Aifinautilus icanus* gen. et sp. nov., *Azarinautilus phorminx* sp. nov., *Liroceras leptum* sp. nov., *Paraliroceras macrogaster* sp. nov., *Permonautilus adelphidus* sp. nov., *Baghuknautilus aplomorphus* gen. et sp. nov., *Shahrezanautilus weyeri* gen. et sp. nov. and *Shahrezanautilus ghaderii* gen. et sp. nov. This nautiloid assemblage is remarkable for its high endemism. Although many genera known from the Transcaucasian region are represented, there is no correspondence at the species level.

**Keywords.** Nautiloidea, Nautilida, Permian, Iran, morphology.

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## Introduction

The faunal transition during the severe mass extinction event at the transition of the Palaeozoic into the Mesozoic is one of the major topics in the study of the evolutionary history of the biosphere, but nautiloids have so far played only a minor role in these studies. This under-representation of nautiloids may be due to the rather patchy state of knowledge; compared to other groups of fossil organisms,

nautiloids have rarely been monographically described and have therefore had little to contribute to the investigation of the largest mass extinction in the Phanerozoic.

It has been shown in recent years that the discovery of new Carboniferous and Permian nautiloid assemblages has led to a significant increase in species numbers (Barskov *et al.* 2014; Niko & Mapes 2016a; Leonova & Shchedukhin 2020; Miao *et al.* 2021; Korn & Bockwinkel 2022; Korn *et al.* 2022; Korn & Klug 2023). Almost every new nautiloid assemblage has yielded predominantly new, previously unknown species. These recent studies have also shown that a stricter application of morphometric methods and more precise stratigraphic assignment can provide a much better insight into the evolutionary history of nautiloids. These studies have also led to improved insights into questions of ontogenetic development, intraspecific variation, and stratigraphic and geographic range.

Late Permian coiled ammonoids were occasionally described in pioneering studies from various regions such as Saxony (Geinitz 1841), England (King 1850) and the Dolomites (Mojsisovics 1869; Stache 1877), but more diverse assemblages were known from only a few regions. Those from the former Armenian part of the Transcaucasus were the first ever described (Abich 1878; von Arthaber 1900), followed by the Salt Range in Pakistan (Waagen 1879) and South China (Kayser 1883). These pioneering studies have been complemented in a larger number of subsequent publications for the Transcaucasus (Shimansky 1965; Teichert & Kummel 1973), the Salt Range (Reed 1931, 1944), the Dolomites (Merla 1930; Prinoth & Posenato 2007) and South China (Zhao *et al.* 1978; Liang 1984; Zheng 1984; Miao *et al.* 2021). These studies have significantly improved our knowledge of nautiloids before the mass extinction at the Permian-Triassic boundary. An overview of their morphological range and morphospace occupation has already been obtained (Korn *et al.* 2020).

It was not until the 1970s that Late Permian nautiloids from the territory of Iran became known. Teichert & Kummel (1973) described a number of taxa, mostly in open nomenclature, from around Julfa (NW Iran) and Taraz *et al.* (1981) listed some nautiloids from the Permian–Triassic boundary sections near Abadeh (central Iran). New finds in the Julfa area allowed Korn & Ghaderi (2025) to carry out a



**Fig. 1.** Geographic position of Permian–Triassic boundary sections, including Baghuk Mountain, in Central Iran (from Korn *et al.* 2021b).

monographic study; 30 species from the Wuchiapingian and Changhsingian intervals were described in that monograph, 24 of them new.

Here, we present a monographic description of the coiled nautiloids from the Wuchiapingian and Changhsingian formations of Baghuk Mountain. This monograph complements the previously published monograph on the fish remains (Hampe *et al.* 2013) and the monograph on the Changhsingian ammonoids (Korn *et al.* 2021a). In a parallel attempt, the coiled nautiloids from the Julfa region are described in another monograph (Korn & Ghaderi 2025).

## Material and methods

A total of 55 nautilid specimens were studied. All but one of the specimens described here are from the Baghuk Mountain area 140 km SSE of Esfahan and 50 km NNW of Abadeh (Fig. 1). The individual sections of Baghuk Mountain have been described by Korn *et al.* (2021b) and Heuer *et al.* (2022). All the material comes from the Hambast Formation, which spans almost the entire Wuchiapingian and Changhsingian stages (Taraz *et al.* 1981).

The majority of the specimens were collected from float material below the outcrops. However, all of the specimens described here can be assigned without doubt to a member of the Hambast Formation on the basis of their lithology. Four members were distinguished from bottom to top (Fig. 2):

(1) *Araxoceras* beds (early Wuchiapingian): dark grey micritic nodular limestone (25 specimens).

- *Domatoceras myloide* sp. nov. – 4 specimens
- *Ocunautilus diplodocus* gen. et sp. nov. – 3 specimens

suborder	superfamily	family	genus species	Arax	Prot	Vedi	Para	
Domatoceratina	Grypoceratoidea	Domatoceratidae	<i>Domatoceras myloide</i>	●				
			<i>Domatoceras canonium</i>			●		
			<i>Domatoceras ocomphalum</i>			●		
		Ocunautilidae	<i>Ocunautilus diplodocus</i>	●				
			<i>Ocunautilus coelodesmus</i>	●				
			<i>Ocunautilus tachytrepus</i>	●				
			<i>Aifinautilus icanus</i>	●				
			<i>Azarinautilus phorminx</i>				●	
Tainoceratina	Pleuronautiloidea	Metacoceratidae	<i>Serometacoceras pentagonum</i>	●				
		Foordiceratidae	<i>Foordiceras eicosacanthum</i>			●		
			<i>Foordiceras decacanthum</i>			●		
			<i>Foordiceras ascetum</i>			●		
			<i>Tardunautilus aperimos</i>		●			
		Pleuronautilidae	<i>Lutonautilus cratus</i>			●		
			<i>Lutonautilus elachus</i>			●		
			<i>Lutonautilus cymus</i>			●		
		Tainoceratoidea	Tainoceratidae	<i>Tainoceras hystatum</i>				●
			<i>Epitainoceras lutense</i>	●				
Liroceratina	Liroceratoidea	Liroceratidae	<i>Liroceras leptum</i>			●		
			<i>Paraliroceras macrogaster</i>	●				
		Permonautilidae	<i>Permonautilus adelphidus</i>	●				
		Julfanautilidae	<i>Baghuknautilus aplomorphus</i>			●		
			<i>Shahrezanautilus weyeri</i>			●		
			<i>Shahrezanautilus ghaderii</i>			●		

**Fig. 2.** Stratigraphical positions of the Late Permian nautiloid taxa from Baghuk Mountain and Shahreza. Arax = *Araxoceras* beds; Prot = *Prototoceras* beds; Vedi = *Vedioceras* beds; Para = *Paratirolites* beds.

- *Ocunautilus coelodesmus* gen. et sp. nov. – 3 specimens
- *Ocunautilus tachytrepheus* gen. et sp. nov. – 1 specimen
- *Aifinautilus icanus* gen. et sp. nov. – 5 specimens
- *Serometacoceras pentagonum* sp. nov. – 1 specimen
- *Epitainoceras lutense* gen. et sp. nov. – 2 specimens
- *Paraliroceras macrogaster* sp. nov. – 2 specimens
- *Permonautilus adelphidus* sp. nov. – 4 specimens

(2) *Prototoceras* beds (early Wuchiapingian): light grey platy limestone with numerous pyrite crystals (one specimen).

- *Tardunautilus aperimos* sp. nov. – 1 specimen

(3) *Vedioceras* beds (late Wuchiapingian): pink or light red nodular limestone (26 specimens).

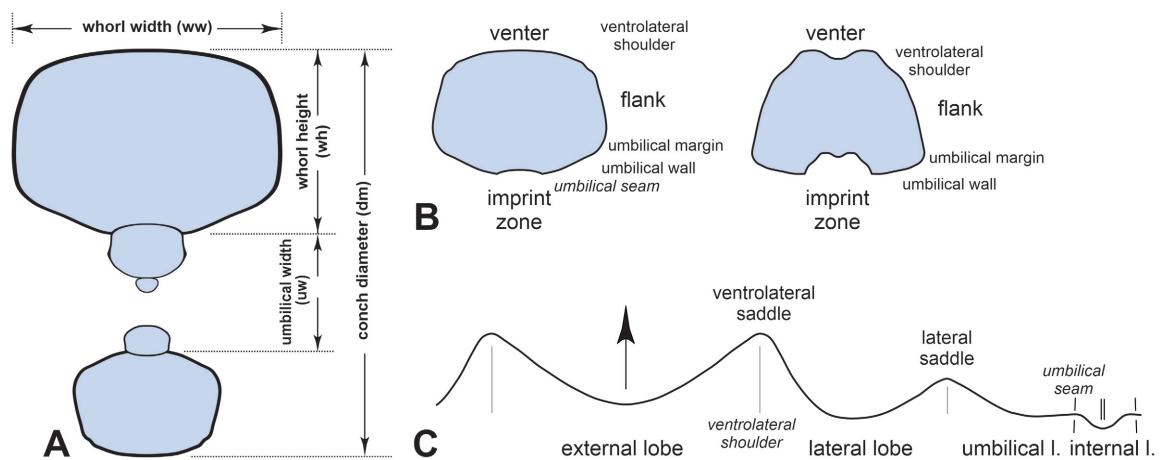
- *Domatoceras canonium* sp. nov. – 5 specimens
- *Domatoceras ocomphalum* sp. nov. – 1 specimen
- *Foordiceras eicosacanthum* sp. nov. – 2 specimens
- *Foordiceras decacanthum* sp. nov. – 1 specimen
- *Foordiceras ascetum* sp. nov. – 1 specimen
- *Lutonautilus cratus* gen. et sp. nov. – 4 specimens
- *Lutonautilus elachus* gen. et sp. nov. – 2 specimens
- *Lutonautilus cymus* gen. et sp. nov. – 3 specimens
- *Liroceras leptum* sp. nov. – 3 specimens
- *Baghuknautilus aplomorphus* gen. et sp. nov. – 2 specimens
- *Shahrezanautilus weyeri* gen. et sp. nov. – 1 specimen
- *Shahrezanautilus ghaderii* gen. et sp. nov. – 1 specimen

(4) *Paratirolites* beds (late Changhsingian): red-grey to grey-violet nodular limestone (three specimens).

- *Azarinautilus phorminx* sp. nov. – 1 specimen
- *Tainoceras hystatum* sp. nov. – 2 specimens

### Taxonomic concept

For the order Nautilida in current understanding, several partially conflicting concepts of systematics have been published and modified over the decades. While Flower & Kummel (1950) and Kummel (1953, 1964) took a more conservative approach, Shimansky (1962a, 1962b, 1965, 1967) proposed a



**Fig. 3.** Conch and suture line parameters used in the taxonomic descriptions. **A.** Conch parameters. **B.** Descriptive terms of whorl profiles. **C.** Suture line terminology.

much more detailed scheme. Dzik (1984) discussed the phylogeny and its implications for the systematic scheme in great detail and drew a much more complex evolutionary history of the coiled nautiloids.

In a revision of the Carboniferous and Permian coiled nautiloids by Korn (2025), a new systematic scheme was presented. This scheme is largely based on the phylogenetic considerations of Ruzhencev & Shimansky (1954) as well as Dzik (1984) and is largely based, with some modifications, on the systematic scheme of Shimansky (1967, 1979). This also means that it differs from the often used scheme of the *Treatise on Invertebrate Paleontology* (Kummel 1964).

The description of the specimens follows the terminology of conch, ornament and suture line proposed by Korn (2010) and Klug *et al.* (2015) for the characterisation of ammonoids (Fig. 3). The terminology of conch geometry used here largely corresponds to that proposed by Teichert (1964). The only differences concern the following terms: umbilical angle or shoulder (= umbilical margin) and umbilical area (= umbilical width in our descriptions).

### **Photography technique**

The photographs for this monograph were taken using Reflectance Transformation Imaging (RTI) techniques with the Broncolor Scope D50 dome to create surface models without previously whitening the specimens. Processing of the images was performed using the Truvis Authentica Creator program. The exported images were processed in Adobe Photoshop.

### **Abbreviations used in the species descriptions**

ah = apertural height  
CLI = chamber length index (in degrees)  
dm = conch diameter  
IZR = imprint zone rate  
uw = umbilical width  
WER = whorl expansion rate  
wh = whorl height  
ww = whorl width

### **Abbreviation of the repository**

MB.C. = Cephalopod collection of the Museum für Naturkunde, Berlin

## **Results**

Class Cephalopoda Cuvier, 1795  
Subclass Nautiloidea Agassiz, 1847

Order **Nautilida** Agassiz, 1847

### **Diagnosis**

Exogastrically curved or coiled nautiloids with a conch shape ranging from gyroconic or cyrtconic to more or less tightly coiled. Shell surface smooth or sculptured with a variety of elements (ribs, nodes, spines, longitudinal ridges or lines). Septa simply domed in most species, with the shape of the whorl profile producing suture lines with variable lobes and saddles. Variations in septal shape with inflexions producing deep lobes in some genera. Septal necks short and straight, rarely slightly widened. Connecting rings cylindrical or beaded. Siphuncular or cameral deposits absent. Juvenile conch with cup-shaped initial chamber and narrow siphuncle. Morphological evolution includes the degree of coiling, the shape and size of the juvenile and adult conch and the suture line (after Shimansky 1962b; emended).

### **Included suborders**

Nautilina Agassiz, 1847 (Jurassic to Recent); Solenochilina Flower, 1950 (Carboniferous to Permian); Liroceratina Flower, 1955 (Carboniferous to Jurassic); Rutoceratina Shimansky, 1957 (Devonian); Tainoceratina Shimansky, 1957 (Carboniferous to Triassic); Temnocheilina Flower, 1963 (Devonian to Permian); Domatoceratina Korn, 2025 (Carboniferous to Triassic).

#### Suborder **Domatoceratina** Korn, 2025

### **Diagnosis**

Suborder of the order Nautilida, in which a ventrolateral shoulder and an umbilical margin are formed early in ontogeny. Conch usually discoidal, subinvolute to evolute. Juvenile whorl profile circular. Adult whorl profile subquadrate or inverted trapezoidal with a distinct ventrolateral shoulder and a distinct umbilical margin in the early species, showing modifications during evolution including a concave venter in some derived species. Dorsal whorl zone always present, but usually very small except for some derived species. Juvenile sculpture sometimes with radial ribs on the flank; adult sculpture is usually lacking except for elongate ventrolateral tubercles in derived species. Septa simply domed in most of the species; with septal inflexion and corrugated septa in some lineages. Suture line usually depending on the whorl profile, usually with shallow lobes and low saddles; with distinct lobes in some derived lineages (from Korn 2025).

### **Included superfamilies**

Grypoceratoidea Hyatt, 1900 (Carboniferous to Triassic); Permoceratoidea Miller & Collinson, 1953 (Permian); Subclymenioidea Shimansky, 1962 (Carboniferous).

### **Remarks**

A detailed discussion of the Domatoceratina has been given by Korn (2025).

#### Superfamily **Grypoceratoidea** Hyatt, 1900

### **Diagnosis**

Superfamily of the suborder Domatoceratina with a discoidal, subinvolute to evolute conch. Whorl profile usually inverted trapezoidal with a distinct ventrolateral shoulder and a distinct umbilical margin. Derived species show a variation of modifications including a concave venter, a skid-like ventrolateral shoulder and an angular umbilical margin. Whorl overlap extremely small to moderate. Sculpture in most species lacking, in some species with short lateral ribs or ventrolateral nodes. Septa simply domed; suture line strongly dependent on the whorl profile, usually with broadly rounded lobes and narrowly rounded or subangular saddles (from Korn 2025).

### **Included families**

Grypoceratidae Hyatt, 1900; Domatoceratidae Miller & Youngquist, 1949; Ocunautilidae fam. nov.

### **Remarks**

A discussion of the Grypoceratoidea has been given by Korn (2025).

#### Family **Domatoceratidae** Miller & Youngquist, 1949

### **Diagnosis**

Family of the superfamily Grypoceratoidea with a thinly to thickly discoidal, subinvolute to evolute conch. Whorl profile in the adult stage usually compressed subquadrate or inverted trapezoidal. Umbilical

margin distinct or sharp; ventrolateral shoulder nearly rectangular to broadly rounded, rarely skid-like. Ornament consisting of fine growth lines; some species have tubercles on the ventrolateral shoulder. Suture line always with rounded but distinct external, lateral and internal lobes separated by a narrowly rounded or subacute saddles; without annular process (from Korn 2025).

### Included genera

*Pselioceras* Hyatt, 1884 (Permian); *Titanoceras* Hyatt, 1884 (Carboniferous); *Domatoceras* Hyatt, 1891 (Carboniferous to Permian); *Pseudometaceras* Miller, Dunbar & Condra, 1933 [synonym of *Domatoceras* Hyatt, 1891]; *Paradomatoceras* Delépine, 1937 (Carboniferous); *Plummeroceras* Kummel, 1953 (Permian); *Neodomatoceras* Ruzhencev & Shimansky, 1954 (Permian); *Neostenopoceras* Zhao, Liang & Zheng, 1978 (Permian); *Parapenascoceras* Ruzhencev & Shimansky, 1954 (Permian); *Parastenopoceras* Ruzhencev & Shimansky, 1954 (Permian); *Penascoceras* Ruzhencev & Shimansky, 1954 (Permian); *Permodomatoceras* Ruzhencev & Shimansky, 1954 (Permian); *Stenodomatoceras* Ruzhencev & Shimansky, 1954 (Permian); *Virgaloceras* Schindewolf, 1954 (Permian); *Neostenopoceras* Zhao, Liang & Zheng, 1978 (Permian); *Shatoceras* Leonova & Shchedukhin, 2020 (Permian); *Omorphoceras* Leonova & Shchedukhin, 2023 (Permian); *Fididomatoceras* Korn & Ghaderi, 2025 (Permian).

### Remarks

A detailed discussion of the Domatoceratidae has been given by Korn (2025).

### Genus *Domatoceras* Hyatt, 1891

#### Type species

*Domatoceras umbilicatum* Hyatt, 1891; original designation.

#### Diagnosis

Genus of the family Domatoceratidae with a subinvolute to evolute conch. High to extremely high coiling rate; whorl profile usually weakly compressed. Venter flattened or weakly concave, flanks usually flattened and slightly convergent; umbilical margin rounded or angular. Without sculpture except for small ventrolateral tubercles in some species. Suture line with small and shallow external lobe and broadly rounded lateral lobe; without annular process.

#### Included Carboniferous species

North America (Meek & Worthen 1865; Worthen & Meek 1875; Gurley 1883; Hyatt 1891; Miller & Owen 1934; Sturgeon & Miller 1948; Tucker 1976; Tucker & Mapes 1978; Sturgeon *et al.* 1982; Niko & Mapes 2016b; Niko *et al.* 2022): *Nautilus Lasallensis* Meek & Worthen, 1865, Kasimovian, Illinois; *Nautilus (Discites) highlandensis* Worthen in Worthen & Meek, 1875, Moscovian, Ohio; *Discites Toddanus* Gurley, 1883, Kasimovian, Missouri; *Domatoceras umbilicatum* Hyatt, 1891, Moscovian, Kansas; *Domatoceras williamsi* Miller & Owen, 1934, Moscovian, Ohio; *Domatoceras obsoletum* Sturgeon, 1946, Moscovian, Ohio; *Domatoceras shepherdii* Sturgeon, 1948, Moscovian, Ohio; *Domatoceras wortheni* Tucker, 1976, Kasimovian, Illinois; *Domatoceras texanum* Tucker & Mapes, 1978, Kasimovian, Texas; *Domatoceras oreskovichi* Sturgeon, Windle, Mapes & Hoare, 1982, Moscovian, Ohio; *Domatoceras collinsvillense* Niko & Mapes, 2016, Moscovian, Oklahoma; *Domatoceras tuckeri* Niko, Mapes & Seuss, 2022, Kasimovian, Texas.

South China (Ruan & Zhou 1987): *Domatoceras quadratum* Ruan & Zhou, 1987, Bashkirian, Ningxia.

West Russia (Tzwetaev 1888, 1898; Shimansky 1967): *Nautilus podolskensis* Tzwetaev, 1888, Moscovian, Moscow Basin; *Nautilus mosquensis* Tzwetaev, 1898, Moscovian, Moscow Basin; *Domatoceras (Domatoceras) magister* Shimansky, 1967, Moscovian, Moscow Basin.

#### Included Permian species

Urals (Leonova & Shchedukhin 2020): *Domatoceras bashkiricum* Leonova & Shchedukhin, 2020, Asselian or Sakmarian, South Urals; *Domatoceras sterlitamakense* Leonova & Shchedukhin, 2020, Asselian or Sakmarian, South Urals.

Transcaucasia and Iran (Abich 1878; Shimansky 1965; this paper): *Nautilus parallelus* Abich, 1878, Wuchiapingian, Azerbaijan; *Nautilus convergens* Abich, 1878, Wuchiapingian, Azerbaijan; *Domatoceras gracile* Shimansky, 1965, Wuchiapingian, Azerbaijan; *Domatoceras atypicum* Shimansky, 1965, Wuchiapingian, Azerbaijan; *Domatoceras multituberculatum* Korn & Ghaderi, 2025, Wuchiapingian, NW Iran; *Domatoceras canonium* sp. nov., Wuchiapingian, Central Iran; *Domatoceras ocomphalum* sp. nov., Wuchiapingian, Central Iran; *Domatoceras myloide* sp. nov., Wuchiapingian, Central Iran.

South China (Zhao *et al.* 1978): *Domatoceras guangxiense* Zhao, Liang & Zheng, 1978, Changhsingian, Guangxi.

Japan (Ehiro & Takizawa 1989): *Domatoceras ogatsuense* Ehiro & Takizawa, 1989, Wuchiapingian, Kitakami Massif.

#### Remarks

The species of the genus *Domatoceras* have a very similar conch morphology from the Moscovian to the Changhsingian, suggesting a very conservative evolutionary lineage. Shimansky (1967) also included some Serpukhovian species in *Domatoceras*, but these differ from the typical representatives of the genus in that they have a wider conch and lack a subangular or angular ventrolateral shoulder. These stratigraphically older species may belong to *Epidomatoceras* Turner, 1954.

The similarity in the morphology of the conchs, the virtual absence of sculptural elements and the fact that the suture line depends essentially on the shape of the whorl profile make it difficult to distinguish the species within *Domatoceras*. Another difficulty is that the species of the genus occur in two phases: the first phase extends from the Moscovian to the Asselian–Sakmarian boundary, and the second phase extends from the Wuchiapingian to the Changhsingian. It should be noted, however, that of the Late Permian species, about ten are known from the Wuchiapingian and only one from the Changhsingian. Apparently, no species are known from the long interval between the Sakmarian and the Capitanian. Some species from the Kungurian and Roadian, which were placed under *Domatoceras* by Miller & Unklesbay (1942) and Miller & Youngquist (1949), have been assigned to other genera such as *Penascoceras* by Ruzhencev & Shimansky (1954).

#### *Domatoceras myloide* sp. nov.

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Fig. 4; Table 1

#### Diagnosis

Species of *Domatoceras* with thinly discoidal, subevolute conch ( $ww/dm \sim 0.35$ ;  $uw/dm \sim 0.35$ ), weakly compressed whorl profile ( $ww/wh \sim 0.90$ ) and very high coiling rate ( $WER \sim 2.45$ ) at a conch diameter of 70 mm. Whorl profile with weakly flattened venter, rounded ventrolateral shoulder, flattened and nearly parallel flanks, subangular umbilical margin and steep and flat umbilical wall. Whorl overlap very small. Without sculpture. Suture line with a small and very shallow external lobe and a much larger and deeper, broadly rounded lateral lobe.

**Table 1.** Conch dimensions (in mm) and ratios of *Domatoceras myloide* sp. nov.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32101	72.1	25.0	27.8	24.6	26.2	0.35	0.90	0.34	2.47	0.06
MB.C.32101	47.2	17.3	19.2	16.0	18.2	0.37	0.90	0.34	2.65	0.05
MB.C.32102	56.3	20.2	21.5	20.5	20.5	0.36	0.94	0.36	2.47	0.05

### Etymology

From the Greek ‘μυλοειδής’= ‘millstone-shaped’; because of the conch shape.

### Type material

#### Holotype

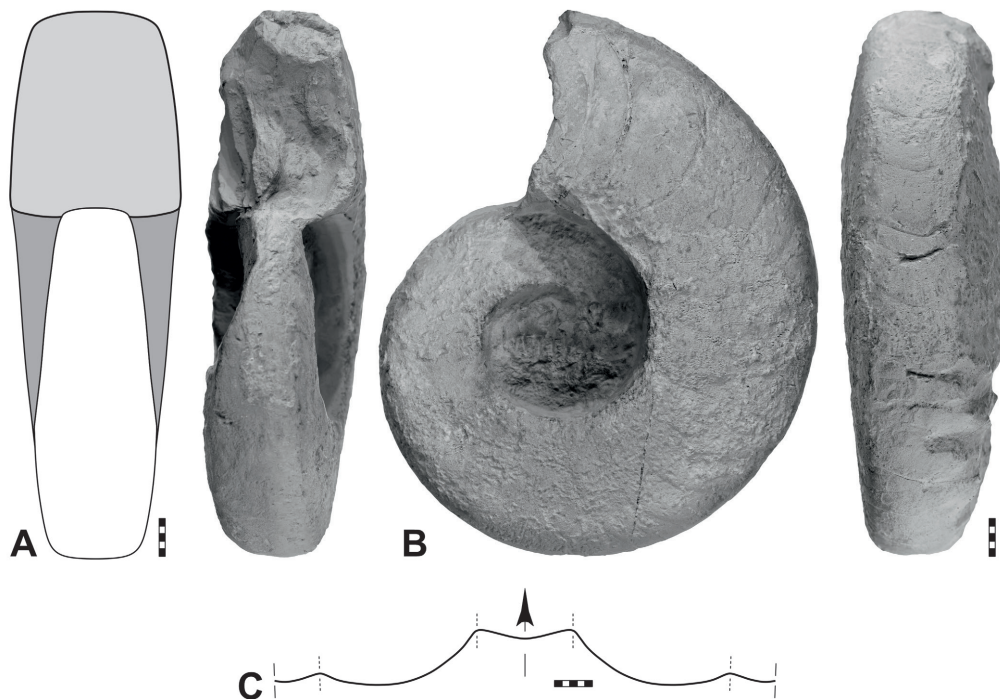
IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Araxoceras* beds (early Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 4; MB.C.32101.

#### Paratypes

IRAN – **Esfahan Province** • 3 specimens; same data as for holotype; 2010; Korn *et al.* leg.; MB.C.32102 to MB.C.32104.

### Description

Holotype MB.C.32101 is a fully chambered internal mould specimen with a conch diameter of 72 mm, which allows the study of one whorl (Fig. 4B). The conch is thinly discoidal and subevolute ( $ww/dm=0.35$ ;  $uw/dm=0.34$ ) with an extremely high coiling rate ( $WER=2.47$ ); the whorl profile is weakly compressed ( $ww/wh=0.90$ ) with a weakly flattened venter, a rounded ventrolateral shoulder, flattened



**Fig. 4.** *Domatoceras myloide* sp. nov., holotype MB.C.32101 (Korn *et al.* 2011 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Dorsal, lateral and ventral views. **C.** Suture line at  $dm=68.5$  mm,  $ww=22.5$  mm,  $wh=26.5$  mm. Scale bar units= 1 mm.

and almost parallel flanks, a subangular umbilical margin and a flattened and steep umbilical wall. The whorl overlap is very small (IZR=0.06) (Fig. 4A). The internal mould appears to be completely lacking sculpture. The suture line is typical for the genus with a shallow external lobe and a much larger and deeper lateral lobe (Fig. 4C). The last half volution of the phragmocone has about 16 chambers (CLI=11).

### Remarks

*Domatoceras myloide* sp. nov. differs from *D. canonium* sp. nov. and *D. ocomphalum* sp. nov. in the nearly parallel flanks, which are convergent in the other two species. Furthermore, *D. myloide* has a broadly rounded venter and a rounded ventrolateral shoulder, while the other two species have an applanate or even slightly concave venter and an angular ventrolateral shoulder.

*Domatoceras myloide* sp. nov. differs from *D. elegantulum* and *D. multituberculatum* from Julfa in the nearly parallel flanks, which are convergent in the other two species. *Domatoceras parallelum* has parallel flanks, but according to the description and illustration by Abich (1878: 17, pl. 2 fig. 2), it has a much wider umbilicus (uw/dm ~0.45) than *D. myloide* (uw/dm ~0.35).

### *Domatoceras canonium* sp. nov.

[urn:lsid:zoobank.org:act:FAC63FFF-26E3-4BF3-9D0B-6701596A9576](https://zoobank.org/urn:lsid:zoobank.org:act:FAC63FFF-26E3-4BF3-9D0B-6701596A9576)

Figs 5–6; Table 2

*Domatoceras* sp. – Korn *et al.* 2021b: text-fig. 17e.

### Diagnosis

Species of *Domatoceras* with extremely discoidal, subevolute conch (ww/dm ~0.25; uw/dm ~0.35), weakly compressed whorl profile (ww/wh ~0.65) and extremely high coiling rate (WER ~2.75) at a conch diameter of 70–80 mm. Whorl profile with weakly concave venter, angular ventrolateral shoulder, flattened convergent flanks, rounded umbilical margin and oblique umbilical wall. Whorl overlap extremely small. Without sculpture, but with small ventrolateral tubercles in the juvenile stage. Suture line with a small and narrow external lobe and a much larger and deeper, broadly rounded lateral lobe.

### Etymology

From the Greek ‘καυονίης’=‘slender’; because of the slender conch.

### Type material

#### Holotype

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2010; Hairapetian leg.; illustrated in Fig. 5; MB.C.32105.

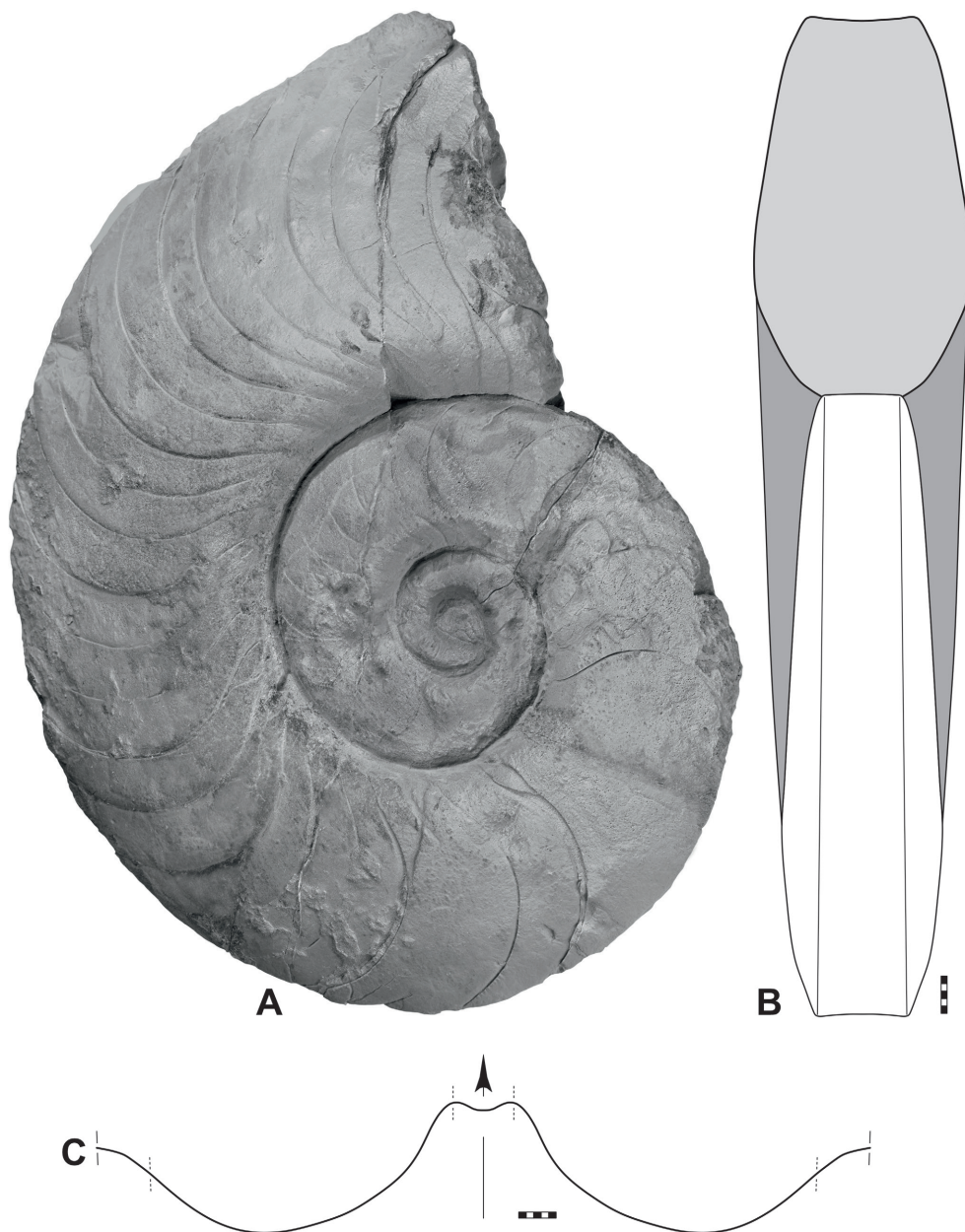
#### Paratypes

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; MB.C.32106 • 1 specimen; same data as for holotype; 2011; Korn *et al.* leg.; illustrated in Fig. 6; MB.C.30227 • 2 specimens; same data as for holotype; 2011; Korn *et al.* leg.; MB.C.32107, MB.C.32108.

### Description

Holotype MB.C.32105 is a slightly corroded, fully chambered internal mould with a conch diameter of 134 mm (Fig. 5A); the total conch diameter inclusive the body chamber must have been at least 200 mm. The specimen has two and a half whorls, but the early ontogenetic stage of the conch is poorly preserved. The conch is, at 134 mm diameter, extremely discoidal and subevolute (ww/dm=0.22; uw/dm=0.37)

with an extremely high coiling rate ( $WER=2.58$ ); the whorl profile is compressed ( $ww/wh=0.57$ ) with a weakly concave venter, an angular ventrolateral shoulder, flattened and convergent flanks, a broadly rounded umbilical margin and a convex and oblique umbilical wall. The last whorl hardly embraces the preceding; the whorl overlap zone is extremely small (Fig. 5B). The specimen shows ontogenetic changes in the conch geometry quite clearly. This can mainly be seen in the lowering of the coiling rate; at a conch diameter of 50 mm, the whorl expansion rate is 2.73, at 80 mm diameter 2.72 and at 134 mm diameter only 2.58.



**Fig. 5.** *Domatoceras canonium* sp. nov., holotype MB.C.32105 (Hairapetian 2010 Coll.) from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Lateral view. **B.** Reconstruction of apertural view. **C.** Suture line at  $dm=120$  mm,  $wh=45$  mm. Scale bar units=1 mm.

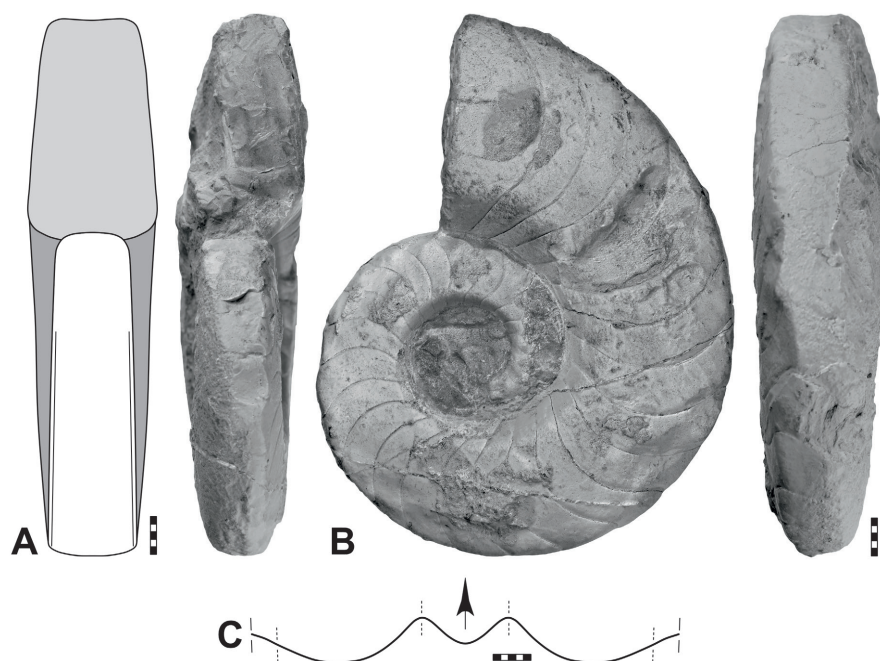
**Table 2.** Conch dimensions (in mm) and ratios of *Domatoceras canonium* sp. nov.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32105	134.0	29.0	50.9	50.0	50.6	0.22	0.57	0.37	2.58	0.01
MB.C.32105	83.4	21.5	33.1	30.0	32.8	0.26	0.65	0.36	2.72	0.01
MB.C.32105	50.6	14.8	20.3	18.2	20.0	0.29	0.73	0.36	2.73	0.01
MB.C.30227	70.9	17.1	29.2	24.4	28.3	0.24	0.59	0.34	2.77	0.03
MB.C.30227	42.7	11.7	18.0	15.5	17.5	0.27	0.65	0.36	2.87	0.03

The conch of the holotype is largely void of sculpture. Only the first whorl has small tubercles on the outer flank. The suture line is characterised by a very small external lobe (owing to the narrow venter) and a much larger, broadly rounded lateral lobe (Fig. 5C). The length of the chambers decreases on the last whorl of the phragmocone. On the first quarter of this whorl there are six septa, on the second seven, on the third there are already nine and on the last there are eleven (CLI decreases from 15 to 8 during one revolution). This increasing septal crowding is probably an indication of adulthood.

Paratype MB.C.30227 is a rather well-preserved, fully chambered internal mould with a conch diameter of 71 mm (Fig. 6B). It largely agrees with the holotype with regard to its conch geometry, if the same conch dimensions are taken into account. However, paratype MB.C.30227 shows a slightly narrower umbilicus ( $uw/dm=0.34$  at 71 mm dm). The shape of the umbilical margin changes during ontogeny. Up to a diameter of 30 mm it is still subangular; with increasing growth of the conch, it becomes less and less distinct and at 71 mm diameter it is evenly rounded (Fig. 6A).

The paratype shows a sculpture with small ventrolateral tubercles in the juvenile stage; these tubercles are clearly visible up to a conch diameter of 30 mm. The suture line shows a small rounded external lobe, a broadly rounded lateral lobe about twice as deep and a very small umbilical lobe (Fig. 6C).



**Fig. 6.** *Domatoceras canonium* sp. nov., paratype MB.C.30227 (Korn *et al.* 2011 Coll.) from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Dorsal, lateral and ventral views. **C.** Suture line at  $dm=57.0$  mm,  $ww=13.5$  mm,  $wh=21.5$  mm. Scale bar units=1 mm.

### Remarks

*Domatoceras canonium* sp. nov. differs from *D. ocomphalum* sp. nov. and *D. myloide* sp. nov. in the shape of the umbilicus. Its wall is convex and oblique in *D. canonium* but flattened and steep in *D. ocomphalum* and *D. myloide*. The umbilical margin is rounded in *D. canonium* but subangular in *D. ocomphalum* and *D. myloide*. Furthermore, *D. canonium* possesses ventrolateral tubercles in the juvenile stage, which are absent in the other two species.

*Domatoceras canonium* sp. nov. differs from the species known from Julfa, such as *D. elegantulum* and *D. multituberculatum*, in the extremely small whorl overlap. Another difference is the extremely high coiling rate of about 2.75 at a conch diameter of about 80 mm in *D. canonium*, while this rate reaches only 2.60 in the species from Julfa.

### *Domatoceras ocomphalum* sp. nov.

[urn:lsid:zoobank.org:act:335740F3-E4E5-4185-8313-8521F9287A28](https://zoobank.org/act:335740F3-E4E5-4185-8313-8521F9287A28)

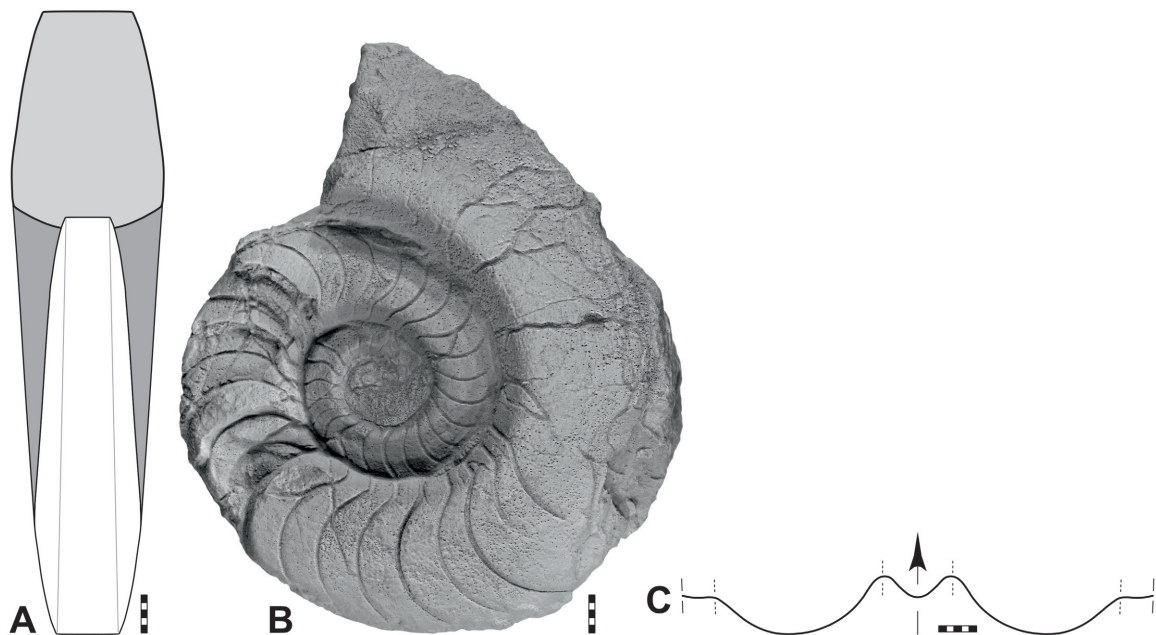
Fig. 7; Table 3

### Diagnosis

Species of *Domatoceras* with extremely discoidal, subevolute conch (ww/dm ~0.28; uw/dm ~0.38), weakly compressed whorl profile (ww/wh ~0.70) and extremely high coiling rate (WER ~2.60) at a conch diameter of 60 mm. Whorl profile with flat venter, angular ventrolateral shoulder, convergent flanks, subangular umbilical margin and steep and flattened umbilical wall. Whorl overlap very small. Without sculpture. Suture line with a small and narrow external lobe and a much larger and deeper, broadly rounded lateral lobe.

### Etymology

From the Greek ‘ομφαλός’=‘umbilicus’ and ‘όξύς’=‘sharp’; because of the subangular umbilical margin.



**Fig. 7.** *Domatoceras ocomphalum* sp. nov., holotype MB.C.32109 (Korn *et al.* 2010 Coll.) from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Lateral view. **C.** Suture line at dm=57.5 mm, ww=17.0 mm, wh=20.5 mm. Scale bar units=1 mm.

**Table 3.** Conch dimensions (in mm) and ratios of *Domatoceras ocomphalum* sp. nov.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32109	62.2	17.2	24.7	23.4	23.5	0.28	0.70	0.38	2.58	0.05

### Type material

#### Holotype

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2010; Korn *et al.* leg.; illustrated in Fig. 7; MB.C.32109.

### Description

Holotype MB.C.32109 is a partially corroded specimen with a conch diameter of about 80 mm. It allows the study of two whorls (Fig. 7B). The conch is, at 62 mm diameter, extremely discoidal and subevolute ( $ww/dm=0.28$ ;  $uw/dm=0.38$ ) with an extremely high coiling rate ( $WER=2.58$ ); the whorl profile is compressed ( $ww/wh=0.70$ ) with a completely flat venter, an angular ventrolateral shoulder, weakly convex and convergent flanks, a subangular umbilical margin and a flattened and steep umbilical wall (Fig. 7A). The specimen is free of sculpture. The suture line shows a shallow, rounded external lobe and a three times larger, broadly rounded lateral lobe. A small, incipient lobe is visible on the umbilical wall (Fig. 7C).

### Remarks

*Domatoceras ocomphalum* sp. nov. differs from *D. canonium* sp. nov. in the shape of the umbilicus. Its wall is flattened and steep in *D. ocomphalum* but convex and oblique in *D. canonium*. The umbilical margin is subangular in *D. ocomphalum* but rounded in *D. canonium*. Furthermore, *D. ocomphalum* lacks ventrolateral tubercles in the juvenile stage.

*Domatoceras ocomphalum* sp. nov. differs from *D. myloide* sp. nov. in the more strongly convergent flanks, which in the latter species are almost parallel and in the flat venter bounded by an angular ventrolateral shoulder, while the venter is convex and bounded by a rounded ventrolateral shoulder in *D. myloide*.

*Domatoceras ocomphalum* sp. nov. has conch proportions similar to *D. elegantulum* and *D. multituberculatum* from Julfa, but differs from these species in the lack of ventrolateral nodes in the intermediate stage and the more angular umbilical margin and ventrolateral shoulder.

Family **Ocunautilidae** fam. nov.

[urn:lsid:zoobank.org:act:AB88B12B-667A-4001-A82B-52ECBFEA5B5D](https://zoobank.org/act:AB88B12B-667A-4001-A82B-52ECBFEA5B5D)

New family – Korn 2025: 65, 69, fig. 42. — Korn & Ghaderi 2025: 25.

### Type genus

*Ocunautilus* gen. nov.

### Diagnosis

Family of the superfamily Grypoceratoidea with a usually discoidal, subinvolute conch. Whorl profile in the adult stage weakly compressed or weakly depressed; flanks and venter usually separated by a distinct ventrolateral shoulder, venter more or less concave. Umbilical margin usually subangular or angular, rarely rounded; umbilical wall steep, often flattened. Ornament usually consisting of fine growth lines. Septum simple in shape, concavely domed; suture line depending on whorl profile with shallow to V-shaped external lobe and shallow lateral lobe.

### Etymology

Named after the type genus *Ocunutilus* gen. nov.

### Included genera

*Pseudotitanoceras* Shimansky, 1965 (Permian); *Azarinautilus* Korn & Ghaderi, 2025 (Permian); *Ocunutilus* gen. nov. (Permian); *Aifinautilus* gen. nov. (Permian).

### Remarks

Grypoceratids with a whorl profile characterised by a concave venter, a pronounced ventrolateral shoulder with skid-like extensions, strongly convergent flanks and an angular umbilical margin occurred iteratively in the Late Carboniferous and the Late Permian. It is not clear whether they are phylogenetically related with each other or belong to independent evolutionary lineages.

The Late Permian forms are morphologically closely related; they are characterised by an ontogenetically rather late transformation of the juvenile growth stage with rounded or flattened venter into the adult stage with concave venter. Furthermore, the Late Permian forms have rather stout conchs (ww/dm between 0.40 and 0.55), whereas the conchs of the Late Carboniferous forms are usually more slender. The umbilical margin is more pronounced in the Late Permian genera. These are probably good reasons to assume that the Late Permian forms evolved independently of the Late Carboniferous forms and not represent a long-ranging evolutionary lineage.

The family *Ocunutilidae* fam. nov. is characterised by a transformation of the originally broadly rounded venter into a more or less concave venter in the middle ontogenetic stage. The new family can therefore easily be derived from the family *Domatoceratidae*, some species of which also show a similar transformation. In addition to the modification of the venter, some members of the family *Ocunutilidae* show a narrowing of the umbilicus and a subangular or angular shape of the umbilical margin.

Genus *Ocunutilus* gen. nov.

[urn:lsid:zoobank.org:act:1E0C7C57-E989-44E6-998D-730ECB2C672E](https://zoobank.org/urn:lsid:zoobank.org:act:1E0C7C57-E989-44E6-998D-730ECB2C672E)

New genus A – Korn 2025: 43. — Korn & Ghaderi 2025: 28.

### Type species

*Ocunutilus diplodocus* gen. et sp. nov.

### Diagnosis

Genus of the family *Ocunutilidae* fam. nov. with a subinvolute conch. Extremely to extraordinarily high coiling rate; whorl profile inverted trapezoidal, weakly compressed or weakly depressed with concave or flat venter and flattened, convergent flanks. Sculpture in the adult stage absent; in the juvenile stage sometimes with short ribs on the flank. Suture line with a shallow to deep V-shaped external lobe and a broadly rounded lateral lobe.

### Etymology

From Greek ‘ὄξύς’= ‘sharp’ and ‘ναυτίλος’; because of the angular ventrolateral shoulder.

### Included species

Central Iran (this paper): *Ocunutilus diplodocus* gen. et sp. nov., Wuchiapingian; *Ocunutilus coelodesmus* gen. et sp. nov., Wuchiapingian; *Ocunutilus tachytrepheus* gen. et sp. nov., Wuchiapingian.

## Remarks

*Ocunautilus* gen. nov. can hardly be confused with any other genus of Late Permian nautilids because of its very characteristic conch shape. The rather sharp umbilical margin, the flattened and rapidly converging flanks, the angular, skid-like ventrolateral shoulder and the more or less clearly concave venter allow a clear separation. *Pseudotitanoceras* is similar to *Ocunautilus*, but this genus is distinguished by the presence of tubercles on the ventrolateral shoulder. Shimansky (1965) mentioned that among his *P. armeniacum* material there were also specimens without ventrolateral tubercles. Perhaps these do belong to *Ocunautilus* rather than *Pseudotitanoceras*.

*Ocunautilus diplodocus* gen. et sp. nov.

[urn:lsid:zoobank.org:act:46279074-DA8A-42D6-B45C-8C639250C01A](https://zoobank.org/act:46279074-DA8A-42D6-B45C-8C639250C01A)

Fig. 8; Table 4

## Diagnosis

Species of *Ocunautilus* gen. nov. with thinly discoidal, subinvolute conch ( $ww/dm \sim 0.42$ ;  $uw/dm \sim 0.20$ ), weakly compressed whorl profile ( $ww/wh \sim 0.85$ ) and extremely high coiling rate ( $WER \sim 2.95$ ) at a conch diameter of 100 mm. Whorl profile inverted trapezoidal with deeply concave venter, angular ventrolateral shoulder, flattened and weakly convergent flanks, angular umbilical margin and steep and weakly concave umbilical wall. Whorl overlap small ( $IZR \sim 0.12$ ). Without sculpture. Suture line with a very deep, rounded V-shaped external lobe, an angular ventrolateral saddle, a shallow and broadly rounded lateral lobe and a very small umbilical lobe.

## Etymology

From the Greek ‘διπλόος’=‘double’ and ‘ὄξύς’=‘sharp’; because of the double-keeled venter.

## Type material

### Holotype

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Araxoceras* beds (early Wuchiapingian); 2013; Korn *et al.* leg.; illustrated in Fig. 8; MB.C.32110.

### Paratypes

IRAN – **Esfahan Province** • 2 specimens; same data as for holotype; 2010; Korn *et al.* leg.; MB.C.32111, MB.C.32112.

## Description

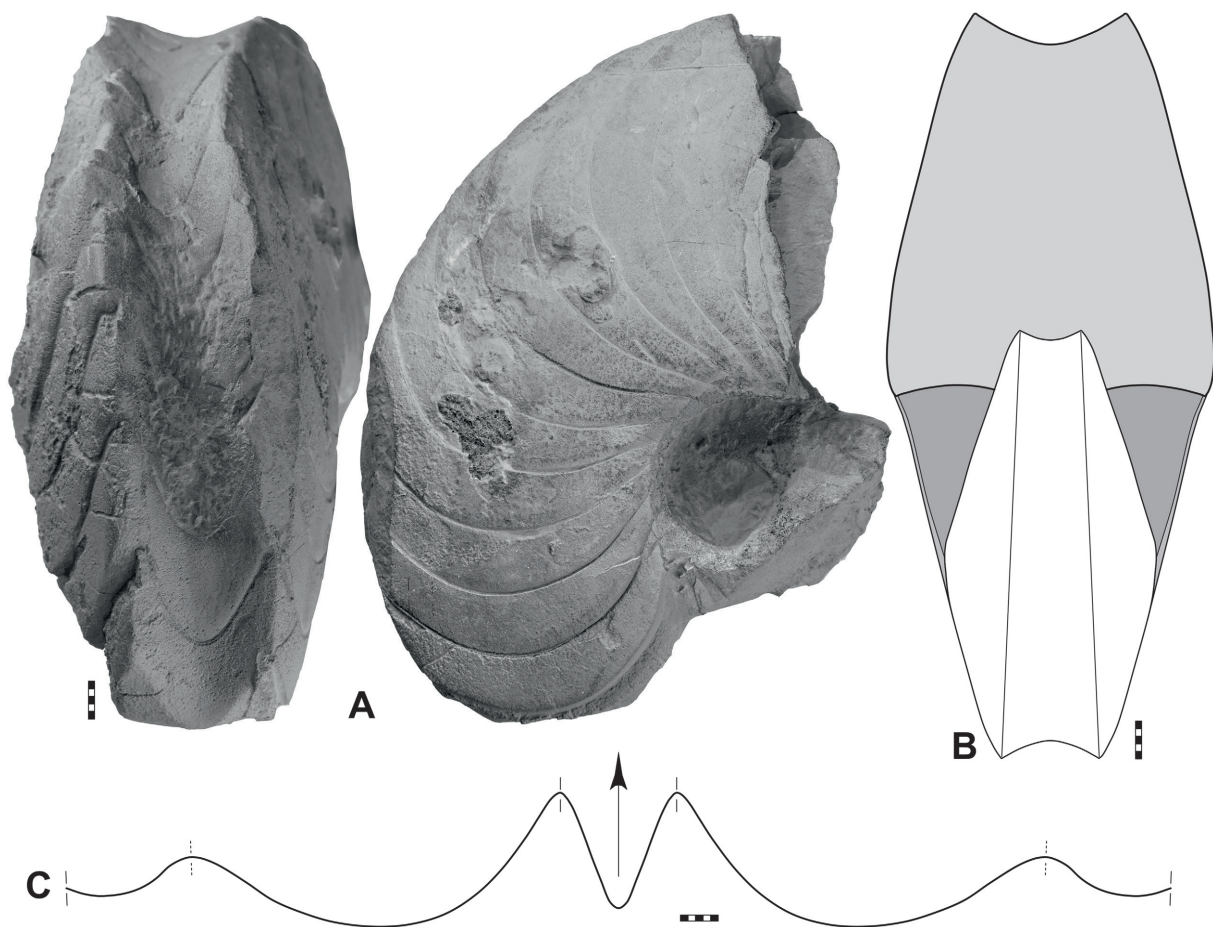
Holotype MB.C.32110 is a fragment showing slightly more than a quarter whorl of the phragmocone and a poorly preserved piece of the penultimate whorl (Fig. 8A). The fragment has a maximum whorl height of 51 mm; from this, a diameter of 105 mm can be reconstructed. On the basis of this calculated diameter, the conch parameters can be determined. The conch is thinly discoidal and subinvolute ( $ww/dm \sim 0.42$ ;  $uw/dm \sim 0.21$ ) with an extremely high coiling rate ( $WER \sim 2.96$ ). The whorl profile is weakly compressed ( $ww/wh=0.87$ ) with a deeply concave venter that is bordered by a sharp, skid-like ventrolateral shoulder; the flanks are flattened and convergent. Most conspicuous is the angular umbilical margin, which borders the weakly concave, incurved umbilical wall (Fig. 8B). The whorl overlap is small ( $IZR=0.14$ ). The specimen does not show any sculpture. The suture line is strongly influenced by the outline of the whorl profile; it is characteristic because of the narrow and deep, V-shaped external lobe, which is separated from the broadly rounded lateral lobe by a subangular ventrolateral saddle (Fig. 8C). The last quarter volution of the phragmocone consists of seven chambers ( $CLI=13$ ); there occurs weak septal approximation toward the aperture.

**Table 4.** Conch dimensions (in mm) and ratios of *Ocunautilus diplodocus* gen. et sp. nov.; reconstructed values in italics.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32110	<i>105.0</i>	44.5	50.9	22.5	44.0	<i>0.42</i>	0.87	<i>0.21</i>	2.96	0.14
MB.C.32111	84.0	32.2	38.2	23.3	34.4	0.38	0.84	0.28	2.87	0.10

**Remarks**

*Ocunautilus diplodocus* gen. et sp. nov. differs from the other two species *O. coelodesmus* gen. et sp. nov. and *O. tachytrepus* gen. et sp. nov. from Baghuk Mountain by the much more deeply concave venter; accordingly, the external lobe of *O. diplodocus* is also much deeper and narrower.



**Fig. 8.** *Ocunautilus diplodocus* gen. et sp. nov., holotype MB.C.32110 (Korn *et al.* 2013 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Ventral and lateral views. **B.** Reconstruction of apertural view. **C.** Suture line at  $ww=42.5$  mm,  $wh=46.0$  mm. Scale bar units=1 mm.

*Ocunautilus coelodesmus* gen. et sp. nov.

urn:lsid:zoobank.org:act:FC07FF9A-4B9C-4162-8BFD-9B43A2E3052C

Fig. 9; Table 5

**Diagnosis**

Species of *Ocunautilus* gen. nov. with thickly discoidal, subinvolute conch (ww/dm ~0.55; uw/dm ~0.25), weakly depressed whorl profile (ww/wh ~1.10) and extraordinarily high coiling rate (WER ~3.40) at a conch diameter of 60 mm. Whorl profile inverted trapezoidal with moderately concave venter, subangular ventrolateral shoulder, flattened and strongly convergent flanks, angular umbilical margin and steep and flat umbilical wall. Whorl overlap small (IZR ~0.08). Without sculpture, but juvenile conch with weak, backwardly directed ribs on the inner flank, ending in low and blunt nodes on the midflank. Suture line with a rather deep, rounded V-shaped external lobe, an angular ventrolateral saddle, a shallow and broadly rounded lateral lobe and a very small umbilical lobe.

**Etymology**

From the Greek ‘κόιλος’= ‘hollow’ and ‘δεσμός’= ‘band, brace’; because of the shape of the venter.

**Type material**

**Holotype**

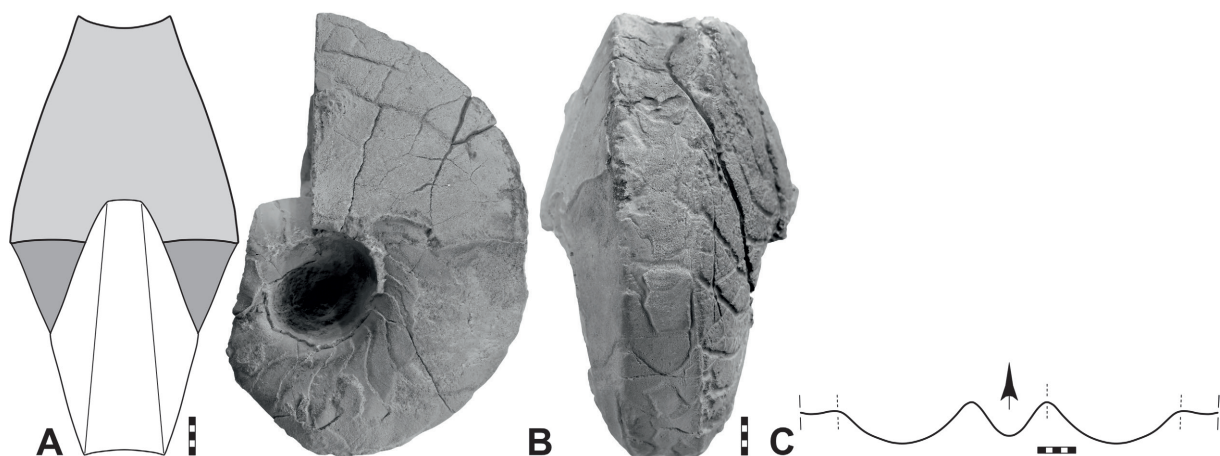
IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Araxoceras* beds (early Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 9; MB.C.32113.

**Paratypes**

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; MB.C.32114.

**Description**

Holotype MB.C.32113 is an incomplete, almost fully chambered specimen with a conch diameter of 57 mm (Fig. 9B). It is preserved as an internal mould, but shows some shell remains. The conch is, at a conch diameter of 57 mm, thickly discoidal and subinvolute (ww/dm=0.55; uw/dm=0.23) with an extraordinarily high coiling rate (WER=3.38). There occurs an ontogenetic decrease of the coiling rate;



**Fig. 9.** *Ocunautilus coelodesmus* gen. et sp. nov., holotype MB.C.32113 (Korn *et al.* 2011 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Lateral and ventral views. **C.** Suture line at dm=37.0 mm, ww=22.2 mm, wh=19.6 mm. Scale bar units=1 mm.

**Table 5.** Conch dimensions (in mm) and ratios of *Ocunautilus coelodesmus* gen. et sp. nov.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32113	57.0	31.5	28.2	12.9	26.0	0.55	1.12	0.23	3.38	0.08
MB.C.32113	37.5	21.3	19.4	9.5	18.0	0.57	1.10	0.25	3.70	0.07

at a conch diameter of 37.5 mm, it has even a value of 3.70. The whorl profile is weakly depressed ( $ww/wh=1.12$ ) with a weakly concave venter that is bordered by a sharp ventrolateral shoulder; the flanks are nearly flat and strongly convergent. The umbilical margin is subangular and the umbilical wall is steep and flat (Fig. 9A). The whorl overlap is small ( $IZR=0.08$ ). The few preserved shell remains of the holotype show no ornamentation or sculpture. The internal mould, however, has very small tubercles on the angular ventrolateral shoulder in the preadult stage up to a diameter of about 35 mm. The flanks bear very shallow, from the umbilical margin backwardly directed ribs, which strengthen in the middle of the flank to form very low, broad conical nodes. The suture line is dependent on the cross-sectional shape of the whorl; it has a rather deep, rounded V-shaped external lobe, an angular saddle on the ventrolateral shoulder and a broadly rounded lateral lobe (Fig. 9C). The last quarter revolution of the phragmocone has about seven chambers ( $CLI=13$ ).

### Remarks

*Ocunautilus coelodesmus* gen. et sp. nov. occupies an intermediate position between *O. diplococus* gen. et sp. nov. and *O. tachytrepheus* gen. et sp. nov. as far as the concavity of the venter is concerned; in *O. diplococus* the venter is much more deeply concave and in *O. tachytrepheus* it is nearly flat. *Ocunautilus coelodesmus* gen. et sp. nov. has very similar conch proportions to *O. tachytrepheus*, but differs in the concave umbilical wall, which is weakly convex in *O. tachytrepheus*.

### *Ocunautilus tachytrepheus* gen. et sp. nov.

[urn:lsid:zoobank.org:act:3C21BF76-5C82-4F5E-B39F-43499C76950D](https://zoobank.org/act:3C21BF76-5C82-4F5E-B39F-43499C76950D)

Fig. 10; Table 6

### Diagnosis

Species of *Ocunautilus* gen. nov. with thickly discoidal, subinvolute conch ( $ww/dm \sim 0.50$ ;  $uw/dm \sim 0.25$ ), weakly depressed whorl profile ( $ww/wh \sim 1.10$ ) and extraordinarily high coiling rate ( $WER \sim 3.35$ ) at a conch diameter of 80 mm. Whorl profile inverted trapezoidal with weakly concave venter, angular ventrolateral shoulder, flattened and weakly convergent flanks, angular umbilical margin and steep and weakly convex, flattened umbilical wall. Whorl overlap very small ( $IZR \sim 0.04$ ). Without sculpture, but first whorl with low, blunt nodes on the ventrolateral shoulder. Suture line with a very shallow external lobe, a subangular ventrolateral saddle, a shallow and broadly rounded lateral lobe and a very small umbilical lobe.

### Etymology

From the Greek ‘ταχύς’=‘rapid’ and ‘τρέφω’=‘enlarge’; because of the high coiling rate.

### Type material

#### Holotype

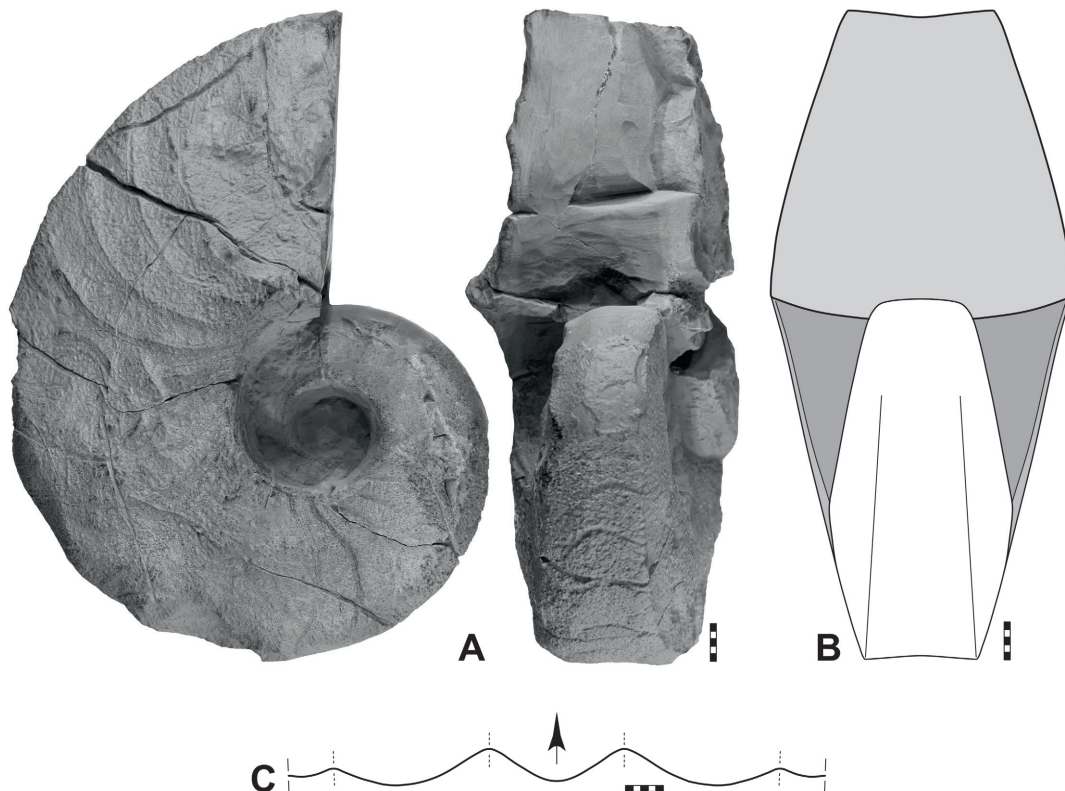
IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Araxoceras* beds (early Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 10; MB.C.32115.

## Description

Holotype MB.C.32115 is a fully chambered, partially corroded specimen with a conch diameter of 85 mm (Fig. 10A). It has slightly more than two volutions; the first volution has a diameter of about 24 mm and an umbilical foramen of about 4 mm diameter. The conch is, at a conch diameter of 85 mm, thickly discoidal and subinvolute ( $w/w/dm=0.51$ ;  $u/w/dm=0.24$ ) with an extraordinarily high coiling rate ( $WER=3.35$ ). Measurements from a position half a volution before result in similar ratios of conch geometry, but there occurs an ontogenetic decrease of the coiling rate; at a conch diameter of 48 mm, it has a value of about 3.50. The whorl profile is weakly depressed ( $w/w/h=1.08$ ) with a very weakly concave venter that is bordered by a sharp ventrolateral shoulder; the flanks are nearly flat and convergent. The umbilical margin is angular and the umbilical wall is steep and weakly convex. The whorl overlap is very small ( $IZR=0.04$ ). The specimen shows that the venter is still convex at a conch diameter of 24 mm, although it is already slightly flattened; the venter is completely applanate at a conch diameter of 48 mm (Fig. 10B). The conch is largely free of sculpture and ornament. On the first half of the last volution, the ventrolateral shoulder bears very low and blunt conical nodes. The suture line extends with a broadly rounded external lobe, a subangular ventrolateral saddle, a shallow lateral lobe and a very small umbilical lobe (Fig. 10C).

## Remarks

*Ocunautilus tachytrepheus* gen. et sp. nov. differs from the other two species *O. diplodocus* gen. et sp. nov. and *O. coelodesmus* gen. et sp. nov. from Baghuk Mountain in the shape of the umbilical wall (convex in *O. tachytrepheus*, but concave in the other species) and in the only weakly developed concavity of the venter. *Ocunautilus tachytrepheus* has similar conch proportions as *O. coelodesmus*, but shows a flattening



**Fig. 10.** *Ocunautilus tachytrepheus* gen. et sp. nov., holotype MB.C.32115 (Korn *et al.* 2011 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Lateral and dorsal views. **B.** Reconstruction of apertural view. **C.** Suture line at  $w/w=23.5$  mm,  $w/h=22.4$  mm. Scale bar units=1 mm.

**Table 6.** Conch dimensions (in mm) and ratios of *Ocunautilus tachytrepheus* gen. et sp. nov.; reconstructed values in italics.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32115	85.0	43.5	40.1	20.8	38.6	<i>0.51</i>	<i>1.08</i>	0.24	3.35	0.04
MB.C.32115	48.4	25.4	23.4	12.4	22.5	0.52	1.09	0.26	3.49	0.04

of the venter only at a larger conch diameter. This flattening occurs at about 35 mm in *O. tachytrepheus*, but already at about 20 mm in *O. coelodesmus*.

*Pseudotitanoceras armeniacus* (Abich, 1878) has similar conch proportions, but differs from *O. tachytrepheus* gen. et sp. nov. by a distinctly concave venter as well as the presence of tubercles on the ventrolateral shoulder and umbilical margin. Some of the specimens without tubercles mentioned by Shimansky (1965) may belong to *O. coelodesmus* gen. et sp. nov.

Genus *Aifinautilus* gen. nov.

[urn:lsid:zoobank.org:act:C251419E-4EF4-4D59-BBAA-FEEA876287CC](https://zoobank.org/urn:lsid:zoobank.org:act:C251419E-4EF4-4D59-BBAA-FEEA876287CC)

New genus B – Korn 2025: 43. — Korn & Ghaderi 2025: 30.

### Type species

*Aifinautilus icanus* gen. et sp. nov.

### Diagnosis

Genus of the family Ocunautilidae fam. nov. with a subinvolute conch. High coiling rate; whorl profile rounded rectangular, weakly depressed with concave venter. Without sculpture. Suture line with shallow external lobe and broadly rounded lateral lobe; without annular process.

### Etymology

From the Greek ‘αἴφνης’= ‘suddenly, unexpected’; because of the unexpected conch form of a Permian nautiloid.

### Included species

NW Iran (Korn & Ghaderi 2025): *Aifinautilus hebes* Korn & Ghaderi, 2025, Wuchiapingian.

Central Iran (this paper): *Aifinautilus icanus* gen. et sp. nov., Wuchiapingian.

### Remarks

*Aifinautilus* gen. nov. is difficult to confuse with any other genus of Palaeozoic nautiloids because of its peculiar conch morphology with the box-shaped whorl profile, the concave venter, the skid-like ventrolateral shoulder, parallel flanks and flattened umbilical wall. *Ocunautilus* gen. nov. differs from *Aifinautilus* by its clearly convergent flanks, resulting in a much narrower venter; it has an angular ventrolateral shoulder and an angular umbilical margin. *Pseudotitanoceras* also has convergent flanks and is characterised by a row of nodes on the ventrolateral shoulder and sometimes also at the umbilical margin (Shimansky 1965: 163).

The conch of *Aifinautilus* gen. nov. is very similar to that of some species of the Triassic genus *Germanonautilus* Mojsisovics, 1902 (e.g., Mojsisovics 1902; Dzik 1984; Sobolev 1989). The main difference between the two genera is the presence of an annular lobe in *Germanonautilus*, which is absent in *Aifinautilus*. The siphuncle has a more dorsal position in *Germanonautilus*.

The Late Carboniferous genus *Titanoceras* has a superficially similar conch shape with a concave venter and almost parallel flanks. However, the conch of *Titanoceras* has almost non-overlapping whorls and the sculpture is characterised by ventrolateral tubercles. Shimansky (1965: 163) has already suggested that the Late Carboniferous (*Titanoceras*) and Late Permian forms (*Pseudotitanoceras*) belong to two independent, homoeomorphic evolutionary lineages and that both arose from *Domatoceras*.

*Aifinautilus icanus* gen. et sp. nov.

[urn:lsid:zoobank.org:act:8E2C5B5B-1C6B-4492-8D76-89F957B1DCC1](https://doi.org/10.21203/rs.3.rs-4825551/v1)

Figs 11–13; Table 7

### Diagnosis

Species of *Aifinautilus* gen. nov. with thickly discoidal, subinvolute conch (ww/dm  $\sim 0.50$ ; uw/dm  $\sim 0.25$ ), weakly depressed whorl profile (ww/wh  $\sim 1.10$ ) and very high coiling rate (WER  $\sim 2.30$ ) at a conch diameter of 110 mm. Whorl profile with weakly concave venter, rounded ventrolateral shoulder, weakly convergent flanks, rounded umbilical wall, weakly concave umbilical wall and moderately deep imprint zone (IZR  $\sim 0.25$ ). Without sculpture. Suture line with a very shallow external lobe and a very shallow lateral lobe.



**Fig. 11.** *Aifinautilus icanus* gen. et sp. nov., holotype MB.C.32116 (Korn *et al.* 2010 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain, ventral and lateral views. Scale bar units = 1 mm.

**Etymology**

From the Greek ‘ικανός’ = ‘competent’; because of the robust conch.

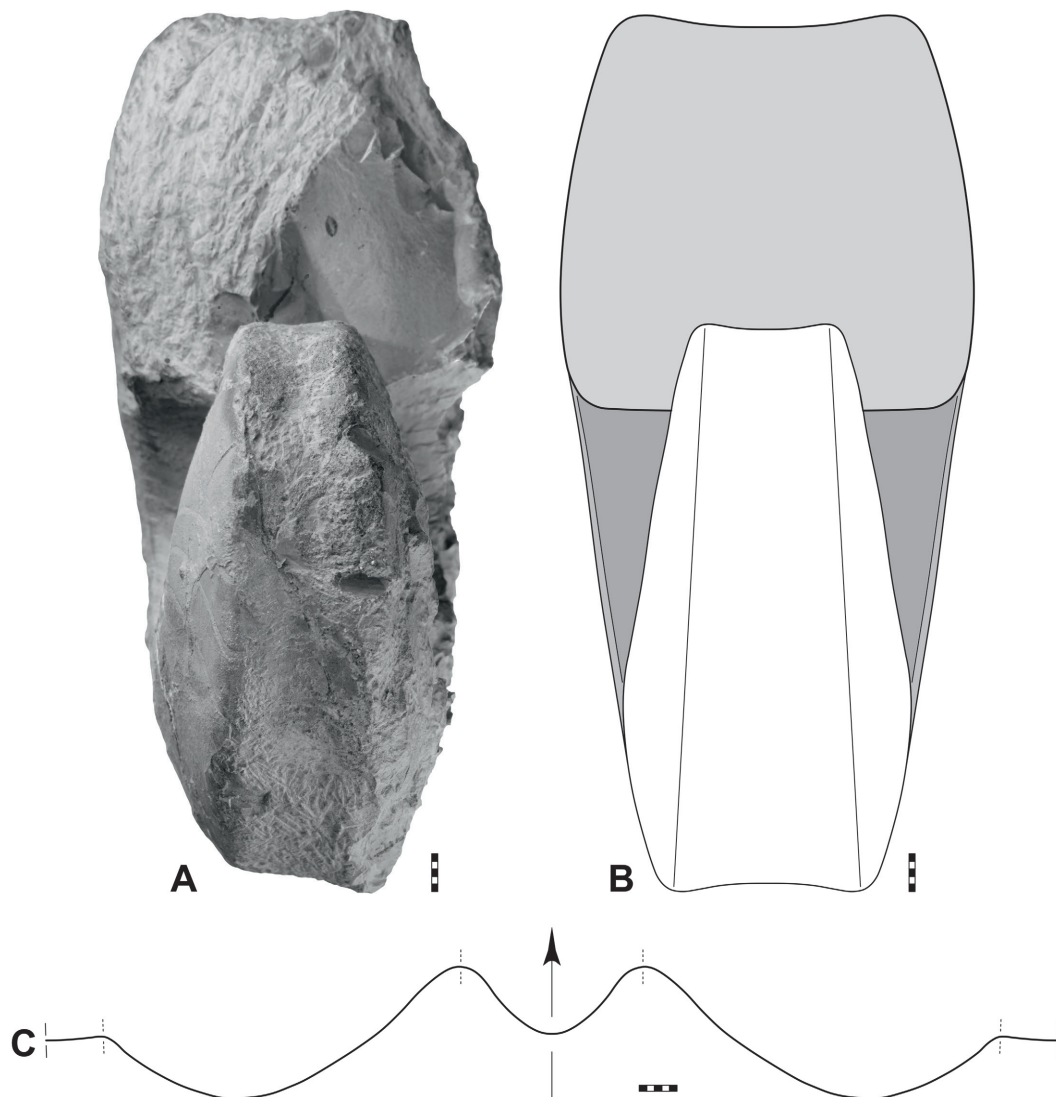
**Type material**

**Holotype**

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Araxoceras* beds (early Wuchiapingian); 2010; Korn *et al.* leg.; illustrated in Figs 11–12; MB.C.32116.

**Paratypes**

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; 2011; Korn *et al.* leg.; illustrated in Fig. 13; MB.C.32117 • 3 specimens; same data as for holotype; 2011; Korn *et al.* leg.; MB.C.32118 to MB.C.32120.



**Fig. 12.** *Aifinautilus icanus* gen. et sp. nov., holotype MB.C.32116 (Korn *et al.* 2010 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Dorsal view. **B.** Reconstruction of apertural view. **C.** Suture line at  $dm=105$  mm,  $ww=53$  mm,  $wh=47$  mm. Scale bar units=1 mm.

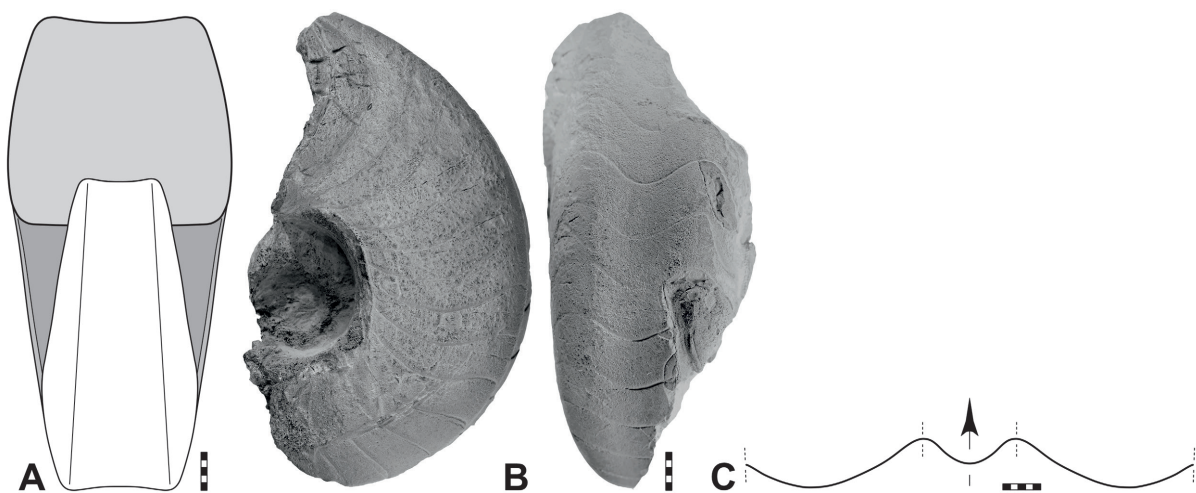
## Description

Holotype MB.C.32116 is an almost complete, but partially corroded specimen with a conch diameter of 114 mm (Figs 11, 12A). It is largely chambered; only a small part of the specimen belongs to the body chamber. The conch is, at a conch diameter of 114 mm, thickly discoidal and subinvolute ( $ww/dm=0.48$ ;  $uw/dm=0.24$ ) with a very high coiling rate ( $WER=2.31$ ) and moderately wide whorl overlap ( $IZR=0.23$ ). The whorl profile is weakly depressed ( $ww/wh=1.09$ ) with a slightly concave venter that is bordered by a rounded ventrolateral shoulder; the flanks are broadly convex and weakly convergent. The umbilical margin is narrowly rounded and the umbilical wall is steep and weakly incurved. The last whorl shows a modification in the profile. At the beginning it is inverted trapezoidal with fairly convergent flanks and a subangular ventrolateral shoulder (Fig. 12B). The specimen does not show any traces of sculpture. The length of the phragmocone chambers shows considerable changes during the last volution. The first quarter of this whorl consists of six chambers ( $CLI=15$ ); considerable septal crowding at the end of the phragmocone causes the number to increase to about 12 ( $CLI=7.5$ ). Especially the last six septa are very closely spaced. The suture line shows a shallow and broadly rounded external lobe, a narrowly rounded ventrolateral saddle, a shallow lateral lobe twice as deep than the external lobe and a very small umbilical lobe (Fig. 12C).

Paratype MB.C.32117 is an incomplete, fully chambered specimen with a conch diameter of 63 mm (Fig. 13B). It corresponds largely to the holotype in its conch proportions and also shows a weakly concave umbilical wall, almost parallel flanks, a rounded but pronounced ventrolateral shoulder and a weakly concave venter (Fig. 13A). The suture line has a shallow external lobe, a narrowly rounded ventrolateral saddle and a broadly rounded lateral lobe that is twice as deep as the external lobe (Fig. 13C).

## Remarks

Specimens of *Aifinautilus icanus* gen. et sp. nov. can hardly be confused with any other species of Baghuk Mountain. Species of the genus *Ocunautilus* gen. nov. show similarities in conch shape, but there are some easily recognisable differences. In *A. icanus*, the flanks are almost parallel, while in the species of *Ocunautilus* they are distinctly convergent. Another distinguishing criterion is the coiling rate, which is considerably lower in *A. icanus* ( $WER \sim 2.25$ ) than in *Ocunautilus* ( $WER$  mostly over 3.00).



**Fig. 13.** *Aifinautilus icanus* gen. et sp. nov., paratype MB.C.32117 (Korn *et al.* 2011 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Lateral and ventral views. **C.** Suture line at  $ww=26.5$  mm,  $wh=25.5$  mm. Scale bar units = 1 mm.

**Table 7.** Conch dimensions (in mm) and ratios of *Aifinautilus icanus* sp. nov.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32116	114.0	55.2	50.5	27.0	39.0	0.48	1.09	0.24	2.31	0.23
MB.C.32116	75.0	40.3	38.3	18.6	–	0.54	1.05	0.25	–	–
MB.C.32119	79.2	38.0	34.5	22.1	–	0.48	1.10	0.28	–	–
MB.C.32117	63.0	31.0	27.4	16.6	20.6	0.49	1.13	0.26	2.21	0.25

There are great similarities of *A. icanus* gen. et sp. nov. to species of the Triassic genus *Germanonautilus*. For example, *A. icanus* shows very close agreement in conch morphology with *G. bidorsatus* (Schlotheim, 1820), as was shown by Dzik (1984: 166, text-fig. 64). However, *Germanonautilus* differs from *Aifinautilus* gen. nov. by the presence of an annular lobe.

### Genus *Azarinautilus* Korn & Ghaderi, 2025

#### Type species

*Azarinautilus nahidae* Korn & Ghaderi, 2025; original designation.

#### Diagnosis

Genus of the family Ocucaulidae fam. nov. with a rather small, subinvolute or subevolute conch; whorl profile lyriform, venter moderately to deeply concave and bordered by raised keels, umbilical margin broadly rounded or subangular. Sculpture with conical nodes or shallow ribs in the midflank area. Suture line with narrow, rounded external lobe and broadly rounded lateral lobe (from Korn & Ghaderi 2025).

#### Included species

NW Iran (Korn & Ghaderi 2025): *Azarinautilus nahidae* Korn & Ghaderi 2025, Wuchiapingian.

Central Iran (this paper): *Azarinautilus phorminx* sp. nov., Changhsingian.

#### Remarks

*Azarinautilus* has an isolated position within the family Domatoceratidae because of its conch shape and sculpture. A comparably distinctly concave venter has apparently not been described from any other genus of the family; however, species of *Fididomatoceras* show a flat or slightly concave venter bordered laterally by low ridges.

#### *Azarinautilus phorminx* sp. nov.

[urn:lsid:zoobank.org:act:91FE758E-E2BC-45B0-BE73-90A885833281](https://zoobank.org/act:91FE758E-E2BC-45B0-BE73-90A885833281)

Fig. 14; Table 8

#### Diagnosis

Species of *Azarinautilus* with thickly discoidal, subevolute conch ( $ww/dm \sim 0.40$ ;  $uw/dm \sim 0.32$ ), equidimensional whorl profile ( $ww/wh \sim 1.00$ ) and very high coiling rate ( $WER \sim 2.30$ ) at a conch diameter of 45 mm. Whorl profile rounded lyriform with strongly convergent, broadly convex flanks; venter moderately concave, umbilical margin subangular. Whorl overlap small ( $IZR \sim 0.15$ ). Sculpture with short ribs in the midflank area. Suture line with a very shallow external lobe and a very shallow lateral lobe.

#### Etymology

From the Greek ‘φόρμιγγς’=the ancient Greek lyre; because of the whorl profile.

**Table 8.** Conch dimensions (in mm) and ratios of *Azarinautilus phorminx* sp. nov. from Baghuk Mountain.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32121	46.0	18.5	18.6	14.7	15.8	0.40	0.99	0.32	2.32	0.15

### Type material

#### Holotype

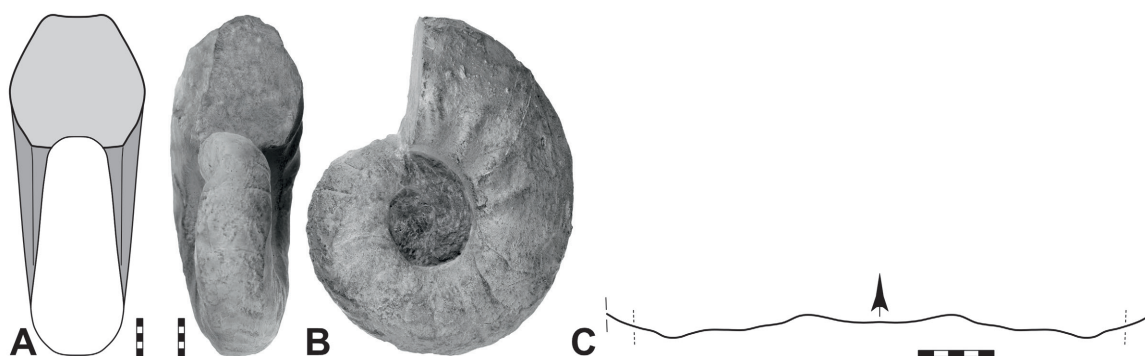
IRAN – **Esfahan Province** • Baghuk Mountain section G; Hambast Formation, *Paratirolites* beds (late Changhsingian), 2 m below top; 2012; Korn *et al.* leg.; illustrated in Fig. 14; MB.C.32121.

### Description

Holotype MB.C.32121 is a somewhat corroded internal mould with a diameter of 46 mm (Fig. 14B). About 135 degrees of the last whorl belong to the body chamber. The conch is thinly discoidal and subevolute ( $ww/dm=0.40$ ;  $uw/dm=0.32$ ) with a very high coiling rate ( $WER=2.32$ ). The whorl profile is almost equidimensional ( $ww/wh=0.99$ ) and shows a narrow, slightly concave venter that is separated by a rounded ventrolateral shoulder from the convex flanks. The whorl profile is widest near the rounded umbilical margin; the flanks are strongly convergent. The umbilical margin is pronounced and subangular and the low umbilical wall is steep. The whorl overlap rate is small ( $IZR \sim 0.15$ ). The shape of the whorl profile changes significantly in the last volution. At the beginning it shows almost parallel flanks and a flattened venter with a shallow longitudinal depression (Fig. 14A). The sculpture also changes on the last volution. At the beginning there are only very fine riblets on the inner flank; these grade into rather strong, sharp ribs. They start directly at the umbilical margin and are directed forward. In the middle of the flank they become weaker and disappear completely. The suture line shows a very shallow, broadly rounded external lobes as well as two very shallow lobes on the flank (Fig. 14C). This course strongly depends on the shape of the respective whorl profile at the position of the septum. There are about 12 chambers in the last half volution of the phragmocone ( $CLI=15$ ).

### Remarks

*Azarinautilus phorminx* sp. nov. differs from *A. nahidae* from Julfa in the much less concave venter, the subangular umbilical margin and the slightly wider umbilicus ( $uw/dm > 0.30$  in *A. phorminx*, but only 0.25 in *A. nahidae*). The suture line of *A. phorminx* shows a very shallow external lobe, which is much deeper in *A. nahidae*.



**Fig. 14.** *Azarinautilus phorminx* sp. nov., paratype MB.C.32121 (Korn *et al.* 2012 Coll.) from the *Paratirolites* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Dorsal and lateral and views. **C.** Suture line at  $dm=38.7$  mm,  $ww=14.5$  mm,  $wh=12.8$  mm. Scale bar units=1 mm.

Suborder **Tainoceratina** Shimansky, 1957

**Diagnosis**

Suborder of the order Nautilida, in which a ventrolateral shoulder and an umbilical margin are formed early in ontogeny in the advanced species. Conch usually discoidal, subinvolute to evolute. Juvenile whorl profile depressed oval or circular. Adult whorl profile depressed oval or reniform in the early species, showing numerous modifications during evolution (inverted trapezoidal, trapezoidal or polygonal whorl profiles or with ventral depression). Dorsal whorl zone always present, but usually very small. Juvenile sculpture with radial ribs on the flank; adult sculpture with radial ribs on the flank, ventrolateral nodes or several rows of nodes in derived species. Septa simply domed; with dorsal inflexion in advanced species. Suture line depending on the whorl profile, with shallow lobes and low saddles (from Korn 2025).

**Included superfamilies**

Tainoceratoidea Hyatt, 1883 (Carboniferous to Triassic); Pleuronautiloidea Hyatt, 1900 (Carboniferous to Triassic).

**Remarks**

A detailed discussion of the suborder Tainoceratina has been given by Korn (2025).

Superfamily **Pleuronautiloidea** Hyatt, 1900

**Diagnosis**

Superfamily of the suborder Tainoceratina with a discoidal, subinvolute to subevolute conch. Whorl profile in phylogenetically early species subquadrate with distinct ventrolateral shoulder and distinct umbilical margin. Derived species show a variation of modifications including trapezoidal, inverted trapezoidal or hexagonal whorl profiles with a less angular ventrolateral shoulder and umbilical margin. Whorl overlap is always very small. Sculpture in phylogenetically early species with transverse ribs and ventrolateral nodes, in derived species often with ribs and several rows of nodes. Septa simply domed, in derived species with a dorsal inflexion that produces an annular process. Suture line with broadly rounded lateral lobe and shallow lobe or low saddle on the venter (from Korn 2025).

**Included families**

Pleuronautilidae Hyatt, 1900 (Permian to Triassic); Gzheloceratidae Ruzhencev & Shimansky, 1954 (Carboniferous to Permian); Mosquoceratidae Ruzhencev & Shimansky, 1954 (Carboniferous to Permian); Aktubonautilidae Ruzhencev & Shimansky, 1954 (Permian); Rhiphaeoceratidae Ruzhencev & Shimansky, 1954 (Permian); Metacoceratidae Korn, 2025 (Carboniferous to Permian); Foordiceratidae Korn, 2025 (Permian).

**Remarks**

A detailed discussion of the superfamily Pleuronautiloidea has been given by Korn (2025).

Family **Metacoceratidae** Korn, 2025

**Diagnosis**

Family of the superfamily Pleuronautiloidea with an equidimensional or more commonly weakly depressed, trapezoidal to inverted trapezoidal whorl profile. Venter usually flattened, but ranging from

slightly convex to slightly concave. Ventrolateral shoulder often prominent, ranging from broadly rounded to subangular. Flanks weakly convergent, parallel or weakly divergent, usually flattened and ranging from weakly convex to weakly concave. Umbilical margin usually pronounced, usually subangular in the intermediate growth stage. Sculpture with ventrolateral conical nodes, often with dorsolateral nodes and low ribs on the flank. Suture line with shallow lobes and low saddles. Internal lobe very shallow, without annular process (from Korn 2025).

### Included genera

*Metacoceras* Hyatt, 1883 (Carboniferous to Triassic); *Mojsvaroceras* Hyatt, 1883 (Triassic); *Huanghoceras* Yin, 1933 (Permian); ? *Shansinautilus* Yabe & Mabuti, 1935 (Permian); *Cooperoceras* Miller, 1945 (Permian); *Epimetacoceras* Librovtich, 1946 (Carboniferous) (nomen nudum); *Pseudofoordiceras* Ruzhencev & Shimansky, 1954 (Permian); *Pseudotemnocheilus* Ruzhencev & Shimansky, 1954 (Permian); *Tanchiashanites* Zhao, 1954 (Permian); *Mahoningoceras* Murphy, 1974 (Carboniferous); *Lichuanoceras* Xu, 1977 (Permian); *Sinotitanoceras* Pan, 1983 (Permian); *Anthodiscoceras* Qin, 1986 (Permian); *Serometacoceras* Korn & Ghaderi, 2025 (Permian).

### Remarks

A detailed account of the research history of *Metacoceras* and genera with similar morphology has been given by Korn (2025). Therefore, only the differences between the new genus *Serometacoceras* and *Metacoceras* will be discussed here.

Genus *Serometacoceras* Korn & Ghaderi, 2025

### Type species

*Pleuromutilus Verae* von Arthaber, 1900: 216; original designation.

### Diagnosis

Genus of the family Metacoceratidae with a subinvolute or subevolute conch; whorl profile equidimensional or more or less strongly depressed, usually trapezoidal with weakly divergent flanks. Venter usually weakly convex or flattened; ventrolateral shoulder narrowly or broadly rounded. Umbilical margin pronounced and subangular in the intermediate growth stage, rounded in the adult stage. Sculpture with conical nodes on the ventrolateral shoulder or on the umbilical margin or both, sometimes connected by low ribs on the flank. Suture line with a shallow external lobe or a very low external saddle and a broadly rounded lateral lobe; without annular process. Siphuncle small with subcentral position ventrad of septum centre (from Korn & Ghaderi 2025).

### Included species

Transcaucasia and NW Iran (Abich 1878; von Arthaber 1900; Shimansky 1965; Kotlyar *et al.* 1989; Korn & Ghaderi 2025): *Nautilus dorso armatus* Abich, 1878, Wuchiapingian, Azerbaijan; *Nautilus tubercularis* Abich, 1878, Wuchiapingian, Azerbaijan; *Nautilus incertus* Abich, 1878, Wuchiapingian, Azerbaijan; *Pleuromutilus Verae* von Arthaber, 1900, Wuchiapingian, Azerbaijan; *Metacoceras dorashamense* Shimansky, 1965, Wuchiapingian, Azerbaijan; *Pleuromutilus dzhulfensis* Shimansky, 1965, Wuchiapingian, Azerbaijan [synonym of *Serometacoceras verae*]; *Pleuromutilus costalis* Shimansky, 1965, Wuchiapingian, Armenia; *Pleuromutilus dzhagadzurensis* Zakharov in Kotlyar *et al.*, 1989, Capitanian, Azerbaijan; *Serometacoceras inflatum* Korn & Ghaderi, 2025, Wuchiapingian, NW Iran; *Serometacoceras cingulum* Korn & Ghaderi, 2025, Wuchiapingian, NW Iran; *Serometacoceras parvituberculatum* Korn & Ghaderi, 2025, Wuchiapingian, NW Iran; *Serometacoceras arasense* Korn & Ghaderi, 2025, Changhsingian, NW Iran.

Central Iran (this paper): *Serometacoceras pentagonum* sp. nov., Wuchiapingian.

Pakistan (Waagen 1879; Reed 1931, 1944): *Nautilus latissimus* Waagen, 1879, Wuchiapingian, Salt Range; *Gyroceras Medlicottianum* Waagen, 1879, Wuchiapingian, Salt Range; *Metacoceras warchense* Reed, 1931, Wuchiapingian, Salt Range; *Metacoceras chittidilense* Reed, 1944, Wuchiapingian, Salt Range; *Parametacoceras venustum* Reed, 1944, Wuchiapingian, Salt Range.

South China (Xu 1977; Zheng 1984; Ma 1997): *Metacoceras hunanense* Xu, 1977, Changhsingian, Hunan; *Pleurometacoceras changxingensis* Zhao, Liang & Zheng, 1978, Changhsingian, Zhejiang; *Pleurometacoceras zhongyingensis* Zheng, 1984, Changhsingian, Guizhou; *Pleurometacoceras magnus* Zheng, 1984, Changhsingian, Guizhou; *Pleurometacoceras anfuensis* Ma, 1997, Wuchiapingian, Jiangxi; *Pleurometacoceras curvatus* Ma, 1997, Wuchiapingian, Jiangxi; *Pleurometacoceras robustus* Ma, 1997, Wuchiapingian, Jiangxi.

### Remarks

Korn & Ghaderi (2025) placed the morphocline with “*Nautilus dorso armatus*” and “*Pleurometacoceras Verae*” entirely in the genus *Serometacoceras*. Some representatives of these Late Permian forms, previously attributed to *Pleurometacoceras*, do in fact have a sculpture very reminiscent of *Pleurometacoceras*, but they lack the annular process. They may also belong to *Serometacoceras*.

### *Serometacoceras pentagonum* sp. nov.

[urn:lsid:zoobank.org:act:2FF8B350-39A8-46CF-AD42-1C10F79C1820](https://zoobank.org/act:2FF8B350-39A8-46CF-AD42-1C10F79C1820)

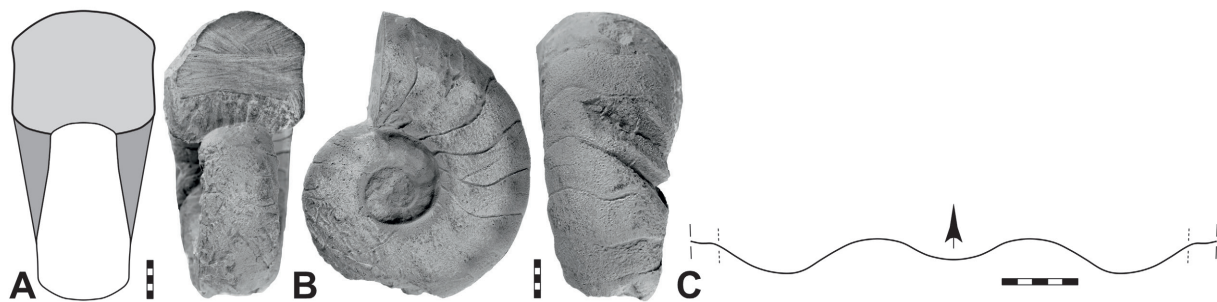
Fig. 15; Table 9

### Diagnosis

Species of *Serometacoceras* with thickly discoidal, subevolute conch (ww/dm ~0.50; uw/dm ~0.32), weakly depressed whorl profile (ww/wh ~1.15) and extremely high coiling rate (WER ~2.65) at a conch diameter of 40 mm. Whorl profile weakly depressed with nearly parallel flanks; venter broadly convex, flanks weakly concave. Sculpture with pairs of about 20 low ventrolateral nodes and weak umbilical nodes per volution; the nodes are connected by weak ribs on the midflank. Suture line with a shallow external lobe and a broadly rounded lateral lobe.

### Etymology

From the Greek ‘πέντε’= ‘five’ and ‘γόνυ’= ‘knee, angle’; because of the pentagonal whorl profile.



**Fig. 15.** *Serometacoceras pentagonum* sp. nov., holotype MB.C.32122 (Ghaderi 2011 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Dorsal, lateral and ventral views. **C.** Suture line at dm=30.0 mm, ww=17.4 mm, wh=11.8 mm. Scale bar units=1 mm.

**Table 9.** Conch dimensions (in mm) and ratios of *Serometacoceras pentagonum* sp. nov.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32122	38.1	18.8	16.2	12.1	14.7	0.49	1.16	0.32	2.65	0.09
MB.C.32122	23.4	12.4	9.9	7.3	–	0.53	1.25	0.31	–	–

### Type material

#### Holotype

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Araxoceras* beds (early Wuchiapingian); 2011; Ghaderi leg.; illustrated in Fig. 15; MB.C.32122.

### Description

Holotype MB.C.32122 is a rather small phragmocone with a conch diameter of only 38 mm (Fig. 15B). The conch is thickly discoidal and subevolute ( $ww/dm=0.49$ ;  $uw/dm=0.32$ ) with an extremely high coiling rate ( $WER=2.65$ ). The whorl profile is weakly depressed ( $ww/wh=1.16$ ) with a slightly convex venter and a broadly rounded ventrolateral shoulder. The flanks are very slightly flattened and slowly divergent; the umbilical margin is narrowly rounded and the umbilical wall is steep and convex (Fig. 15A). The sculpture consists of very low, about ten conical ventrolateral nodes on a half volution, which show a very weak continuation across the flanks and are connected to barely visible umbilical nodes. The suture line has shallow, broadly rounded external and lateral lobes and a very small lobe on the umbilical wall (Fig. 15C).

### Remarks

*Serometacoceras pentagonum* sp. nov. is similar to the Transcaucasian species *S. verae* in conch shape. However, the two species differ in the suture line (external saddle in *S. verae*, external lobe in *S. pentagonum*) and the sculpture (midflank nodes in *S. verae*). *Serometacoceras pentagonum* differs from the other Transcaucasian species in the more robust conch ( $ww/dm \sim 0.50$  in contrast to 0.40–0.45), the narrower umbilicus ( $uw/dm \sim 0.30$  in contrast to  $\sim 0.35$ ) and the convexly rounded venter.

## Family Foordiceratidae Korn, 2025

### Diagnosis

Family of the superfamily Tainoceratoidea with a trapezoidal whorl profile; ventrolateral shoulder rounded, flanks strongly divergent. Sculpture with ventrolateral conical nodes, sometimes with low ribs on the flank. Suture line with shallow lobes and low saddles. Internal lobe very shallow, without annular process (from Korn 2025).

### Included genera

*Araxonautilus* Shimansky, 1979 (Permian); *Foordiceras* Hyatt, 1893 (Permian); *Tardunautilus* Korn & Ghaderi 2025 (Permian).

### Remarks

A detailed discussion of *Foordiceras* and genera with similar morphology has been given by Korn (2025).

Genus *Foodiceras* Hyatt, 1893

**Type species**

*Nautilus goliathus* Waagen, 1879; original designation.

**Diagnosis**

Genus of the family Foodiceratidae with a subevolute conch with equidimensional or depressed trigonal or trapezoidal whorl profile. Umbilical margin in the intermediate stage pronounced and subangular, in the adult stage missing. Sculpture with coarse nodes on the ventral shoulder. Suture line with shallow external lobe or low external saddle and broadly rounded lateral lobe; without annular process. Siphuncle with subcentral position ventrad of septum centre.

**Included Permian species**

Pakistan (de Koninck 1863; Waagen 1879; Reed 1931): *Nautilus Flemingianus* de Koninck, 1863, Wuchiapingian, Salt Range; *Nautilus goliathus* Waagen, 1879, Wuchiapingian, Salt Range; *Foodiceras grypoceroides* Reed, 1931, Wuchiapingian, Salt Range.

Central Europe (Prinoth & Posenato 2007): *Foodiceras dolomiticum* Prinoth & Posenato, 2007, Changhsingian, Dolomites.

Central Iran (this paper): *Foodiceras eicosacanthum* sp. nov., Wuchiapingian; *Foodiceras decacanthum* sp. nov., Wuchiapingian; *Foodiceras ascetum* sp. nov., Wuchiapingian.

**Remarks**

*Foodiceras* is a genus that has been interpreted in very different ways. Miller & Youngquist (1949) defined it very broadly and included a number of species that are now placed in other genera such as *Pseudofoodiceras* (Ruzhencev & Shimansky 1954). Here, *Foodiceras* is reduced to a narrow morphological circle, which is mainly defined by the rounded triangular or trapezoidal whorl profile and a sculpture with coarse ventrolateral nodes.

*Foodiceras eicosacanthum* sp. nov.

[urn:lsid:zoobank.org:act:439D1047-04C8-45E8-A26D-7B8F74784441](https://doi.org/10.3897/zoobank.org/act:439D1047-04C8-45E8-A26D-7B8F74784441)

Fig. 16; Table 10

*Endolobus* sp. – Korn *et al.* 2021: text-fig. 17a.

**Diagnosis**

Species of *Foodiceras* with thickly discoidal, evolute conch ( $ww/dm \sim 0.47$ ;  $uw/dm \sim 0.47$ ), moderately depressed whorl profile ( $ww/wh \sim 1.75$ ) and moderately high coiling rate ( $WER \sim 1.80$ ) at a conch diameter of 60 mm. Whorl profile rounded trapezoidal with strongly divergent, flattened flanks; venter flattened. Sculpture with about 20 weak, blunt ventrolateral ribs per volution. Suture line with a very wide and shallow external lobe and a very shallow, broadly rounded lateral lobe.

**Etymology**

From the Greek ‘εἴκοσι’=‘twenty’ and ‘ἄκανθα’=‘thorn, spine’; because of the 20 ventrolateral nodes.

**Type material**

**Holotype**

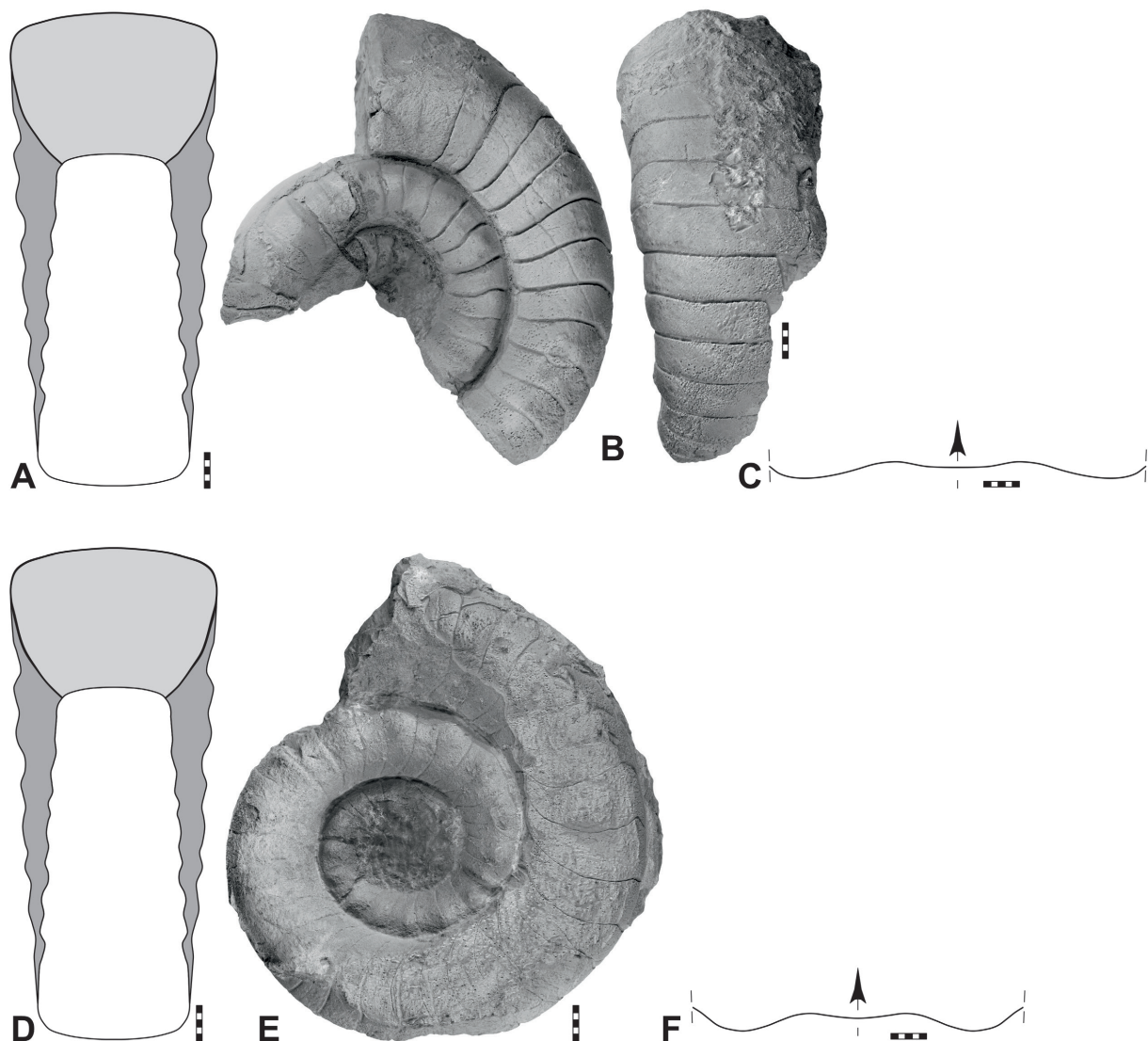
IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2013; Korn *et al.* leg.; illustrated in Fig. 16A–C; MB.C.30223.

**Paratype**

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; 2011; Korn *et al.* leg.; illustrated in Fig. 16D–F; MB.C.32123.

**Description**

Holotype MB.C.30223 is an incomplete internal mould with a conch diameter of 57 mm; it is fully chambered (Fig. 16B). The conch width had to be reconstructed; it appears that the conch is thickly discoidal and subevolute ( $ww/dm \sim 0.48$ ;  $uw/dm = 0.47$ ) with a moderately high coiling rate ( $WER = 1.81$ ). The whorl profile is moderately depressed ( $ww/wh \sim 1.80$ ) and rounded trapezoidal with a flatly rounded venter and a broadly rounded ventrolateral shoulder. The divergent flanks are slightly flattened; an



**Fig. 16.** *Foordiceras eicosacanthum* sp. nov. from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Holotype MB.C.30223 (Korn *et al.* 2013 Coll.), reconstruction of apertural view. **B.** The same specimen, lateral and ventral views. **C.** The same specimen, suture line at  $wh = 17.2$  mm. **D.** Paratype MB.C.32123 (Korn *et al.* 2011 Coll.), reconstruction of apertural view. **E.** The same specimen, lateral view. **F.** The same specimen, suture line at  $dm = 50.0$  mm,  $ww = 22.0$  mm,  $wh = 15.0$  mm. Scale bar units = 1 mm.

**Table 10.** Conch dimensions (in mm) and ratios of *Foordiceras eicosacanthum* sp. nov. from Baghuk Mountain; reconstructed value in italics.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32123	61.3	28.0	16.2	29.0	15.6	<i>0.46</i>	<i>1.73</i>	0.47	1.80	0.04
MB.C.30223	56.5	27.2	15.1	26.8	14.5	0.48	1.80	0.47	1.81	0.04

umbilical margin is not present (Fig. 16A). The sculpture consists of low conical ventrolateral nodes, of which there are 10 on half a volution. They are entirely confined to the ventrolateral shoulder and the outer flank and are as wide as their interspaces. The suture line shows a very wide, very shallow external lobe and a very shallow lateral lobe (Fig. 16C). The septa are rather short in the last quarter volution of the phragmocone has about eight chambers (CLI=11); in the penultimate volution, there are only six chambers on a quarter whorl (CLI=15).

Paratype MB.C.32123 is a partially corroded specimen with a conch diameter of 68 mm (Fig. 16E). One whorl between a conch diameter of 20 and 37 mm is rather well-preserved and allows the study of the conch geometry and sculpture. In both features as well as in the suture line (Fig. 16F) the paratype agrees well with the holotype. The number of chambers remains the same in the last volution; in both last half volutions the phragmocone has 15 chambers each (CLI=12). The third last half volution has 12 chambers (CLI=15).

### Remarks

*Foordiceras eicosacanthum* sp. nov. differs from *F. decacanthum* sp. nov. and *F. ascetum* sp. nov. in the rather small and more numerous ventrolateral nodes, of which there are ten on half a volution, while there are only five very coarse nodes on half a volution in the other two species. Furthermore, *F. eicosacanthum* has a more strongly depressed whorl profile ( $ww/wh \sim 1.75$ ) than *F. decacanthum* ( $ww/wh \sim 1.25$ ) and *F. ascetum* ( $ww/wh \sim 1.00$ ).

### *Foordiceras decacanthum* sp. nov.

[urn:lsid:zoobank.org:act:FEB57A12-32B4-461B-968A-0037BCC865E6](https://zoobank.org/urn:lsid:zoobank.org:act:FEB57A12-32B4-461B-968A-0037BCC865E6)

Fig. 17; Table 11

*Metacoceras* sp. – Korn *et al.* 2021: text-fig. 17b.

### Diagnosis

Species of *Foordiceras* with thinly discoidal, subevolute conch ( $ww/dm \sim 0.40$ ;  $uw/dm \sim 0.44$ ), weakly depressed whorl profile ( $ww/wh \sim 1.25$ ) and high coiling rate (WER  $\sim 2.10$ ) at a conch diameter of 60 mm. Whorl profile trapezoidal with divergent, convex flanks; venter flattened, umbilical margin incipient. Sculpture with about 10 very coarse, blunt ventrolateral ribs per volution. Suture line with a very shallow external lobe and a very shallow, broadly rounded lateral lobe.

### Etymology

From the Greek ‘δέκα’=‘ten’ and ‘ἄκανθα’=‘thorn, spine’; because of the ten ventrolateral nodes per volution.

### Type material

#### Holotype

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2010; Korn *et al.* leg.; illustrated in Fig. 17; MB.C.30224.

**Table 11.** Conch dimensions (in mm) and ratios of *Foordiceras decacanthum* sp. nov. from Baghuk Mountain.

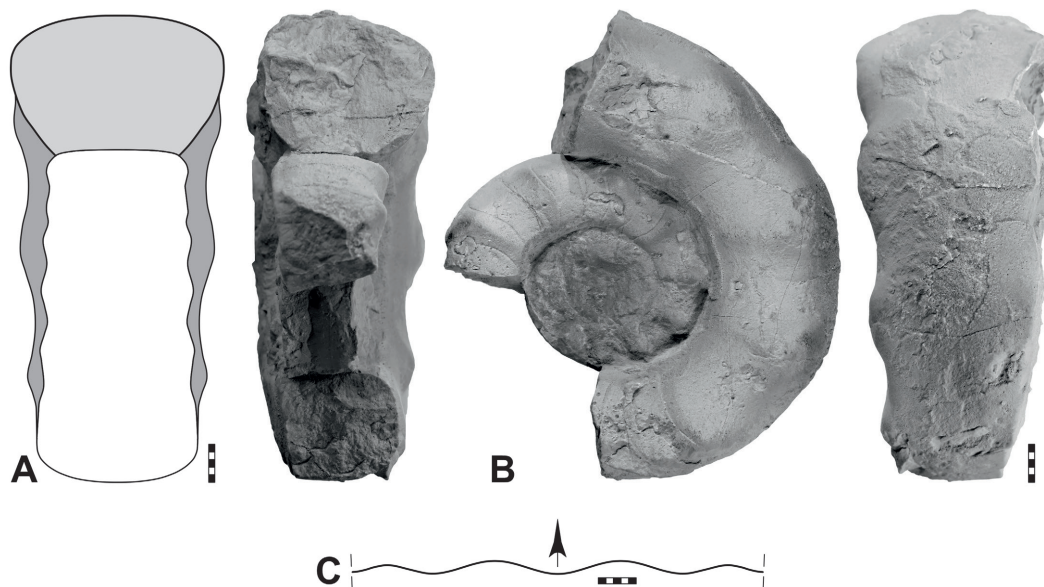
Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.30224	61.9	25.1	19.7	27.5	19.0	0.41	1.27	0.44	2.08	0.04

### Description

Holotype MB.C.30224 is an incomplete, but rather well-preserved internal mould with a diameter of 62 mm (Fig. 17B). The conch is thinly discoidal and subevolute ( $ww/dm=0.41$ ;  $uw/dm=0.44$ ) with a high coiling rate ( $WER=2.08$ ); the whorl profile is weakly depressed ( $ww/wh=1.27$ ) and rounded trapezoidal with a flatly rounded venter and a broadly rounded ventrolateral shoulder. The divergent flanks are convex; a rudimentary umbilical margin is developed (Fig. 17A). The sculpture consists of about 10 very large, but low ventrolateral nodes per volution; these nodes have a rounded conical shape and continue as very low ribs on the flank. They are much wider than the spaces between them. These ribs are considerably more prominent on the penultimate whorl, at a conch diameter of about 25 mm, than on the last whorl. The suture line shows a very shallow external lobe and a very shallow lateral lobe (Fig. 17C). The last half volution of the phragmocone has about 12 chambers ( $CLI=15$ ).

### Remarks

*Foordiceras decacanthum* sp. nov. differs from *F. eicosacanthum* sp. nov., which possesses a similar conch geometry, in the number and formation of the ventrolateral nodes. *Foordiceras decacanthum* has only five very coarse nodes on half a whorl, whereas *F. eicosacanthum* has ten much smaller nodes. *Foordiceras decacanthum* has a very similar sculpture to *F. ascetum* sp. nov., but shows a depressed whorl profile ( $ww/wh \sim 1.25$ ), whereas in *F. ascetum* this is almost equidimensional ( $ww/wh \sim 1.00$ ). Another criterion to separate *F. decacanthum* from the rather similar *F. ascetum* is in the width of the nodes; in *F. decacanthum* they are wider than the interspaces, while they are only half as wide as their interspaces in *F. ascetum*.



**Fig. 17.** *Foordiceras decacanthum* sp. nov., holotype MB.C.30224 (Korn *et al.* 2010 Coll.) from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Dorsal, lateral and ventral views. **C.** Suture line at  $wh=10.8$  mm. Scale bar units = 1 mm.

*Foordiceras decacanthum* sp. nov. differs from the superficially similar *F. goliathus*, which also possesses very coarse ventrolateral nodes, in the much wider umbilicus. The uw/dm ratio is about 0.45 in *F. decacanthum*, but only around 0.30 in *F. goliathus*.

*Foordiceras ascetum* sp. nov.

[urn:lsid:zoobank.org:act:B448394B-F0E2-42D2-9EFA-FA09D8C8E1A7](https://zoobank.org/urn:lsid:zoobank.org:act:B448394B-F0E2-42D2-9EFA-FA09D8C8E1A7)

Fig. 18; Table 12

**Diagnosis**

Species of *Foordiceras* with thinly discoidal, subevolute conch (ww/dm ~0.33; uw/dm ~0.43), nearly equidimensional whorl profile (ww/wh ~1.00) and high coiling rate (WER ~2.20) at a conch diameter of 60 mm. Whorl profile trapezoidal with weakly divergent, flattened flanks; venter flattened, umbilical margin incipient. Sculpture with about 10 coarse, blunt ventrolateral ribs per revolution. Suture line with a very shallow external lobe and a very shallow, broadly rounded lateral lobe.

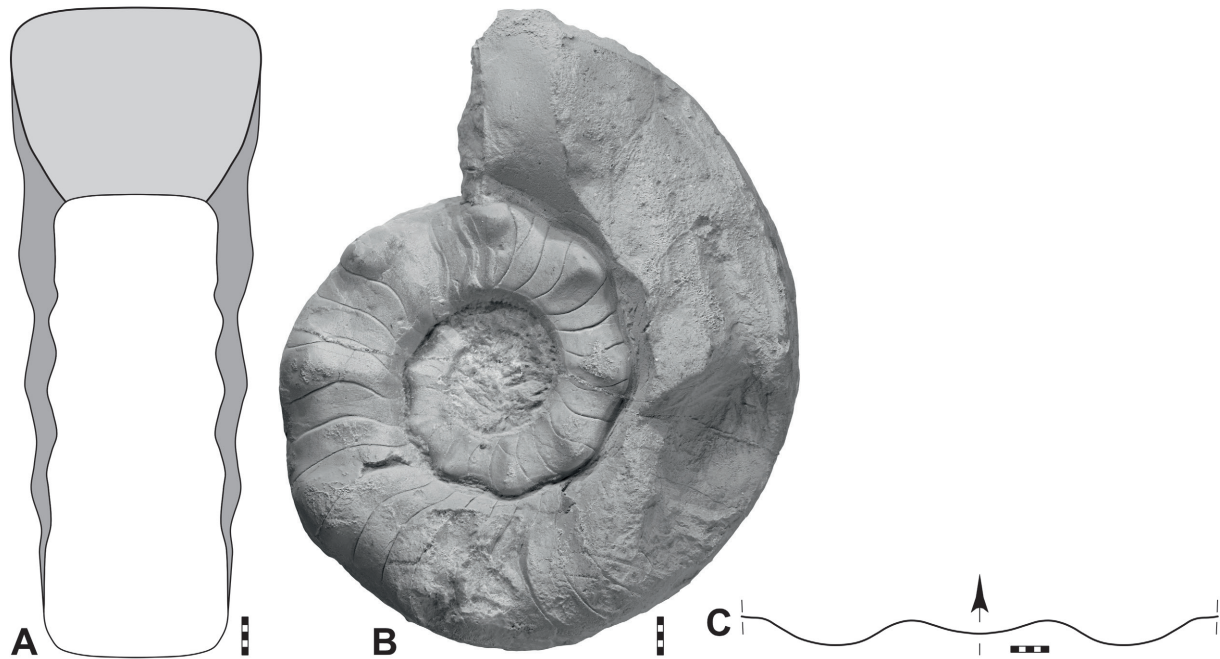
**Etymology**

From the Greek ‘ἀσκητός’= ‘decorated’; because of the sculpture.

**Type material**

**Holotype**

IRAN – Esfahan Province • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 18; MB.C.32124.



**Fig. 18.** *Foordiceras ascetum* sp. nov., holotype MB.C.32124 (Korn *et al.* 2011 Coll.) from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Lateral view. **C.** Suture line at dm=61.4 mm, wh=19.6 mm. Scale bar units=1 mm.

**Table 12.** Conch dimensions (in mm) and ratios of *Foordiceras ascetum* sp. nov. from Baghuk Mountain.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32124	61.6	20.5	21	26.5	20.2	0.33	0.98	0.43	2.21	0.04

### Description

Holotype MB.C.32124 is an internal mould with a diameter of 86 mm, but the last portion is poorly preserved (Fig. 18B). The conch is, at 62 mm diameter, thinly discoidal and subevolute ( $ww/dm=0.33$ ;  $uw/dm=0.43$ ) with a high coiling rate ( $WER=2.21$ ). The whorl profile is weakly compressed ( $ww/wh=0.98$ ) and rounded trapezoidal with a nearly flat venter and a broadly rounded ventrolateral shoulder. The weakly divergent flanks are flattened; an umbilical margin is only barely visible (Fig. 18A). The sculpture has five prominent conical nodes per half volution in the outer area of the flank; these nodes show a low extension on the flank towards the umbilicus. The nodes are narrower than their interspaces. The suture line shows shallow, broadly rounded lobes on venter and flanks (Fig. 18C). The last half volution of the phragmocone has about 16 chambers ( $CLI=11$ ).

### Remarks

*Foordiceras ascetum* sp. nov. differs from *F. eicosacanthum* sp. nov. and *F. decacanthum* sp. nov. in the nearly equidimensional whorl profile ( $ww/wh=1.00$ ), which is depressed in the other two species ( $ww/wh=1.75$  in *F. eicosacanthum* and  $=1.25$  in *F. decacanthum*). Another criterion to separate *F. ascetum* from the rather similar *F. decacanthum* is in the width of the nodes; in *F. ascetum* they are only half as wide as their interspaces, while they are wider than the interspaces in *F. decacanthum*.

## Genus *Tardunautilus* Korn & Ghaderi, 2025

### Diagnosis

Genus of the family Foordiceratidae with evolute conch; whorl profile rounded triangular or rounded trapezoidal, depressed with broadly rounded venter. Sculpture with one or two rows of conical ribs near the ventrolateral shoulder. Suture line with very shallow external lobe and broadly rounded lateral lobe; without annular process (from Korn & Ghaderi 2025).

### Type species

*Tardunautilus nimius* Korn & Ghaderi, 2025; by original designation.

### Included species

NW Iran (Korn & Ghaderi 2025): *Tardunautilus nimius* Korn & Ghaderi, 2025, Wuchiapingian; *Tardunautilus minor* Korn & Ghaderi, 2025, Wuchiapingian.

Central Iran (this paper): *Tardunautilus aperimos* sp. nov., Wuchiapingian.

### Remarks

The new genus can be easily distinguished from all other genera in the assemblage from Baghuk Mountain because of its combination of a conch shape with a wide umbilicus, a rounded triangular or rounded trapezoidal whorl profile and a sculpture consisting of conical nodes. A genus with a similar morphology is *Pseudotemnocheilus*, but this is mostly known from much smaller specimens of about 40–60 mm in diameter. These smaller specimens have a much narrower umbilicus ( $uw/dm \sim 0.40$ ) compared to *Tardunautilus* ( $uw/dm \sim 0.47$ ) and a less depressed whorl profile ( $ww/wh \sim 1.30$ ) than *Tardunautilus* ( $ww/wh \sim 1.40$ – $1.80$ ). The coiling rate is much lower in *Tardunautilus* ( $WER$  below 2.00) when compared to *Pseudotemnocheilus* ( $WER$  greater than 2.25).

*Tardunautilus aperimos* sp. nov.

urn:lsid:zoobank.org:act:E08EF718-C2F6-44E2-9D15-A879DA51D394

Fig. 19; Table 13

**Diagnosis**

Species of *Tardunautilus* with thinly discoidal, evolute conch (ww/dm ~0.35; uw/dm ~0.50), weakly depressed whorl profile (ww/wh ~1.50) and low coiling rate (WER ~1.70) at a conch diameter of 60 mm. Whorl profile rounded trapezoidal with flattened venter, rounded ventrolateral shoulder, strongly divergent flanks and very small imprint zone. Sculpture with 20 conical nodes on the outer flank per revolution. Suture line with a very shallow external lobe and a very shallow lateral lobe.

**Etymology**

From the Greek ‘ἀπό’=‘from’ and ‘ἐρήμιος’=‘desert’; because of the origin of the material.

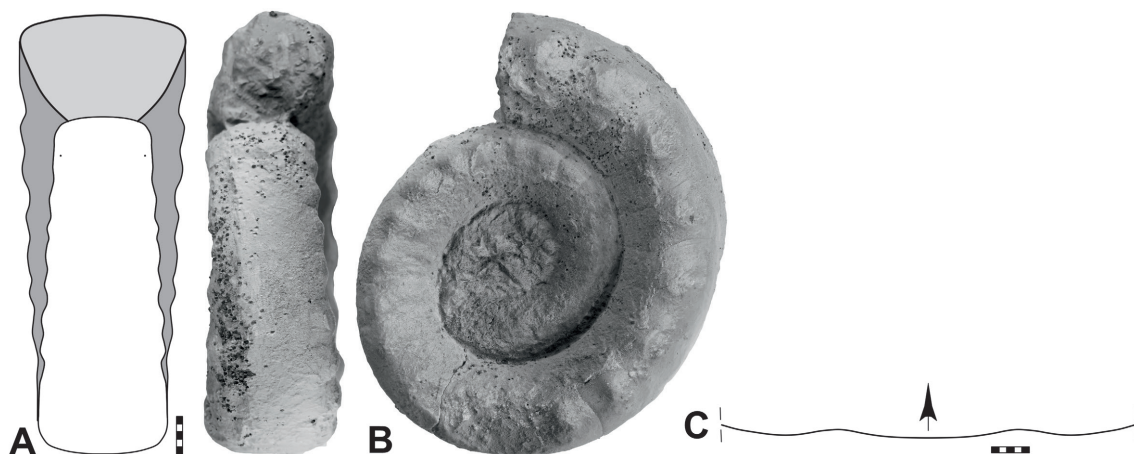
**Type material**

**Holotype**

IRAN – Esfahan Province • Baghuk Mountain; Hambast Formation, *Prototoceras* beds (early Wuchiapingian); 2012; Korn *et al.* leg.; illustrated in Fig. 19; MB.C.32125.

**Description**

Holotype MB.C.32125 is an internal mould with a conch diameter of 58 mm; it is nearly fully chambered (Fig. 19B). The conch is thinly discoidal and evolute (ww/dm=0.37; uw/dm=0.53) with a low coiling rate (WER=1.70); the whorl profile is weakly depressed (ww/wh=1.49) and rounded trapezoidal with a flattened venter, a rounded ventrolateral shoulder and strongly convex and divergent flanks (Fig. 19A). The specimen shows a whorl that only slightly embraces the preceding; the umbilical seam has a position on the venter of the preceding whorl. The sculpture consists of 20 blunt conical nodes in ventrolateral position. These nodes are slightly narrower than their interspaces. The suture line shows very shallow, broadly rounded lobes on the venter and the flank (Fig. 19C).



**Fig. 19.** *Tardunautilus aperimos* sp. nov., holotype MB.C.32125 (Korn *et al.* 2012 Coll.) from the *Prototoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Dorsal and lateral views. **C.** Suture line at dm=43.8 mm, ww=23.8 mm, wh=18.0 mm. Scale bar units=1 mm.

**Table 13.** Conch dimensions (in mm) and ratios of *Tardunautilus aperimos* sp. nov.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32125	57.9	21.5	14.4	30.5	13.5	0.37	1.49	0.53	1.70	0.06
MB.C.32125	44.5	17.1	11.4	21.8	–	0.38	1.50	0.49	–	–

### Remarks

*Tardunautilus aperimos* sp. nov. differs from the similar species *T. minor* of Julfa in the lower number of ventrolateral nodes (20 per whorl, but about 25 in *T. minor*) and the wider umbilicus (uw/dm ~0.53 in *T. aperimos*, but only ~0.47 in *T. minor*) at comparable conch diameters. *Tardunautilus nimius* from Julfa differs in the broader whorls and the double row of ventrolateral nodes.

## Family Pleuronautilidae Hyatt, 1900

### Diagnosis

Family of the superfamily Pleuronautiloidea with a commonly subquadrate or weakly depressed whorl profile; venter ranging from convex to weakly concave, ventrolateral shoulder and umbilical margin often pronounced, flanks usually weakly convergent. Sculpture with numerous ribs on the flank, sometimes with conical tubercles and more rarely with spiral ridges. An annular process is present in the advanced species (from Korn 2025).

### Included genera

*Lutonautilus* gen. nov. (Permian); *Pleuronautilus* Mojsisovics, 1882 (Triassic); *Phloioceras* Hyatt, 1884 (Triassic); *Anoploceras* Hyatt, 1900 (Triassic); *Encoiloceras* Hyatt, 1900 (Triassic); *Enoploceras* Hyatt, 1900 (Triassic); *Holconautilus* Mojsisovics, 1902 (Triassic); *Trachynautilus* Mojsisovics, 1902 (Triassic); *Sibyllonautilus* Diener, 1915 (Triassic); *Phaedrysmocheilus* Shimansky & Erlanger, 1955 (Triassic); *Arctonautilus* Sobolev, 1989 (Triassic); *Grumantoceras* Sobolev, 1989 (Triassic).

### Remarks

A detailed discussion of the Pleuronautilidae and families with similar morphology has been given by Korn (2025).

### Genus *Lutonautilus* gen. nov.

[urn:lsid:zoobank.org:act:6CCC6ECD-ED65-4A11-83AC-666B45EFC1C0](https://zoobank.org/act:6CCC6ECD-ED65-4A11-83AC-666B45EFC1C0)

New genus C – Korn 2025: 57. — Korn & Ghaderi 2025: 7, 61, 63, fig. 33.

### Type species

*Lutonautilus cratus* gen. et sp. nov.

### Diagnosis

Genus of the family Pleuronautilidae with subevolute conch; whorl profile inverted trapezoidal, weakly depressed or equidimensional with broadly rounded venter, parallel or weakly convergent flanks, rounded umbilical margin and convex or flattened umbilical wall. Sculpture with ribs on the flanks, without nodes or tubercles. Suture line with very shallow external lobe and broadly rounded lateral lobe; without annular process.

### Etymology

Named after the Lut desert (Central Iran), at which margin Baghuk Mountain is located.

### Included species

Central Iran (this paper): *Lutonautilus cratus* gen. et sp. nov., Wuchiapingian; *Lutonautilus elachus* gen. et sp. nov., Wuchiapingian; *Lutonautilus cymus* gen. et sp. nov., Wuchiapingian.

### Remarks

*Lutonautilus* gen. nov. is newly introduced here for Permian species with a conch shape and sculpture similar to some Triassic species of *Pleuronautilus*, such as *P. mosis* Mojsisovics, 1882. The main difference, however, is that *Lutonautilus* does not possess the annular lobe that is present in *Pleuronautilus*.

*Lutonautilus* gen. nov. occurs with morphologically similar species in the sections of central Iran and probably also in the Transcaucasian region. But it is also possible that the genus occurs in other regions such as the Salt Range of Pakistan; however, this can only be clarified by revising the corresponding assemblages.

*Lutonautilus cratus* gen. et sp. nov.

[urn:lsid:zoobank.org:act:FA260A86-6965-469D-96FE-D7D6B45B5F8A](https://zoobank.org/act:FA260A86-6965-469D-96FE-D7D6B45B5F8A)

Fig. 20; Table 14

New genus, new species – Korn 2025: 58, fig. 29.

### Diagnosis

Species of *Lutonautilus* gen. nov. with thinly discoidal, subinvolute conch ( $ww/dm=0.35-0.40$ ;  $uw/dm=0.35-0.40$ ), nearly equidimensional whorl profile ( $ww/wh=0.95-1.05$ ) and high to very high coiling rate ( $WER=2.20-2.35$ ) at a conch diameter of 60–80 mm. Whorl profile with gently convergent flanks; venter broadly rounded, flanks slightly flattened, umbilical margin rounded, umbilical wall flattened. Sculpture with about 25 blunt lateral ribs per volution; they begin on the outer umbilical wall and are strengthened on the ventrolateral shoulder to form elongate nodes. Suture line with a shallow external lobe and a shallow, broadly rounded lateral lobe.

### Etymology

From the Greek ‘κρατύς’= ‘strong’; because of the rather robust conch and sculpture.

### Type material

#### Holotype

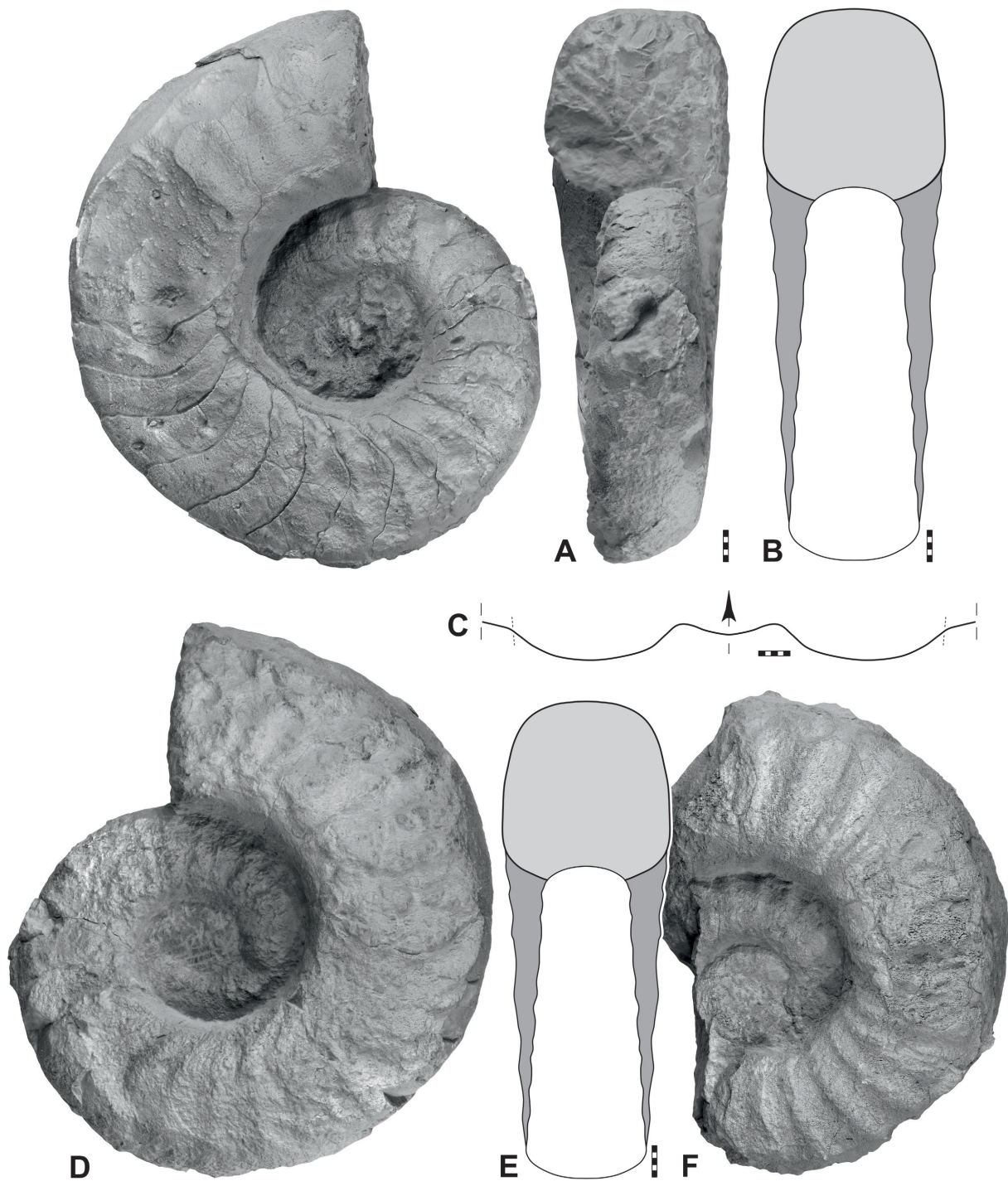
IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 20A–D; MB.C.32126.

#### Paratypes

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; 2010; Korn *et al.* leg.; illustrated in Fig. 20E–F; MB.C.32127 • 2 specimens; same data as for holotype; 2010; Korn *et al.* leg.; MB.C.32128, MB.C.32129.

### Description

Holotype MB.C.32126 is a rather complete, but somewhat corroded specimen with a conch diameter of 88 mm (Fig. 20A, D). It is almost completely chambered and only a little more than a quarter of the last whorl belongs to the body chamber. The conch is thinly discoidal and subevolute ( $ww/dm=0.33$ ;  $uw/dm=0.38$ ) with a high coiling rate ( $WER=2.17$ ). The whorl profile is almost square-shaped ( $ww/wh=0.95$ ) and shows a flatly rounded venter and a broadly rounded ventrolateral shoulder. The flanks are slightly flattened and slowly convergent; the umbilical margin is continuously rounded and the



**Fig. 20.** *Lutonautilus cratus* gen. et sp. nov. from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Holotype MB.C.32126 (Korn *et al.* 2011 Coll.), left side lateral and dorsal views. **B.** The same specimen, reconstruction of apertural view. **C.** The same specimen, suture line at  $dm=76.2$  mm,  $ww=27.0$  mm,  $wh=29.2$  mm. **D.** The same specimen, right side lateral view. **E.** Paratype MB.C.32127 (Korn *et al.* 2010 Coll.), reconstruction of apertural view. **F.** The same specimen, lateral view. Scale bar units=1 mm.

**Table 14.** Conch dimensions (in mm) and ratios of *Lutonautilus cratus* gen. et sp. nov. from Baghuk Mountain; estimated values in italics.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32126	87.6	29.0	30.5	33.2	28.1	0.33	0.95	0.38	2.17	0.08
MB.C.32128	80.5	30.4	30.0	30.0	28.0	0.38	1.01	0.37	2.35	0.07
MB.C.32127	76.1	26.7	28.6	28.1	26.5	0.35	0.93	0.37	2.35	0.07
MB.C.32129	61.6	24.3	22.4	24.4	21.2	0.39	1.08	0.40	2.32	0.05

umbilical wall is steep (Fig. 20B). The sculpture consists of about 25 blunt ribs on the flank; the ribs and their interspaces have almost the same width. These ribs already begin in the outer area of the umbilical wall and from there, they follow a weakly backwardly directed course; they extend across the flank with a broad and shallow sinus and are strengthened to form radially elongated nodes in the area of the ventrolateral shoulder. There they suddenly weaken and diminish; no ribs are visible on the venter. The suture line shows a very shallow external lobe and a broadly rounded lateral lobe (Fig. 20C). The last half whorl of the phragmocone has about 12 chambers (CLI=15).

Paratype MB.C.32127 is a fragment of a specimen with a conch diameter of 76 mm (Fig. 20F). The conch geometry is largely the same as in the holotype, but the paratype has a slightly more compressed whorl profile ( $ww/wh=0.93$ ) and a higher coiling rate ( $WER=2.35$ ). The sculpture is better preserved than in the holotype; it shows 16 rather sharp ribs on the last half volution; these ribs start on the umbilical wall and thin out at the ventrolateral shoulder. The ribs are somewhat narrower than their interspaces; they extend across the flank with a shallow sinus.

### Remarks

*Lutonautilus cratus* gen. et sp. nov. differs from the co-occurring *L. elachus* gen. et sp. nov. in the slenderer whorl profile ( $ww/wh=0.95-1.05$  in *L. cratus* but  $\sim 1.15$  in *L. elachus*), the stronger convergent flanks (nearly parallel in *L. elachus*) and the wider umbilicus ( $uw/dm=0.35-0.40$  in *L. cratus*, but only  $\sim 0.30$  in *L. elachus*). Furthermore, the ribs begin in the outer area of the umbilical wall in *L. cratus*, but at the umbilical margin in *L. elachus*.

*Lutonautilus cratus* gen. et sp. nov. differs from *L. cymus* gen. et sp. nov. in the shape of the ribs, which in *L. cratus* are almost straight on the flanks, while they extend with a concave arch in *L. cymus*. The ribs of *L. cratus* are coarse in the midflank area, while they are weakly developed in the middle of the flank in *L. cymus* and strengthened and forming nodes on the outer and inner flanks.

### *Lutonautilus elachus* gen. et sp. nov.

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Fig. 21; Table 15

*Pleuronautilus* sp. – Korn *et al.* 2021: text-fig. 17c.

### Diagnosis

Species of *Lutonautilus* gen. nov. with thickly discoidal, subevolute conch ( $ww/dm \sim 0.45$ ;  $uw/dm \sim 0.32$ ), weakly depressed whorl profile ( $ww/wh \sim 1.15$ ) and very high coiling rate ( $WER \sim 2.50$ ) at a conch diameter of 50 mm. Whorl profile with nearly parallel flanks; venter flattened, flanks slightly flattened, umbilical margin narrowly rounded, umbilical wall flat. Sculpture with about 20 blunt lateral ribs per volution. Suture line with a shallow external lobe and a shallow, broadly rounded lateral lobe.

## Etymology

From the Greek ‘ἐλαχύς’= ‘small’; because of the rather small conch.

## Type material

### Holotype

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 21A–C; MB.C.30225.

### Paratype

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; 2014; Korn *et al.* leg.; illustrated in Fig. 21D–E; MB.C.32130.

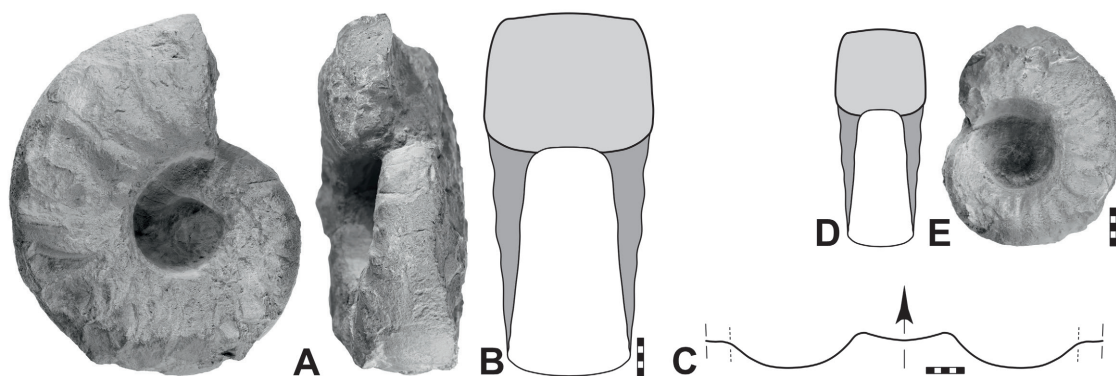
## Description

Holotype MB.C.30225 is a somewhat corroded, largely chambered specimen with a conch diameter of 48 mm (Fig. 21A). The conch is thickly discoidal and subevolute ( $ww/dm=0.47$ ;  $uw/dm=0.31$ ) with a very high coiling rate ( $WER=2.50$ ). The whorl profile is depressed rectangular ( $ww/wh=1.18$ ) with flattened venter and almost parallel flanks. Both the ventrolateral shoulder and the umbilical margin are rounded; the umbilical wall is flat and perpendicular to the plane of symmetry. The sculpture of the holotype is not well-preserved because of corrosion. However, about 20 blunt ribs are present; the ribs appear to be wider than their interspaces. These ribs start on the umbilical margin and run with very shallow sinus across the flank. They become coarser in the middle of the flank and form radially elongated nodes in the ventrolateral area. The suture line shows a very broad, shallow external lobe and a slightly deeper lateral lobe (Fig. 21C).

## Remarks

*Lutonautilus elachus* gen. et sp. nov. differs from *L. cratus* gen. et sp. nov. in the stouter whorl profile ( $ww/wh \sim 1.15$  in *L. elachus* but only 0.95–1.05 in *L. cratus*), the nearly parallel flanks (convergent in *L. cratus*), the narrower umbilicus ( $uw/dm \sim 0.30$  in *L. elachus* but 0.35–0.40 in *L. cratus*). Furthermore, the ribs begin at the umbilical margin in *P. elachus*, but in the outer area of the umbilical wall in *L. cratus*.

*Lutonautilus elachus* gen. et sp. nov. differs from *L. cymus* gen. et sp. nov. in the shape of the ribs, which in *L. elachus* are almost straight on the flanks, while they extend with a concave curve in *L. cymus*. The



**Fig. 21.** *Lutonautilus elachus* gen. et sp. nov. from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Holotype MB.C.30225 (Korn *et al.* 2011 Coll.), lateral and dorsal views. **B.** The same specimen, reconstruction of apertural view. **C.** The same specimen, suture line at  $dm=37.7$  mm,  $ww=19.4$  mm,  $wh=17.0$  mm. **D.** Paratype MB.C.32130 (Korn *et al.* 2014 Coll.), reconstruction of apertural view. **E.** The same specimen, lateral view. Scale bar units=1 mm.

**Table 15.** Conch dimensions (in mm) and ratios of *Lutonautilus elachus* gen. et sp. nov. from Baghuk Mountain.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.30225	47.6	22.5	19.1	14.6	17.5	0.47	1.18	0.31	2.50	0.08
MB.C.32130	28.6	11.9	11.2	9.8	10.2	0.42	1.06	0.34	2.42	0.09

ribs of *L. elachus* are coarse in the midflank area, while they are weakly developed in the middle of the flank in *L. cymus* and reinforced like nodes on the outer and inner flanks.

*Lutonautilus cymus* gen. et sp. nov.

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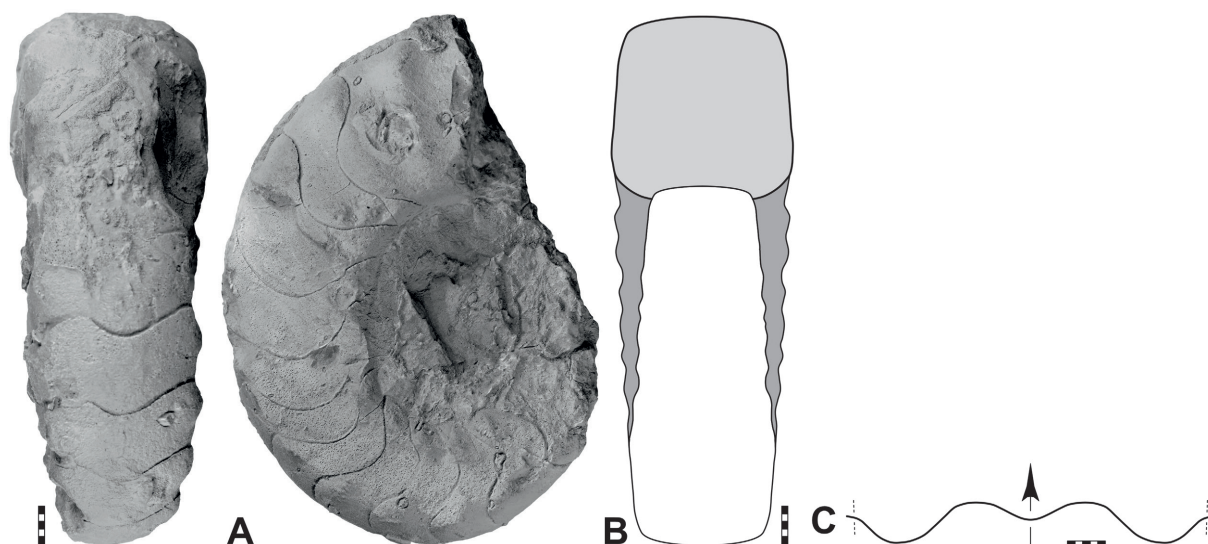
Fig. 22; Table 16

**Diagnosis**

Species of *Lutonautilus* gen. nov. with thinly discoidal, subinvolute conch ( $ww/dm \sim 0.35$ ;  $uw/dm \sim 0.35$ ), nearly quadrate whorl profile ( $ww/wh \sim 0.95$ ) and high to very high coiling rate ( $WER \sim 2.30$ ) at a conch diameter of 70–80 mm. Whorl profile with nearly parallel flanks; venter flatly rounded, flanks flattened, umbilical margin rounded, umbilical wall rounded. Sculpture with about 20 blunt lateral ribs per volution; they begin at the umbilical margin and are strengthened on the inner and outer flank to form elongate nodes. Suture line with a moderately deep external lobe and a moderately deep, broadly rounded lateral lobe.

**Etymology**

From the Greek ‘κῶμα’=‘wave’; because of the undulated suture line.



**Fig. 22.** *Lutonautilus cymus* gen. et sp. nov., holotype MB.C.32131 (Korn *et al.* 2010 Coll.) from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Ventral and lateral views. **B.** Reconstruction of apertural view. **C.** Suture line at  $ww=19.2$  mm,  $wh=20.4$  mm. Scale bar units=1 mm.

**Table 16.** Conch dimensions (in mm) and ratios of *Lutonautilus cymus* gen. et sp. nov. from Baghuk Mountain.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32132	80.2	28.5	29.7	28.7	27.8	0.36	0.96	0.36	2.34	0.06
MB.C.32131	70.7	24.8	25.6	25.5	24.0	0.35	0.97	0.36	2.29	0.06

### Type material

#### Holotype

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2010; Korn *et al.* leg.; illustrated in Fig. 22; MB.C.32131.

#### Paratypes

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; MB.C.32132 • 1 specimen; same data as for holotype; 2010; Ghaderi leg.; MB.C.32133.

### Description

Holotype MB.C.32131 is an incomplete specimen with a conch diameter of 71 mm; it is almost completely chambered (Fig. 22A). The conch is thinly discoidal and subevolute ( $ww/dm=0.35$ ;  $uw/dm=0.36$ ) with a very high coiling rate ( $WER=2.29$ ). The whorl profile is almost as wide as high ( $ww/wh=0.97$ ) and shows a flatly rounded venter and broadly rounded ventrolateral shoulders. The flanks are flattened and nearly parallel; the umbilical margin is continuously rounded (Fig. 22B). The sculpture consists of low, blunt ribs that start at the umbilical margin and extend with a shallow sinus across the flank. Most of these ribs are most coarsely developed on the inner and outer flank, where they form conical nodes, which are as wide as their interspaces. The suture line has a moderately deep, broadly rounded external lobe and a lateral lobe that is about twice as deep and broad (Fig. 22C). There are 10 septa on the last half whorl ( $CLI=18$ ).

### Remarks

*Lutonautilus cymus* gen. et sp. nov. differs from *L. cratus* gen. et sp. nov. and *L. elachus* gen. et sp. nov. in the shape of the ribs, which in *L. cymus* extend with a concave curve across the flanks, but in the other two species are almost straight. Furthermore, the ribs of *L. cymus* are weakly developed in the middle of the flank and strengthened and forming nodes on the outer and inner flanks, while those of *L. cratus* and *L. elachus* do not form nodes and are strongly developed in the middle of the flank.

Superfamily **Tainoceratoidea** Hyatt, 1883

### Diagnosis

Superfamily of the suborder Tainoceratina with a discoidal to pachyconic, subinvolute or subevolute conch. Whorl profile always with midventral longitudinal groove; in phylogenetically early species subquadrate with a distinct ventrolateral shoulder and a distinct umbilical margin, in derived species polygonal with divergent or convergent flanks. Dorsal whorl zone always very small. Sculpture with rows of ventrolateral nodes, in some species with rows of nodes on the flank. Septa simply domed; suture line depending on the whorl profile, usually with shallow lobes and low saddles (from Korn 2025).

### Included family

Tainoceratidae Hyatt, 1883 (Carboniferous to Triassic).

### Remarks

A detailed discussion of superfamily Tainoceratoidea has been given by Korn (2025).

Family **Tainoceratidae** Hyatt, 1883

**Diagnosis**

Family of the superfamily Tainoceratoidea with a discoidal to pachyconic, subinvolute or subevolute conch. Whorl profile always with midventral longitudinal groove; in early species subquadrate with a distinct ventrolateral shoulder and a distinct umbilical margin, in derived species polygonal with divergent or convergent flanks. Dorsal whorl zone always very small. Sculpture with rows of ventrolateral nodes, in some species with rows of nodes on the flank. Septa simply domed; suture line depending on the whorl profile, usually with shallow lobes and low saddles (from Korn 2025).

**Included genera**

*Tainoceras* Hyatt, 1883 (Carboniferous to Permian); *Tainionutilus* Mojsisovics, 1902 (Permian to Triassic); *Tirolonutilus* Mojsisovics, 1902 (Permian); *Tylonutilus* Pringle & Jackson, 1928 (Carboniferous to ?Permian); *Aulametacoceras* Miller & Unklesbay, 1942 (Permian); *Hexagonites* Hayasaka, 1947 (Permian); *Hunanoceras* Chao, 1954 (Permian); *Hefengnutilus* Xu, 1977 (Permian); *Clavinutilus* Zhao, Liang & Zheng, 1978 (Permian); *Eulomacoceras* Zhao, Liang & Zheng, 1978 (Permian); *Lirometacoceras* Zhao, Liang & Zheng, 1978 (Permian); *Neotainoceras* Zhao, Liang & Zheng, 1978 (Permian); *Paratainonutilus* Zhao, Liang & Zheng, 1978 (Permian); *Seironutilus* Zhao, Liang & Zheng, 1978 (Permian); *Neoclavinutilus* Liang, 1984 (Permian); *Nodonutilus* Liang, 1984 (Permian); *Nodopleuroceras* Zheng, 1984 (Permian); *Meixianlingites* Qin, 1986 (Permian); *Paratainoceras* Qin, 1986 (Permian); *Siamnutilus* Ishibashi *et al.*, 1994 (Permian); *Gujaonutilus* Miao *et al.*, 2019 (Permian); *Corotainoceras* Korn & Ghaderi, 2025 (Permian); *Epitainoceras* gen. nov. (Permian).

**Remarks**

A detailed discussion of family Tainoceratidae has been given by Korn (2025).

Genus ***Tainoceras*** Hyatt, 1883

**Type species**

*Nautilus quadrangulus* McChesney, 1860; original designation.

**Diagnosis**

Genus of the family Tainoceratidae with a subinvolute or subevolute conch; whorl profile more or less strongly depressed, ranging from subquadrate and hexagonal to polygonal with a distinct midventral longitudinal groove. Umbilical margin usually pronounced and subangular in the intermediate stage, rounded in the adult stage. Sculpture usually with two rows of conical nodes on the venter and additional rows on the flank. Suture line strongly depending on the shape of the whorl profile, usually with shallow external lobe and broadly rounded lateral lobe. Siphuncle narrow with subcentral position ventrad of septum centre.

**Included Carboniferous species**

North America (McChesney 1860; Miller *et al.* 1933; Miller & Unklesbay 1942; Lintz 1958; Tucker & Mapes 1978; Sturgeon *et al.* 1982): *Nautilus quadrangulus* McChesney, 1860, Gzhelian, Illinois; *Nautilus nodocarinatus* McChesney, 1860, Gzhelian, Illinois; *Tainoceras monilifer* Miller, Dunbar & Condra, 1933, Gzhelian, Texas; *Tainoceras rotundatum* Miller, Dunbar & Condra, 1933, Gzhelian, Texas; *Tainoceras murrayi* Miller & Unklesbay, 1942, Gzhelian, Nebraska; *Metacoceras marylandica* Lintz, 1958, Gzhelian, Maryland; *Tainoceras sexlineatum* Tucker, 1976, Kasimovian, Illinois; *Tainoceras collinsi* Sturgeon, Windle, Mapes & Hoare, 1982, Gzhelian, Ohio.

Donets Basin (Dernov 2024): *Tainoceras luxaeterna* Dernov, 2024, Kasimovian.

Western Russia (Waagen 1879): *Nautilus Trautscholdi* Waagen, 1879, Gzhelian, Moscow Basin.

### Included Permian species

North America (Swallow 1860; Hyatt 1891, 1893; Miller *et al.* 1933; Miller & Thomas 1936; Miller & Unklesbay 1942; Miller & Kemp 1947; Miller & Youngquist 1949): *Nautilus occidentalis* Swallow, 1860, Artinskian, Kansas; *Tainoceras cavatum* Hyatt, 1891, Asselian, Texas; *Tainoceras Duttoni* Hyatt, 1893, Asselian, New Mexico; *Tainoceras nebrascense* Miller, Dunbar & Condra, 1933, Artinskian, Nebraska; *Tainoceras wyomingense* Miller & Thomas, 1936, Asselian, Wyoming; *Tainoceras schellbachi* Miller & Unklesbay, 1942, Kungurian, Arizona; *Tainoceras clydense* Miller & Kemp, 1947, Kungurian, Texas; *Tainoceras unklesbayi* Miller & Youngquist, 1949, Kungurian, Texas.

Alps and Southern Europe (Gemmellaro 1889; Simić 1933; Schréter 1974; Prinoth & Posenato 2007): *Pleuromutilus Toulai* Gemmellaro, 1890, Wordian, Sicily; *Tainoceras zmajevatense* Simić, 1933; Wuchiapingian, Serbia; *Tainoceras bükkense* Schréter, 1974; Changhsingian, Bükk Mountains; *Tainoceras crassicostatum* Schréter, 1974; Changhsingian, Bükk Mountains; *Tainoceras balestense* Prinoth & Posenato, 2007, Changhsingian, Dolomites; *Tainoceras malsineri* Prinoth & Posenato, 2007, Changhsingian, Dolomites.

NW Iran (Korn & Ghaderi 2025): *Tainoceras admonens* Korn & Ghaderi, 2025, Wuchiapingian; *Tainoceras latecostatum* Korn & Ghaderi, 2025, Wuchiapingian; *Tainoceras unitum* Korn & Ghaderi, 2025, Changhsingian.

Central Iran (this paper): *Tainoceras hystatum* sp. nov., Changhsingian.

Pakistan (Reed 1931, 1944): *Tainoceras Noetlingi* var. *subglobosa* Reed, 1931, Wuchiapingian, Salt Range; *Tainoceras comptum* Reed, 1944, Changhsingian, Salt Range; *Tainoceras debile* Reed, 1944, Changhsingian, Salt Range; *Tainoceras trimuense* Reed, 1944, Wuchiapingian, Salt Range.

South China (Kayser 1883; Chao 1954; Zheng 1984): *Nautilus mingshanensis* Kayser, 1883, Wuchiapingian, Jiangxi; *Nautilus orientalis* Kayser, 1883, Wuchiapingian, Jiangxi; *Tainoceras changlingpuense* Chao, 1954, Roadian, Hunan; *Tainoceras hunanense* Chao, 1954, Roadian, Hunan; *Tainoceras gibbosum* Zheng, 1984, Changhsingian, Guizhou; *Tainoceras guizhouense* Zheng, 1984, Changhsingian, Guizhou; *Tainoceras lateronodosum* Zheng, 1984, Changhsingian, Guizhou.

Japan (Hayasaka 1957, 1962; Ehiro & Araki 1997): *Tainoceras abukumense* Hayasaka, 1957, Capitanian; *Tainoceras kitakamiense* Hayasaka, 1962, Roadian; *Tainoceras carinatum* Ehiro & Araki, 1997, Capitanian.

### Remarks

*Tainoceras* is considered one of the cardinal genera within the order Nautilida; it stands as a typical representative for the family, superfamily and suborder named after it. Around 40 species of *Tainoceras* have been described so far and it has a long stratigraphic range, extending from the latest Carboniferous to the latest Permian. Nevertheless, only a few efforts have been made to clearly define the genus in its morphological range. While Miller *et al.* (1933: 147) and Miller & Youngquist (1949: 80) gave detailed characteristics of the genus, Shimansky (1962b: 121) and Kummel (1964: K413) characterised the genus *Tainoceras* with just one sentence: “Like *Metacoceras* but with a double row of nodes on the venter.” Sturgeon *et al.* (1997: 29) became more precise: “Similar to *Metacoceras* but possessing two ventral rows of nodes or ribs separated by a median sulcus.” They gave a more detailed outline of the characters typically present in *Tainoceras*.

It is apparent that a simple definition is not adequate to define the rather complex genus, especially in view of the fact that other tainoceratids have been described in recent decades. A precise morphological delineation and taxonomic interpretation of *Tainoceras* requires a discussion of several questions:

- (1) What are the morphological characters that can be used to clearly distinguish *Tainoceras* from other genera?
- (2) Were the tainoceratids (*Tainoceras* and derived Late Permian genera) really a monophyletic unit?
- (3) Did long-lived evolutionary lines with stable morphologies exist within *Tainoceras*, or did similar conch shapes and sculptures emerge iteratively?

The first question is not easy to answer. The previously used feature of the double row of nodes on the venter cannot be applied universally as the cardinal separating tool, as some species possess only one row of ventral nodes or no ventral nodes at all in the adult stage (e.g., the Late Carboniferous *T. collinsi* Sturgeon, Windle, Mapes & Hoare, 1982 and *T. marylandicum* (Lintz, 1858) and the Late Permian *T. balestense* Prinoth & Posenato, 2007). Rather, other assisting features must be used, such as the presence of the midventral groove. It should be made clear that in *Tainoceras* this groove indents a broadly rounded venter. This is in contrast to genera such as *Metacoceras*, in which a concave venter, if present at all, always occurs as a depression of the entire venter.

The second question is easier to answer. Although the morphological spectrum of *Tainoceras* is rather broad and somewhat variable, the combination of several morphological characters, such as the presence of the midventral groove, the rows of nodes on the venter and ventrolateral shoulder and the pronounced umbilical margin, indicate a monophyletic series of forms. Because of the complexity of the morphology, a polyphyletic origin of *Tainoceras* can be excluded.

To answer the third question, it is necessary to evaluate the characters of conch and sculpture with regard to their variation within the genus *Tainoceras*. The following characters have proven to be particularly variable (with some representative examples):

- General shape of the whorl profile: it can range from rectangular (*T. nebrascense*) to octagonal or polygonal (*T. clydense*, *T. admonens*); the ww/wh ratio can range from approximately equidimensional (*T. cavatum*) to weakly depressed (*T. schellbachi*, *T. admonens*) and moderately depressed (*T. duttoni*).
- General shape of the venter: in all of the species, the venter is more or less tripartite, but the degree of tripartition varies from weak with nearly convex venter (*T. cavatum*) to very strong with clearly defined ventrolateral applanation forming a tectiform venter (*T. clydense*, *T. duttoni*).
- Position and shape of the flanks: the flanks can be divergent (*T. quadrangulum*, *T. admonens*), parallel (*T. quadrangulum*) or convergent (*T. duttoni*). They can be flattened (*T. cavatum*) or weakly concave (*T. duttoni*, *T. admonens*).
- Shape of the umbilical margin and umbilical wall: while the umbilical margin is usually narrowly rounded (*T. nebrascense*) or subangular (*T. duttoni*), the umbilical wall ranges from oblique (*T. cavatum*, *T. clydense*) to steep (*T. duttoni*) and from weakly convex (*T. nebrascense*) to flattened (*T. duttoni*, *T. admonens*).
- Width and depth of the midventral groove: the groove can vary from narrow (*T. nebrascense*, *T. clydense*) to wide (*T. schellbachi*, *T. admonens*) and from shallow (*T. collinsi*, *T. cavatum*, *T. admonens*) to deep (*T. duttoni*, *T. wyomingense*).
- Formation of the ventral nodes: ventral sculptural elements may appear as short plications (*T. collinsi*), small tubercles (*T. monilifer*, *T. nodocarinatum*, *T. admonens*), or also large conical, blunt (*T. clydense*) or pointed nodes or spines (*T. quadrangulum*, *T. schellbachi*). Some species possess coarse ventral radial ribs (*T. unklesbavi*). The ventral tubercles can be arranged symmetrically (*T. nebrascense*) or alternating on the right and left side of the midventral groove (*T. monilifer*).
- Formation of the ventrolateral nodes: ventrolateral sculptural elements are present in most of the species; they range from being small tubercles (*T. nebrascense*, *T. admonens*) to large conical nodes or spines (*T. monilifer*, *T. schellbachi*).

- Formation of lateral ribs: lateral ribs do not occur in many of the North American species, but are present in species from other regions (*T. debile*, *T. admonens*).
- Formation of the umbilical nodes: umbilical sculptural elements are present in some species; they range from being small tubercles (*T. clydense*) to large conical nodes (*T. schellbachi*).

The list of mostly bipolar character pairs shows numerous theoretical possible combinations; however, covariation is very common and some of the characters often appear simultaneously.

*Tainoceras hystatum* sp. nov.

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Fig. 23; Table 17

**Diagnosis**

Species of *Tainoceras* with thinly discoidal, evolute conch (ww/dm ~0.44; uw/dm ~0.32), weakly depressed whorl profile (ww/wh ~1.05) and extremely high coiling rate (WER ~2.55) at a conch diameter of 40 mm. Whorl profile octagonal with shallow longitudinal ventral groove. Sculpture with two rows of tubercles on the ventrolateral shoulder and one row on the umbilical margin. Suture line undulating with very shallow lobes and low saddles.

**Etymology**

From the Greek ‘ὕστατος’=‘latest’; because the species is the stratigraphically latest of the nautiloids from Baghuk Mountain.

**Type material**

**Holotype**

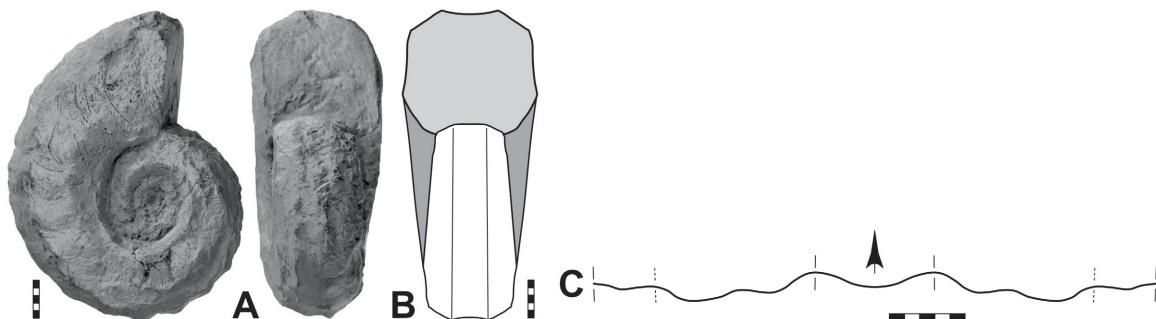
IRAN – **Esfahan Province** • Baghuk Mountain section H; Hambast Formation, *Paratirolites* beds (late Changhsingian), 0.40 m below top; 2013; Korn *et al.* leg.; illustrated in Fig. 23; MB.C.32134.

**Paratype**

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; 2011; Korn *et al.* leg.; MB.C.32135.

**Description**

Holotype MB.C.32134 is a somewhat corroded specimen with a conch diameter of 40 mm (Fig. 23A). It is fairly well preserved only on its left side as an internal mould. The specimen is completely chambered.



**Fig. 23.** *Tainoceras hystatum* sp. nov., holotype MB.C.32134 (Korn *et al.* 2013 Coll.) from the *Paratirolites* beds of the Hambast Formation at Baghuk Mountain. **A.** Lateral and dorsal views. **B.** Reconstruction of apertural view. **C.** Suture line at dm=32.1 mm, ww=18.2 mm, wh=12.3 mm. Scale bar units= 1 mm.

**Table 17.** Conch dimensions (in mm) and ratios of *Tainoceras hystatum* sp. nov.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32134	41.2	17.7	16.2	13.6	15.4	0.43	1.09	0.33	2.55	0.05
MB.C.32135	29.5	11.5	11.0	9.2	–	0.39	1.05	0.31	–	–

The conch is thinly discoidal and subevolute ( $ww/dm=0.43$ ;  $uw/dm=0.33$ ) with an extremely high coiling rate ( $WER=2.55$ ). The whorl profile is generally octagonal and slightly depressed ( $ww/wh=1.09$ ). It has a flattened venter with a shallow longitudinal depression; the ventrolateral shoulder is subangular and the flanks are almost flat and parallel. The umbilical margin is prominent and the umbilical wall is oblique and flat. The areas between the angular margins of the whorl profile are flattened (Fig. 23B).

The sculpture consists of three rows of tubercles, one on the umbilical margin, one on the ventrolateral shoulder and one delimiting the midventral longitudinal groove. The first and the last ones are only very weakly developed; the middle one is much stronger and consists of blunt conical nodes. They are connected to the tubercles on the umbilical wall by very low ribs. The suture line is strongly dependent on the whorl profile; it has shallow lobes at the flattened areas and low saddles at the pronounced margins (Fig. 23C).

### Remarks

*Tainoceras hystatum* sp. nov. shows a morphology of conch and sculpture that can be described as conservative. Even some of the Late Carboniferous species, such as the type species *T. quadrangulum*, show an octagonal shape of the whorl profile with two rows of tubercles each adjacent to the median longitudinal groove. However, *T. quadrangulum* has coarser ventrolateral nodes and a narrower umbilicus ( $uw/dm < 0.30$ ) than *T. hystatum* ( $uw/dm > 0.30$ ).

*Tainoceras hystatum* sp. nov. differs by its wider umbilicus and particularly by the parallel flanks, which are either convergent or divergent in many other species of the genus *Tainoceras*. Another distinguishing feature is the shape of the tubercles, which are much smaller in *T. hystatum* than in most other species.

Genus *Epitainoceras* gen. nov.

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New genus D – Korn 2025: 61. — Korn & Ghaderi 2025: 64, 72, 74.

### Type species

*Epitainoceras lutense* gen. et sp. nov.

### Diagnosis

Genus of the family Tainoceratidae with subinvolute or subevolute conch; whorl profile depressed and polygonal with a shallow or broad midventral longitudinal groove. Umbilical margin pronounced and narrowly rounded, flanks convergent. Sculpture with one row of nodes on the ventrolateral shoulder. Suture line strongly depending on the shape of the whorl profile, with rounded V-shaped external lobe and broadly rounded lateral lobe.

### Etymology

From the Greek ‘ἐπί’=‘on, above’; referring to the late occurrence of this tainoceratid genus.

### Included species

Transcaucasia (Abich 1878): *Nautilus dorso plicatus* Abich, 1878, Wuchiapingian, Azerbaijan.

Central Iran (this paper): *Epitainoceras lutense* gen. et sp. nov., Wuchiapingian.

## Remarks

*Epitainoceras* gen. nov. is a genus with a morphology similar to some species of *Tainoceras*, but with a much weaker sculpture. In contrast to *Tainoceras*, which has at least two rows of nodes or tubercles in the ventrolateral region and sometimes another row of nodes on the inner flank, *Epitainoceras* has only one row of nodes, located immediately adjacent to the median longitudinal groove on each side. With a simplification of the sculpture, the new genus may be derived from *Tainoceras*. *Corotainoceras* also shows simplification of the sculpture, but differs from *Epitainoceras* in the absence of ventrolateral nodes and the presence of very coarse dorsolateral nodes.

*Epitainoceras lutense* gen. et sp. nov.

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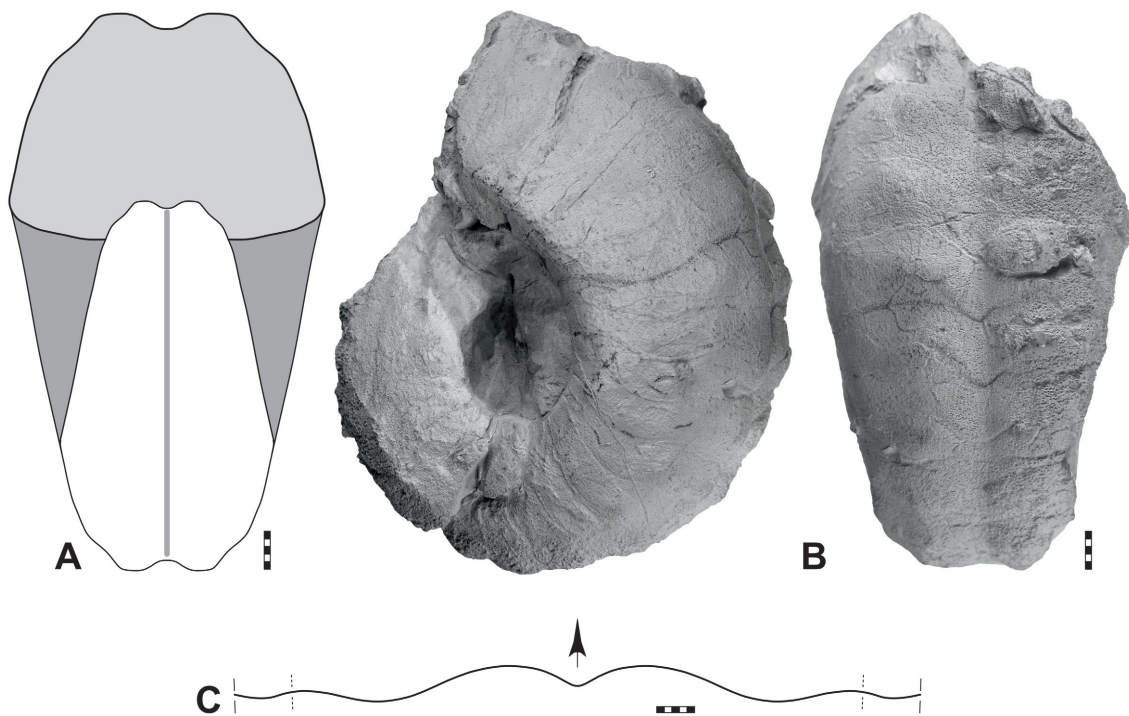
Fig. 24; Table 18

## Diagnosis

Species of *Epitainoceras* gen. nov. with thickly discoidal, subinvolute conch (ww/dm  $\sim$ 0.55; uw/dm  $\sim$ 0.25) and weakly depressed whorl profile (ww/wh  $\sim$ 1.35) and very high coiling rate (WER  $\sim$ 2.35) at a conch diameter of 70 mm. Whorl profile polygonal with convergent flanks; venter tectiform with broad longitudinal midventral groove, flanks flattened, umbilical margin narrowly rounded. Sculpture with about 15 coarse ventrolateral, transversely elongated nodes per volution. Suture line with a small, rounded V-shaped external lobe, a broadly rounded, very shallow lateral lobe and a very shallow umbilical lobe.

## Etymology

Named after the Lut desert (Central Iran), at which margin Baghuk Mountain is located.



**Fig. 24.** *Epitainoceras lutense* gen. et sp. nov., holotype MB.C.32136 (Korn *et al.* 2011 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Lateral and ventral views. **C.** Suture line at dm=63.6 mm, wh=28.2 mm. Scale bar units = 1 mm.

**Table 18.** Conch dimensions (in mm) and ratios of *Epitainoceras lutense* gen. et sp. nov. from Baghuk Mountain; reconstructed dimensions and ratios in italics.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32136	74.6	<i>41.6</i>	30.2	17.8	26.0	<i>0.56</i>	<i>1.38</i>	0.24	2.36	0.14
MB.C.32137	<i>73.0</i>	<i>38.5</i>	29.0	20.5	25.5	<i>0.53</i>	<i>1.33</i>	<i>0.28</i>	2.36	0.12

**Type material****Holotype**

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Araxoceras* beds (early Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 24; MB.C.32136.

**Paratype**

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; MB.C.32137.

**Description**

Holotype MB.C.32136 is a corroded phragmocone specimen with a diameter of 75 mm (Fig. 24B). It allows the conch form, sculpture and suture line to be studied, but some conch dimensions can only be estimated. The conch is thickly discoidal and subinvolute ( $ww/dm \sim 0.55$ ;  $uw/dm \sim 0.25$ ) with a very high coiling rate ( $WER \sim 2.35$ ). The whorl profile is slightly depressed ( $ww/wh \sim 1.35$ ) and widest at the narrowly rounded umbilical margin. The venter possesses a moderately wide median groove; the ventrolateral shoulder is flattened and oblique, the flanks are weakly flattened and convergent and the umbilical margin is narrowly rounded (Fig. 24A).

Because of partial corrosion of the specimen, the sculpture cannot be examined in detail. It consists of two rows of nodes arranged on each side of the ventrolateral shoulder. The ventral row has nodes that are elongated in a lateral direction to form short ribs; the dorsal row consists of much weaker, circular nodes.

The suture line of the holotype has a shallow, broadly V-shaped external lobe, a low and broadly rounded, slightly asymmetric ventrolateral saddle, a shallow and very wide lateral lobe and a very shallow and small lobe on the umbilical wall (Fig. 24C). The last half volution has 15 phragmocone chambers ( $CLI=12$ ).

**Remarks**

*Epitainoceras lutense* gen. et sp. nov. is similar to the Transcaucasian species *E. dorsoplicatum* comb. nov., but differs in having a much wider midventral groove and significantly larger ventral nodes. These nodes are laterally elongated in *E. lutense*, whereas they are simply conical in *E. dorsoplicatum*.

Suborder **Liroceratina** Flower, 1955

**Diagnosis**

Suborder of the order Nautilida, in which an umbilical margin is formed early in ontogeny; advanced species may regress this character. Conch usually pachyconic and rarely discoidal or globular, subinvolute to involute. Juvenile whorl profile circular. Adult whorl profile usually circular or depressed oval without distinct ventrolateral shoulder in the phylogenetically early species, showing modifications during evolution (inverted trapezoidal with convergent flanks and flattened venter). Dorsal whorl zone always present, small to moderately deep. Juvenile sculpture with spiral lines that may be restricted to the umbilical area in the phylogenetically early species; adult sculpture usually lacking except for spiral lines in some species. Septa simply domed in the early species; with dorsal inflexion in advanced species

and with corrugated septa in two derived clades. Suture line depending on the whorl profile, usually with shallow lobes and low saddles; with distinct lobes in two clades (from Korn 2025).

#### **Included superfamilies**

Liroceratoidea Hyatt, 1900 (Carboniferous to Triassic); Ehippioceratoidea Miller & Youngquist, 1949 (Carboniferous to Permian); Clydonautiloidea Hyatt, 1900 (Triassic to Jurassic).

#### **Remarks**

A discussion of the suborder Liroceratina has been given by Korn (2025).

### Superfamily **Liroceratoidea** Hyatt, 1900

#### **Diagnosis**

Superfamily of the suborder Liroceratina with a pachyconic and rarely discoidal or globular, subinvolute to involute conch. Whorl profile usually circular or depressed oval without distinct ventrolateral shoulder; in some species with a pronounced but rounded ventrolateral shoulder. Dorsal whorl zone usually small to moderately deep. Juvenile sculpture in the early species with spiral lines that may be restricted to the umbilical area; derived species are often smooth. Suture line very simple, almost straight across flanks and venter (from Korn 2025).

#### **Included families**

Liroceratidae Miller & Youngquist, 1949 (Carboniferous to Triassic); Coloceratidae Hyatt, 1893 [homonym, synonym of Liroceratidae Miller & Youngquist, 1949]; Paranautilidae Kummel in Flower & Kummel, 1950 (Triassic); Permonautilidae Barskov & Shilovsky, 2014 (Permian); Planetoceratidae Korn, 2025 (Carboniferous); Julfanautilidae Korn & Ghaderi, 2025 (Permian).

#### **Remarks**

A discussion of the superfamily Liroceratoidea has been given by Korn (2025).

### Family **Liroceratidae** Miller & Youngquist, 1949

#### **Diagnosis**

Family of the superfamily Liroceratoidea with a usually pachyconic or globular, subinvolute to subevolute conch. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter form a continuous arch in the early species, the venter can be flattened or concave in advanced species. Umbilical margin rounded; umbilical wall usually convex. Ornament usually consisting of fine growth lines; spiral lines occur in some genera. Septum simple in shape, concavely domed; suture line very simple, almost straight across flanks and venter or with small lobes and saddles (from Korn 2025).

#### **Included genera**

*Solenoceras* Hyatt, 1884 (homonym of *Solenoceras* Conrad, 1860, objective synonym of *Coelogasteroceras*); *Coelogasteroceras* Hyatt, 1893 (Carboniferous to Permian); *Coloceras* Hyatt, 1893 [homonym of *Coloceras* Taschenberg, 1882, synonym of *Liroceras* Teichert, 1940]; *Stearoceras* Hyatt, 1893 (Carboniferous to Permian); *Peripetoceras* Hyatt, 1894 (Carboniferous to Permian); *Potoceras* Hyatt, 1894 (Carboniferous); *Nannoceras* Hyatt, 1894 (nomen nullum, synonym of *Peripetoceras*); *Conradiceras* Cossmann, 1900 (objective synonym of *Coelogasteroceras*); *Liroceras* Teichert, 1940 (Carboniferous to Permian); *Condraoceras* Miller, Lane & Unklesbay, 1947 (Carboniferous)

to Permian); *Periptoceras* Chao, 1954 (nomen nullum, synonym of *Peripetoceras*); *Hemiliroceras* Ruzhencev & Shimansky, 1954 (Carboniferous to Permian); *Bistrialites* Turner, 1954 (Carboniferous); *Pseudophacoceras* Turner, 1966 (Carboniferous); *Neobistrialites* Tucker, Mapes & Aronoff, 1978 (Carboniferous); *Jianoceras* Ma, 1997 (Permian); *Nemdoceras* Barskov & Shilovsky, 2014 (Permian); *Paraliroceras* Barskov & Shilovsky, 2014 (Permian); *Tatianautilus* Barskov & Shilovsky, 2014 (Permian); *Leniceras* Leonova & Shchedukhin, 2020 (Permian); *Shikhanonautilus* Leonova & Shchedukhin, 2020 (Permian); *Thyoceras* Leonova & Shchedukhin, 2020 (Permian); *Celeroliroceras* Korn & Ghaderi, 2025 (Permian); *Perunautilus* Crick & Sobolev, 1994 (Triassic); *Tomponautilus* Sobolev, 1989 (Triassic).

### Remarks

A discussion of the family Liroceratidae has been given by Korn (2025).

### Genus *Liroceras* Teichert, 1940

#### Type species

*Coloceras liratum* Girty, 1911; original designation.

#### Diagnosis

Genus of the family Liroceratidae with pachyconic to globular, involute or subinvolute conch; umbilicus closed by a plug in some species. The first whorl is 10–20 mm in diameter with a very small umbilical foramen; the conch is rapidly increasing in height with a high coiling rate (WER usually higher than 2.50). Whorls weakly embracing, their profile ranges from reniform to nearly circular. Juvenile conch with longitudinal ridges or lines; adult ornament with growth lines with a fairly deep ventral sinus and spiral lines in some species. Septa without inflexions, slightly concave. Suture line simple, nearly straight with a shallow, broadly rounded internal lobe. The siphuncle has a position between the centre of the septum and the venter (after Gordon 1965; Shimansky 1967).

#### Included Carboniferous species

North America (Shumard & Swallow 1858; Miller & Gurley 1897; Girty 1911; Miller *et al.* 1933; Newell 1936; Unklesbay 1962; Gordon 1965): *Nautilus Missouriensis* Swallow, 1858, Bashkirian, Missouri; *Solenochilus henryvillense* Miller & Gurley, 1897, Viséan, Indiana; *Coloceras liratum* Girty, 1911, Moscovian, Oklahoma; *Coloceras liratum* var. *obsoletum* Girty, 1911, Moscovian, Oklahoma; *Coloceras greenei* Miller, Dunbar & Condra, 1933, Kasimovian, Oklahoma; *Coloceras milleri* Newell, 1936, Kasimovian, Kansas; *Coloceras reticulatum* Miller & Owen, 1937, Kasimovian, Oklahoma; *Liroceras patulum* Unklesbay, 1962, Bashkirian, Arkansas; *Liroceras bicostatum* Gordon, 1965, Serpukhovian, Arkansas.

British Isles (Foord 1891; Hind 1910; Turner 1954; Ramsbottom & Moore 1961): *Coelonautilus Derbiensis* Foord, 1891, Viséan, Derbyshire; *Coelonautilus Derbiensis* var. *globulare* Foord, 1891, Viséan, Isle of Man; *Solenocheilus globosus* Hind, 1910, Bashkirian, Lancashire; *Liroceras lunense* Turner, 1954, Serpukhovian, Yorkshire; *Liroceras leitrimense* Ramsbottom & Moore, 1961, Viséan, Ireland.

Central Europe (Trenkner 1868; Hyatt 1894; Miller *et al.* 1933; Schmidt 1951): *Nautilus grundensis* Trenkner, 1868, Viséan, Harz Mountains; *Coloceras globatum* Hyatt, 1894, Viséan, Belgium; *Coloceras hyatti* Miller, Dunbar & Condra, 1933, Viséan, Belgium; *Liroceras oclusor* Schmidt, 1951, Viséan, Harz Mountains; *Liroceras schaelkense* Schmidt, 1951, Viséan, Rhenish Mountains.

North Africa (Korn & Klug 2023): *Liroceras karaouii* Korn & Klug, 2023, Viséan, Anti-Atlas; *Liroceras vermis* Korn & Klug, 2023, Serpukhovian, Anti-Atlas.

Western Russia (Eichwald 1857; Shimansky 1967): *Nautilus excentricus* Eichwald, 1857, Serpukhovian, Western Russia; *Liroceras fornicatum* Shimansky, 1967, Serpukhovian, Western Russia; *Liroceras devjatovense* Shimansky, 1967, Moscovian, Moscow Basin.

Urals (Shimansky 1967): *Liroceras praelunense* Shimansky, 1967, Viséan, North Urals; *Liroceras ruzhencevi* Shimansky, 1967, Serpukhovian, South Urals.

North China (Ruan & Zhou 1987): *Liroceras reniforme* Ruan & Zhou, 1987, Bashkirian, Ningxia.

### Included Permian species

North America (Hyatt 1893): *Coloceras globulare* Hyatt, 1893, Artinskian, Texas.

Central and Southern Europe (Gemmellaro 1889; Prinoth & Posenato 2007): *Endolobus salomonensis* Gemmellaro, 1889, Wordian, Sicily; *Liroceras gardenense* Prinoth & Posenato, 2007, Changhsingian, Dolomites.

Western Russia, Urals (Yakovlev 1899; Kruglov 1928; Barskov *et al.* 2014; Leonova & Shchedukhin 2020): *Asymptoceras korulkense* Yakovlev, 1899, Sakmarian, South Urals; *Coloceras* (?) *sarvaensis* Kruglov, 1928, Sakmarian (?), South Urals; *Coloceras abichi* var. *tastubense* Kruglov, 1928, Sakmarian (?), South Urals; *Liroceras volgense* Barskov & Shilovsky, 2014, Roadian, Western Russia; *Liroceras shakhtauense* Leonova & Shchedukhin, 2020, Asselian or Sakmarian, South Urals.

NW Iran (Korn & Ghaderi 2025): *Liroceras reticulum* Korn & Ghaderi, 2025, Wuchiapingian.

Central Iran (this paper): *Liroceras leptum* sp. nov., Wuchiapingian.

Pakistan (Reed 1944): *Liroceras bakhense* Reed, 1944, Wuchiapingian, Salt Range.

South China (Chao 1940, 1954; Xu 1977; Zhao *et al.* 1978; Liang 1984; Wu & Kuang 1992): *Coloceras sinense* Chao, 1940, Kungurian, Hunan; *Peripetoceras hsueyuechiani* Chao, 1954, Kungurian, Hunan; *Liroceras orientale* Chao, 1954, Kungurian, Hunan; *Ephippioceras hunanense* Chao, 1954, Kungurian, Hunan; *Liroceras didmyoaurise* Xu, 1977, Kungurian, Hunan; *Liroceras meishanense* Zhao, Liang & Zheng, 1978, Changhsingian, Zhejiang; *Liroceras chenxianense* Liang, 1984, Changhsingian, Hunan; *Liroceras lichuanense* Wu & Kuang, 1992, Changhsingian, Hubei.

Indo-Pacific (Haniel 1915): *Nautilus Molengraaffi* Haniel, 1915, Wuchiapingian, Timor.

Madagascar (Vaillant-Couturier Treat 1933): *Nautilus waterloti* Vaillant-Couturier Treat, 1933, Wuchiapingian.

### Remarks

The genus *Liroceras* was introduced by Teichert (1940) for those Carboniferous and Permian nautiloids that were previously mostly included in the genus *Coloceras* Hyatt, 1893. The name *Coloceras* had already been used by Taschenberg (1882) as a subgenus for recent Mallophaga.

*Liroceras* has a stratigraphic range from the Viséan to the Changhsingian and is represented by species at almost all stages of this long interval. At the same time, *Liroceras* is geographically widespread, both in the Carboniferous and in the Permian. *Liroceras* is also known from different facies areas; Early

Carboniferous species are known from shallower and deeper areas of the shelf. In the Late Permian, the genus was more common in the shallower areas of the sea, as suggested by the occurrences at Julfa, where it co-occurs with the morphologically similar and closely related genus *Permonautilus*.

*Liroceras leptum* sp. nov.

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Fig. 25; Table 19

**Diagnosis**

Species of *Liroceras* with thinly pachyconic, subinvolute conch (ww/dm ~0.68; uw/dm ~0.17), moderately depressed whorl profile (ww/wh ~1.45) and very high coiling rate (WER ~2.30) at a conch diameter of 40 mm. Whorl profile with broadly arched venter and flanks, broadly rounded umbilical margin, convex umbilical wall and moderately deep imprint zone (IZR ~0.28). Without sculpture. Suture line with very shallow and wide external, lateral and umbilical lobes.

**Etymology**

From Greek ‘λεπτός’= ‘small, weak’; because of the rather small-sizes material.

**Type material**

**Holotype**

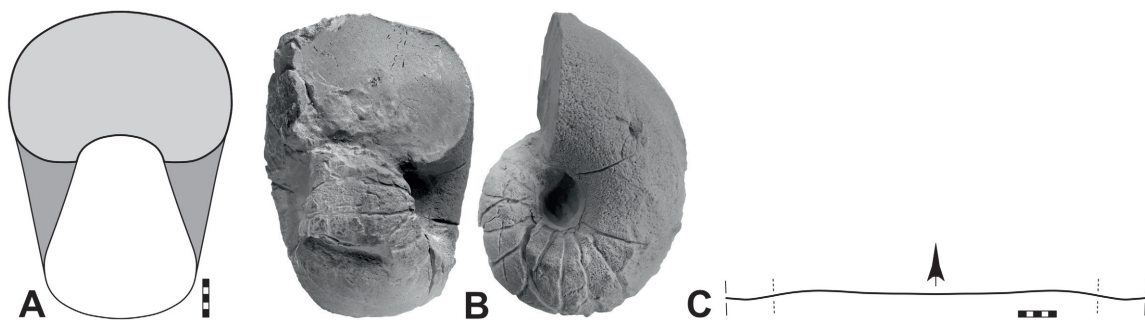
IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 25; MB.C.32138.

**Paratypes**

IRAN – **Esfahan Province** • 2 specimens; same data as for holotype; 2010; Korn *et al.* leg.; MB.C.32139, MB.C.32140.

**Description**

The best-preserved specimen is the obliquely deformed small holotype MB.C.32138 with a conch diameter of 41 mm (Fig. 25B). The conch geometry can only be reconstructed. According to this, the conch is thinly pachyconic and subinvolute (ww/dm=0.68; uw/dm=0.17) with a very high coiling rate (WER=2.31) and a moderately wide whorl overlap (IZR=0.28). The whorl profile is weakly depressed (ww/wh=1.44) with a broadly convex venter that merges continuously with the flanks the flanks. The umbilical margin is broadly rounded and the umbilical wall is convex (Fig. 25A). The suture line is



**Fig. 25.** *Liroceras leptum* sp. nov., holotype MB.C.32138 (Korn *et al.* 2011 Coll.) from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Dorsal and lateral views. **C.** Suture line at dm=25.8 mm, ww=21.2 mm, wh=12.8 mm. Scale bar units = 1 mm.

**Table 19.** Reconstructed conch dimensions (in mm) and ratios of *Liroceras leptum* sp. nov. from Baghuk Mountain.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32139	53.0	34.0	23.0	10.5	17.0	0.64	1.48	0.20	2.17	0.26
MB.C.32138	41.0	28.0	19.5	7.0	14.0	0.68	1.44	0.17	2.31	0.28

nearly straight and shows very broad and shallow lobes on the area consisting of venter and flanks and the umbilical wall (Fig. 25C).

### Remarks

The material of the new species does not show whether the umbilical extensions characteristic of the genus was present in the adult stage; therefore, assignment to *Liroceras* is not entirely certain. *L. leptum* sp. nov. differs from the other Late Permian species of the genus in the opened umbilicus and the slenderer conch; ww/dm ratio for a conch diameter of 40–50 mm is below a value of 0.70, but in the other species it is above 0.80.

Genus *Paraliroceras* Barskov & Shilovsky in Barskov *et al.*, 2014

### Type species

*Paraliroceras kazanicum* Barskov & Shilovsky in Barskov *et al.*, 2014; original designation.

### Diagnosis

Genus of the family Liroceratidae with pachyconic, subinvolute conch. The conch is rapidly increasing in height with a high coiling rate (WER=2.30–2.90). Whorls moderately embracing, whorl profile reniform; umbilical margin pronounced, narrowly rounded. Adult ornament with fine growth lines with a fairly deep ventral sinus. Septa without inflexions, slightly concave. Suture line simple, nearly straight to straight with a shallow, broadly rounded internal lobe. The siphuncle has a position between the centre of the septum and the venter.

### Included species

Western Russia (Barskov *et al.* 2014): *Paraliroceras kazanicum* Barskov & Shilovsky in Barskov *et al.*, 2014, Roadian.

Central Iran (this paper): *Paraliroceras macrogaster* sp. nov., Wuchiapingian.

### Remarks

*Paraliroceras* is similar to *Liroceras* and differs mainly in the pronounced umbilical margin, which is narrowly rounded in *Paraliroceras* but usually broad and evenly rounded in *Liroceras*. The species of *Paraliroceras* are more widely umbilicate than most known species of *Liroceras*.

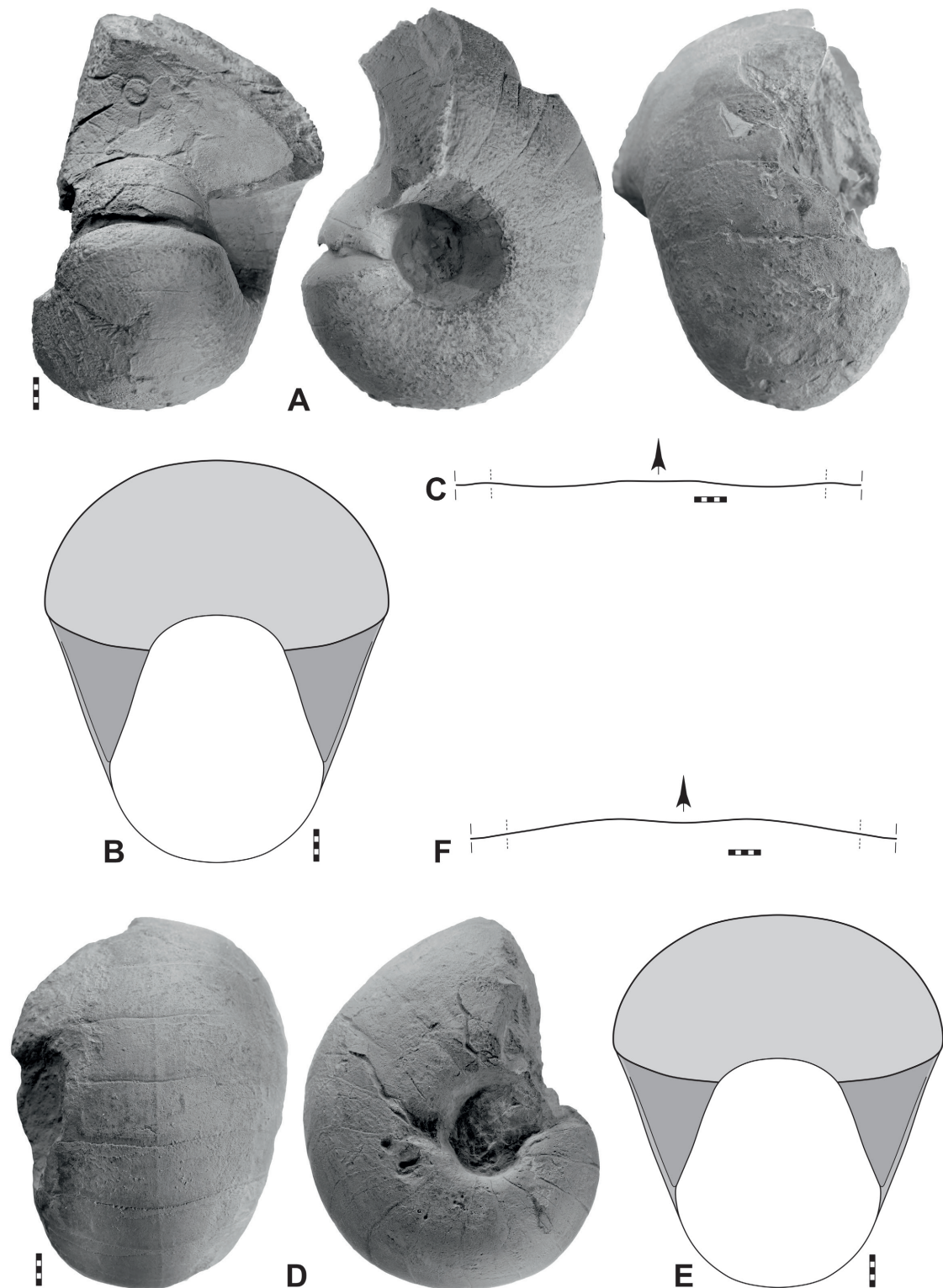
*Paraliroceras macrogaster* sp. nov.

[urn:lsid:zoobank.org:act:0AF97520-0593-4555-9D0F-96A5FBF603A6](https://zoobank.org/urn:lsid:zoobank.org:act:0AF97520-0593-4555-9D0F-96A5FBF603A6)

Fig. 26; Table 20

### Diagnosis

Species of *Paraliroceras* with thinly globular, subinvolute conch (ww/dm ~0.86; uw/dm ~0.23), moderately depressed whorl profile (ww/wh ~1.90) and very high coiling rate (WER ~2.35) at a conch diameter of 60 mm. Whorl profile with broadly arched venter and flanks, narrowly rounded umbilical



**Fig. 26.** *Paraliroceras macrogaster* sp. nov. from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Holotype MB.C.32141 (Korn *et al.* 2011 Coll.), dorsal, lateral and ventral views. **B.** The same specimen, reconstruction of apertural view. **C.** The same specimen, suture line at  $dm=54.5$  mm,  $wh=23.5$  mm. **D.** Paratype MB.C.32142 (Korn *et al.* 2011 Coll.), ventral and lateral views. **E.** The same specimen, reconstruction of apertural view. **F.** The same specimen, suture line at  $dm=40.5$  mm,  $ww=35.8$  mm,  $wh=21.6$  mm. Scale bar units = 1 mm.

**Table 20.** Conch dimensions (in mm) and ratios of *Paraliroceras macrogaster* sp. nov. from Baghuk Mountain; reconstructed values in italics.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32141	62.3	<i>54.5</i>	28.5	14.0	22.0	<i>0.87</i>	<i>1.91</i>	0.22	2.39	0.23
MB.C.32141	41.5	<i>35.5</i>	21.0	10.5	–	<i>0.86</i>	<i>1.69</i>	0.25	–	–
MB.C.32142	60.4	<i>52.0</i>	27.0	14.7	21.0	<i>0.86</i>	<i>1.93</i>	0.24	2.35	0.22

margin, flattened and steep umbilical wall and moderately wide imprint zone (IZR ~0.22). Without sculpture. Suture line with very shallow and wide external, lateral and umbilical lobes.

### Etymology

From the Greek ‘μακρός’=‘large’ and ‘γαστήρ’=‘abdomen’; because of the broadly rounded flanks and venter.

### Type material

#### Holotype

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Araxoceras* beds (early Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 26A–C; MB.C.32141.

#### Paratype

IRAN – **Esfahan Province** • 1 specimen; Baghuk Mountain; same data as for holotype; illustrated in Fig. 26D–F; MB.C.32142.

### Description

Holotype MB.C.32141 is a fully chambered, incomplete specimen with a conch diameter of 62 mm, in which the right side is incomplete. Some conch dimensions can thus only be reconstructed (Fig. 26A). The conch is thinly globular and subinvolute (ww/dm ~0.87; uw/dm=0.22) with a very high coiling rate (WER=2.39) and a moderately deep whorl overlap (IZR=0.23). The whorl profile is moderately depressed (ww/wh ~1.91) with a broadly convex venter that merges continuously with the flanks. The umbilical margin is narrowly rounded and pronounced; the umbilical wall is steep and almost flat (Fig. 26B). The suture line shows very broad and shallow lobes on venter, flanks and umbilical wall (Fig. 26C). The last volution possesses 15 phragmocone chambers without an indication of crowding (CLI=24). The siphuncle has a dorsocentral position.

Paratype MB.C.32142 is almost completely chambered and, with a conch diameter of 60 mm (Fig. 26D–E), has very similar conch parameters to the holotype. The umbilical margin is slightly more rounded and the suture line has a slightly deeper external lobe (Fig. 26F). The last volution of the phragmocone has about 15 chambers (CLI=24).

### Remarks

*Paraliroceras macrogaster* sp. nov. with its pronounced, narrowly rounded umbilical margin makes a separation from the other late Permian representatives of the family Liroceratidae rather easy. *Paraliroceras macrogaster* has a very similar conch to *P. kazanicum*, but differs from *P. kazanicum* (with IZR=0.15 and WER=2.80) in the higher whorl overlap rate of the whorls (IZR=0.22) and the lower coiling rate (WER=2.35).

Family **Permonautilidae** Barskov & Shilovsky in Barskov *et al.*, 2014

**Diagnosis**

Family of the superfamily Liroceratoidea with a pachyconic or globular, usually subinvolute to subevolute conch. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter form a continuous arch in the early forms, the venter can be flattened or concave in advanced forms. Terminal aperture with long lateral shell processes emerging from the umbilical margin. Ornament consisting of fine or coarse growth lines. Septum simple in shape, concavely domed; suture line very simple, almost straight across flanks and venter or with small lobes and saddles (from Korn 2025).

**Included genera**

*Permonautilus* Kruglov, 1933 (Permian); *Alexandronautilus* Shimansky, 1962 (Permian) [synonym of *Permonautilus* Kruglov, 1933].

**Remarks**

A detailed discussion of the family Permonautilidae has been given by Korn (2025).

Genus ***Permonautilus*** Kruglov, 1933

**Type species**

*Nautilus cornutus* Golovkinsky, 1868; original designation.

**Diagnosis**

Genus of the family Permonautilidae with pachyconic or globular, usually subinvolute to subevolute conch. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter form a continuous arch in the early forms, the venter can be flattened or concave in advanced forms. Terminal aperture with long lateral shell processes emerging from the umbilical margin. Ornament consisting of fine or coarse growth lines. Septum simple in shape, concavely domed; suture line very simple, almost straight across flanks and venter or with small lobes and saddles (from Korn & Ghaderi 2025).

**Included species**

Greenland (Tichy 1975): *Permonautilus halleri* Tichy, 1975, Wuchiapingian.

Western Russia (Golovkinsky 1868; Kruglov 1933; Barskov *et al.* 2014): *Nautilus cornutus* Golovkinsky 1868, Roadian; *Permonautilus pinegaensis* Kruglov, 1933, Roadian; *Permonautilus parapinegaensis* Barskov & Shilovsky, 2014, Roadian; *Permonautilus kruglovi* Barskov & Shilovsky, 2014, Roadian.

Transcaucasia (Kruglov 1933): *Coloceras Abichi* Kruglov, 1928, Wuchiapingian, Azerbaijan.

Central Iran (this paper): *Permonautilus adelphidus* sp. nov., Wuchiapingian.

**Remarks**

The species of *Permonautilus* have very similar morphology; differences lie in the width of the conch, the width of the umbilicus and the shape of the whorl profile. The genus is currently only known from the two Permian stages Roadian and Wuchiapingian; no representatives have yet been reported from the Wordian and Capitanian stages in between.

*Permonautilus adelphidus* sp. nov.

urn:lsid:zoobank.org:act:C05CE182-FAC1-48A2-8930-80AC19A205B6

Figs 27–28; Table 21

*Permonautilus* sp. – Korn *et al.* 2021: text-fig. 17d.

### Diagnosis

Species of *Permonautilus* with thinly globular, subinvolute conch ( $ww/dm=0.90–1.00$ ;  $uw/dm=0.18–0.25$ ), strongly depressed whorl profile ( $ww/wh=2.00–2.20$ ) and extremely high coiling rate ( $WER=2.50–2.70$ ) at a conch diameter of 20–60 mm. Whorl profile with broadly arched venter and flanks, broadly rounded umbilical margin, convex umbilical wall and moderately wide imprint zone ( $IZR\sim 0.20$ ). Without sculpture. Suture line nearly straight.

### Etymology

From the Greek ‘ἀδελφή’=‘sister’ and ‘εἶδος’=‘species’; because of its close relationship with *P. abichi*.

### Type material

#### Holotype

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Araxoceras* beds (early Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 27; MB.C.30226.

#### Paratypes

IRAN – **Esfahan Province** • 1 specimen; same data as for holotype; 2011; Korn *et al.* leg.; illustrated in Fig. 28A–C; MB.C.32143 • 1 specimen; same data as for holotype; 2011; Ghaderi leg.; illustrated in Fig. 28D; MB.C.32144 • 1 specimen; same data as for holotype; 2011; Korn *et al.* leg.; illustrated in Fig. 28E–F; MB.C.32145.

### Description

Holotype MB.C.30226 is a strongly corroded, fully chambered specimen with a conch diameter of 48 mm (Fig. 27A). The conch is globular and subinvolute ( $ww/dm=0.91$ ;  $uw/dm=0.25$ ) with an extremely high coiling rate ( $WER=2.62$ ) and a moderately wide whorl overlap ( $IZR=0.16$ ). The whorl profile is reniform and very strongly depressed ( $ww/wh=2.02$ ) with a broadly convex venter that merges continuously with the flanks. The umbilical margin is broadly rounded and the umbilical wall is steep and convex (Fig. 27B). The suture line describes an almost straight line (Fig. 27C). The last volution possesses 18 phragmocone chambers ( $CLI=20$ ).

Paratype MB.C.32143 is an incomplete, in part strongly corroded specimen with a conch diameter of 58 mm (Fig. 28B). About  $135^\circ$  of the final whorl belong to the body chamber. It has similar conch proportions to holotype MB.C.30226, but it is stouter; the conch is thickly globular and subinvolute ( $ww/dm=1.02$ ;  $uw/dm=0.21$ ) with an extremely high coiling rate ( $WER=2.69$ ) and a moderately wide whorl overlap ( $IZR=0.18$ ). The whorl profile is very strongly depressed ( $ww/wh=2.15$ ) with a broadly convex venter that merges continuously with the flanks. The umbilical margin is broadly rounded and the umbilical wall is steep and convex (Fig. 28A). The suture line extends almost linearly across flanks and venter (Fig. 28C). The last half volution possesses 8 phragmocone chambers ( $CLI=22.5$ ).

Paratype MB.C.32144 is a small, incomplete phragmocone specimen with a conch diameter of 38 mm (Fig. 28D). Part of the final whorl is missing; therefore, it allows an insight into the earlier ontogenetic conch growth. It shows that the basic conch proportions seem to change little during ontogeny; only the umbilicus becomes narrower. The conch is, at 38 mm diameter, globular and subinvolute ( $ww/dm=0.95$ ;  $uw/dm=0.22$ ) with an extremely high coiling rate ( $WER=2.59$ ) and a moderately wide whorl overlap

**Table 21.** Conch dimensions (in mm) and ratios of *Permonautilus adelphidus* sp. nov.

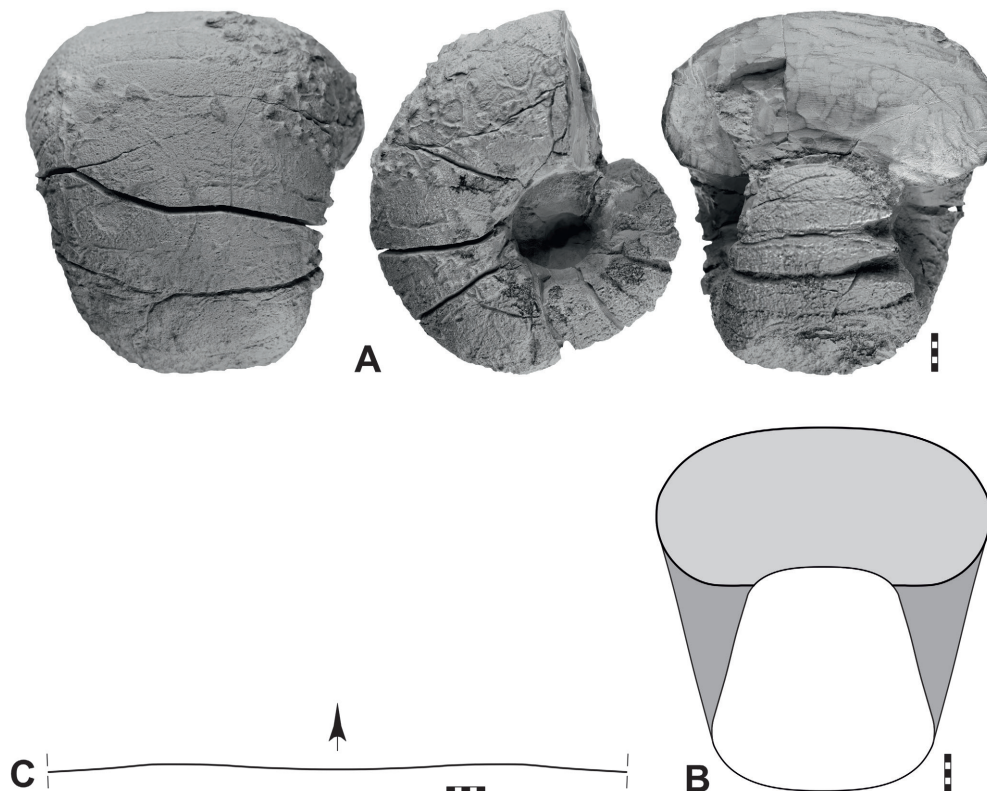
Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32145	77.4	64.0	32.2	19.0	27.2	0.83	1.99	0.25	2.38	0.16
MB.C.32143	57.7	58.8	27.3	12.1	22.5	1.02	2.15	0.21	2.69	0.18
MB.C.30226	48.2	44.1	21.8	11.9	18.4	0.91	2.02	0.25	2.62	0.16
MB.C.30226	34.4	33.0	15.3	7.5	–	0.96	2.16	0.22	–	–
MB.C.32144	37.8	35.8	17.2	8.4	14.3	0.95	2.08	0.22	2.59	0.17
MB.C.32144	21.0	20.0	9.8	6.2	8.0	0.95	2.04	0.30	2.61	0.18

(IZR=0.17). The whorl profile is very strongly depressed ( $ww/wh=2.08$ ) with a broadly convex venter that merges continuously with the flanks. The geometry is almost identical at a conch diameter of 21 mm.

Paratype MB.C.32145 is the largest individual with a conch diameter of 77 mm. It is a rather strongly weathered fragmentary specimen, but it allows the study of conch geometry at the transition to the adult stage, which is characterised by flattening of the venter (Fig. 28E). The conch is, with a  $ww/dm$  ratio of 0.83, slenderer than the other specimens. Its suture line extends almost linearly across flanks and venter (Fig. 28F).

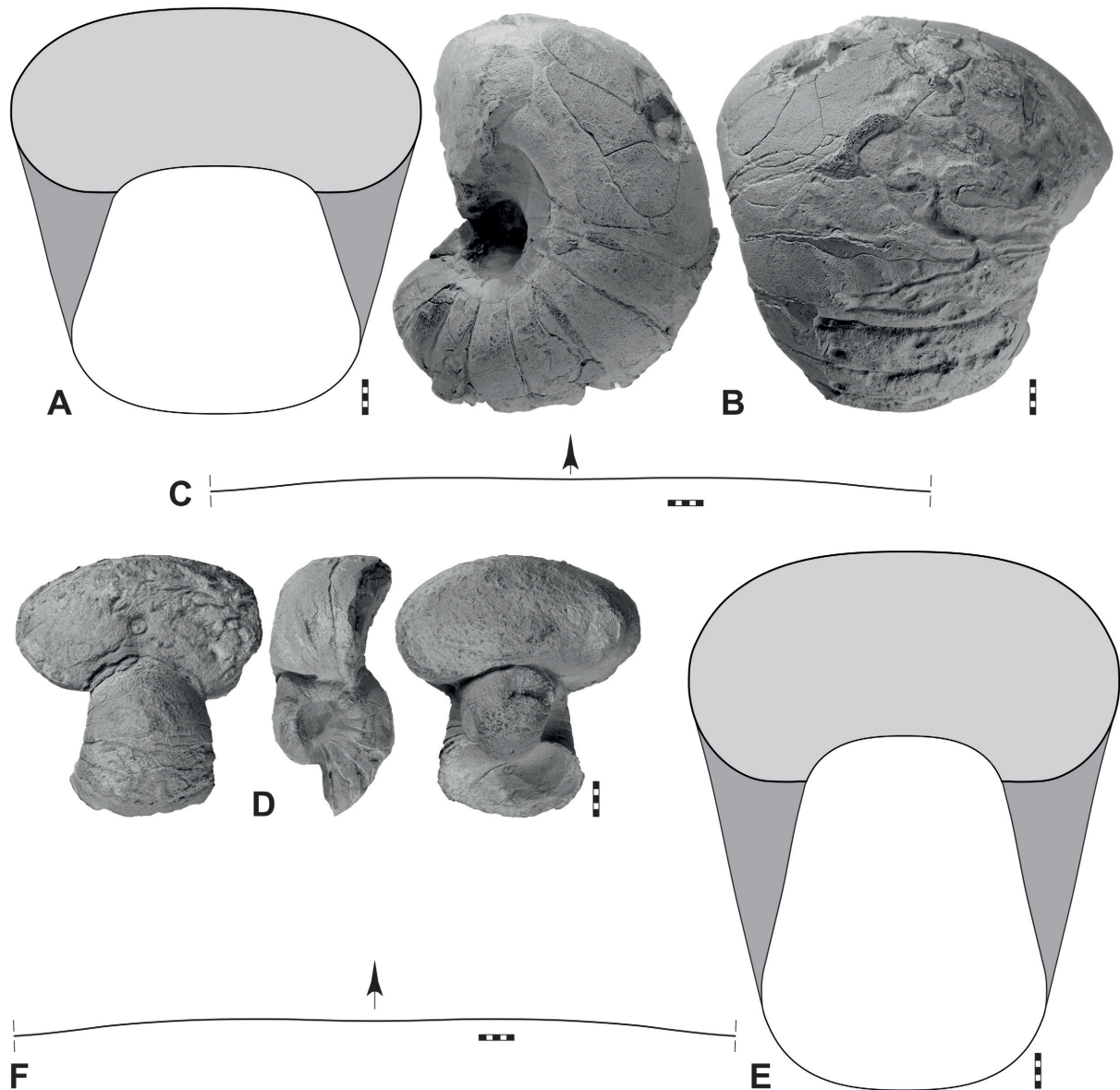
#### Remarks

*Permonautilus adelphidus* sp. nov. is very similar to *P. abichi*, but differs in that it has a significantly higher whorl expansion rate at apparently all ontogenetic stages. In the growth interval between a conch



**Fig. 27.** *Permonautilus adelphidus* sp. nov., holotype MB.C.30226 (Korn *et al.* 2011 Coll.) from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Ventral, lateral and dorsal views. **B.** Reconstruction of apertural view. **C.** Suture line at  $dm=42.5$  mm,  $ww=38.6$  mm,  $wh=21.4$  mm. Scale bar units= 1 mm.

diameter of 20 and 60 mm, the whorl expansion rate for *P. adelphidus* is always higher than 2.50, while for *P. abichi* it is only about 2.25–2.35. Another distinguishing feature is the shape of the shell: The ww/dm ratio in *P. adelphidus* is higher than 0.90 in the interval between 20 and 60 mm shell diameter, while in *P. abichi* it is somewhat lower (0.80–0.90).



**Fig. 28.** *Permonautilus adelphidus* sp. nov. from the *Araxoceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Paratype MB.C.32143 (Korn *et al.* 2011 Coll.), reconstruction of apertural view. **B.** The same specimen, lateral and ventral views. **C.** The same specimen, suture line at ww=46.0 mm, wh=22.0 mm. **D.** Paratype MB.C.32144 (Ghaderi 2011 Coll.), dorsal and lateral views. **E.** Paratype MB.C.32145 (Korn *et al.* 2011 Coll.), reconstruction of apertural view. **F.** The same specimen, suture line at ww=49.5 mm, wh=25.8 mm. Scale bar units=1 mm.

Family **Julfanautilidae** Korn & Ghaderi, 2025

**Diagnosis**

Family of the superfamily Liroceratoidea with a usually pachyconic, subinvolute to involute conch. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter usually separated by distinct ventrolateral shoulder, venter or concave. Umbilical margin subangular or angular; umbilical wall steep, flattened. Ornament usually consisting of fine growth lines. Septum simple in shape, concavely domed; suture line with shallow lobes on venter and flank (from Korn & Ghaderi 2025).

**Included genera**

*Julfanautilus* Korn & Ghaderi, 2025 (Wuchiapingian); *Baghuknautilus* gen. nov. (Wuchiapingian); *Shahrezanautilus* gen. nov. (Wuchiapingian).

**Remarks**

The family Julfanautilidae is characterised by a combination of characters not found in any other family of Palaeozoic nautilids. This is the combination of a rather stout conch with a very pronounced umbilical margin and also sometimes pronounced ventrolateral shoulder. While the first character suggests a placement in the superfamily Liroceratoidea, the second and third characters show a closer morphological relationship to the superfamilies Pleuronautiloidea and Grypoceratoidea. Unfortunately, the early ontogenetic development of the conch in the species of the Julfanautilidae is not known. However, the material shows that the pronounced umbilical margin is present early in ontogeny and that this feature can therefore be considered apomorphic, whereas the ventrolateral shoulder does not assume a subangular shape until a late ontogenetic stage, if at all. Therefore, these forms are included here as a new family of the superfamily Liroceratoidea (from Korn & Ghaderi 2025).

Genus *Baghuknautilus* gen. nov.

[urn:lsid:zoobank.org:act:DEB59642-18B0-46BE-ABD2-6D373AE0B857](https://zoobank.org/act:DEB59642-18B0-46BE-ABD2-6D373AE0B857)

New genus F – Korn 2025: 69. — Korn & Ghaderi 2025: 8, 98, 102–103.

**Type species**

*Baghuknautilus aplomorphus* gen. et sp. nov.

**Diagnosis**

Genus of the family Julfanautilidae with discoidal, involute conch. The conch rapidly increases in height with a very high to extremely high coiling rate (WER usually higher than 2.50). Whorls moderately strongly embracing, their profile ranges from compressed to weakly depressed. Adult ornament with extremely fine growth lines. Septa without inflexions, slightly concave. Suture line simple, nearly straight to straight with a low external saddle, broadly rounded internal lobe. The siphuncle has a dorsocentral position.

**Etymology**

Named after the type locality of the type species.

**Included species**

Central Iran (this paper): *Baghuknautilus aplomorphus* gen. et sp. nov., Wuchiapingian.

**Remarks**

In terms of conch morphology, *Baghuknautilus* gen. nov. shows some similarities to the genera *Julfanautilus* and *Shahrezanautilus* gen. nov. This is particularly true for the shape of the whorl profile with slightly flattened, converging flanks and the slightly flattened umbilical wall. However, the other

two genera show a much higher coiling rate (WER above 3.00) than *Baghuknautilus* (WER around 2.50) and a much more pronounced subangular to angular umbilical margin.

*Baghuknautilus* gen. nov. also has similarity to the Triassic genus *Paranautilus* (Kummel 1953; Sobolev 1989), but this differs in the more dorsal position of the siphuncle and the presence of an annular process. In addition, most species of *Paranautilus* have a convex umbilical wall.

***Baghuknautilus aplomorphus* gen. et sp. nov.**

[urn:lsid:zoobank.org:act:0E6D1116-BB35-4615-832A-A52849FB4934](https://doi.org/10.3897/ejt.1019.1116-BB35-4615-832A-A52849FB4934)

Fig. 29; Table 22

**Diagnosis**

Species of *Baghuknautilus* gen. nov. with thinly discoidal, involute conch (ww/dm ~0.40; uw/dm ~0.10), weakly compressed whorl profile (ww/wh ~0.65) and extremely high coiling rate (WER ~2.55) at a conch diameter of 60 mm. Whorl profile with convex venter, convex and convergent flanks, narrowly rounded umbilical margin, a steep umbilical wall and moderately wide imprint zone (IZR ~0.30). Suture line with a very shallow external lobe and an asymmetric, broadly rounded lateral lobe.

**Etymology**

From the Greek ‘ἀπλός’=‘simple’ and ‘μορφή’=‘form’; because of the rather simple conch morphology.

**Type material**

**Holotype**

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 29A–C; MB.C.32146.

**Paratype**

IRAN – **Esfahan Province** • 1 specimen; Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 29D–E; MB.C.32147.

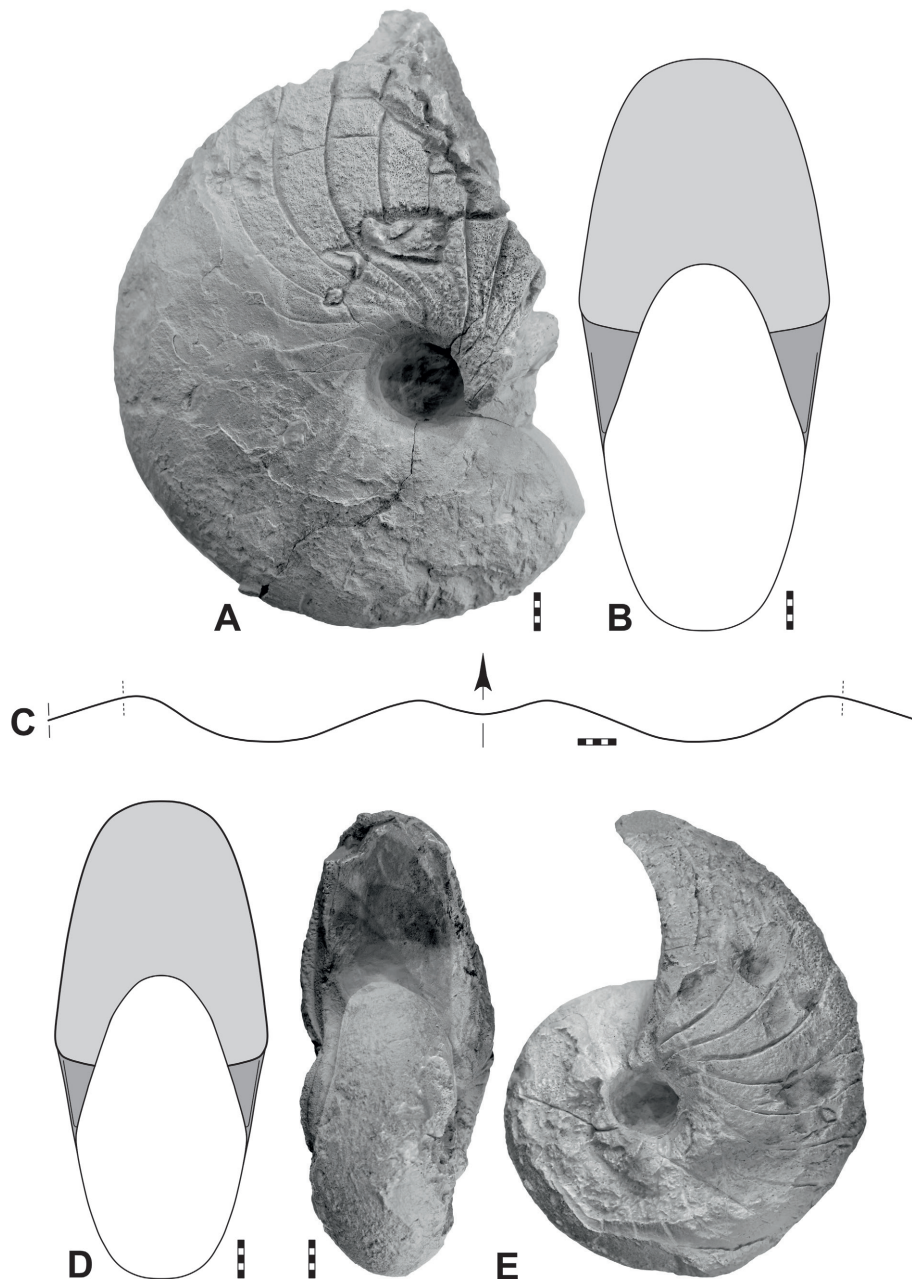
**Description**

Holotype MB.C.32146 is an incomplete, but on the left side rather well-preserved fully chambered specimen with a conch diameter of 83 mm (Fig. 29A). Some conch parameters can only be reconstructed. The conch is thinly discoidal and involute (ww/dm ~0.40; uw/dm=0.10). The whorl profile is weakly compressed (ww/wh ~0.64) with a convex venter and convex, convergent flanks. The umbilical margin is narrowly rounded and the umbilical wall is steep and convex (Fig. 29B). The last volution possesses about 22 phragmocone chambers (CLI=16.5) with an indication of crowding at the end. The siphuncle has a dorsocentral position. The suture line shows a small and very shallow lobe on venter, a broadly rounded asymmetric lateral lobe with steeper dorsal flanks and a shallow umbilical lobe (Fig. 29C).

Paratype MB.C.32147 is a bilaterally corroded, fully chambered specimen with a conch diameter of 60 mm (Fig. 29E). Some conch parameters on the last half volution can only be reconstructed. The conch is thinly discoidal and involute (ww/dm=0.42; uw/dm=0.12) with an extremely high coiling rate (WER=2.54) and a deep whorl overlap (IZR=0.32). The whorl profile is moderately compressed (ww/wh=0.76) with a convex venter and convex convergent flanks (Fig. 29D). The suture line shows a shallow, rounded lobe on venter and a broadly rounded slightly asymmetric lateral lobe with steeper dorsal flanks.

**Table 22.** Conch dimensions (in mm) and ratios of *Baghuknautilus aplomorphus* gen. et sp. nov.; reconstructed values in italics.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32146	83.4	<i>33.0</i>	51.5	8.2	–	<i>0.40</i>	<i>0.64</i>	0.10	–	–
MB.C.32147	60.1	25.0	33.0	7.3	22.4	0.42	0.76	0.12	2.54	0.32



**Fig. 29.** *Baghuknautilus aplomorphus* gen. et sp. nov. from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Holotype MB.C.32146 (Korn *et al.* 2011 Coll.), lateral view. **B.** The same specimen, reconstruction of apertural view. **C.** The same specimen, suture line at dm=72.5 mm, wh=38.8 mm. **D.** Paratype MB.C.32147 (Korn *et al.* 2011 Coll.), reconstruction of apertural view. **E.** The same specimen, dorsal and lateral views. Scale bar units=1 mm.

### Remarks

*Baghuknautilus aplomorphus* gen. et sp. nov. differs from *Shahrezanautilus ghaderii* gen. et sp. nov. by the considerably slenderer conch; the ww/dm ratio is about 0.40 in *B. aplomorphus* but about 0.60 in *S. ghaderii*. The coiling rate is much lower in *B. aplomorphus* (WER higher about 2.50 in comparison with more than 3.00 in *S. ghaderii*).

Genus *Shahrezanautilus* gen. nov.

[urn:lsid:zoobank.org:act:449ADF07-95B8-481E-8C4B-4114FD3DC347](https://zoobank.org/act:449ADF07-95B8-481E-8C4B-4114FD3DC347)

New genus E – Korn 2025: 69.

### Type species

*Shahrezanautilus weyeri* gen. et sp. nov.

### Diagnosis

Genus of the family Julfanautilidae with thinly pachyconic, subinvolute conch. Conch rapidly increasing in height with an extraordinarily high coiling rate (WER higher than 3.00). Whorls weakly embracing, whorl profile weakly depressed. Venter broadly rounded, umbilical wall flat and steep. Adult ornament with extremely fine growth lines. Septa without inflexions, slightly concave. Suture line simple with a shallow external lobe and a broadly rounded lateral lobe.

### Etymology

Named after the city of Shahreza, the type locality of the type species.

### Included species

Central Iran (this paper): *Shahrezanautilus weyeri* gen. et sp. nov., Wuchiapingian; *Shahrezanautilus ghaderii* gen. et sp. nov., Wuchiapingian.

### Remarks

*Shahrezanautilus* gen. nov. differs from *Julfanautilus* in the broadly rounded venter, which in *Julfanautilus* has a concave shape.

*Shahrezanautilus weyeri* gen. et sp. nov.

[urn:lsid:zoobank.org:act:FBA54AF0-D7E6-4EBB-BBFA-2563F160A99D](https://zoobank.org/act:FBA54AF0-D7E6-4EBB-BBFA-2563F160A99D)

Fig. 30; Table 23

### Diagnosis

Species of *Shahrezanautilus* gen. nov. with a thinly pachyconic, subinvolute conch (ww/dm ~0.70; uw/dm ~0.25), weakly depressed whorl profile (ww/wh ~1.40) and extraordinarily high coiling rate (WER ~3.40) at a conch diameter of 60 mm. Whorl profile with a weakly convex venter, a pronounced ventrolateral shoulder, flatly convex and weakly convergent flanks, a subangular umbilical margin, a steep and flattened umbilical wall and a small imprint zone (IZR ~0.10). Suture line with a broadly rounded and shallow external lobe and a broadly rounded lateral lobe.

### Etymology

Named after Dieter Weyer (Berlin), who collected the holotype of the new species.

### Type material

#### Holotype

IRAN – **Esfahan Province** • Shahreza; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2002; D. Weyer leg.; illustrated in Fig. 30; MB.C.32148.

**Table 23.** Conch dimensions (in mm) and ratios of *Shahrezanautilus weyeri* gen. et sp. nov.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32148	57.0	39.0	28.0	15.0	26.0	0.68	1.39	0.26	3.38	0.07

**Paratype**

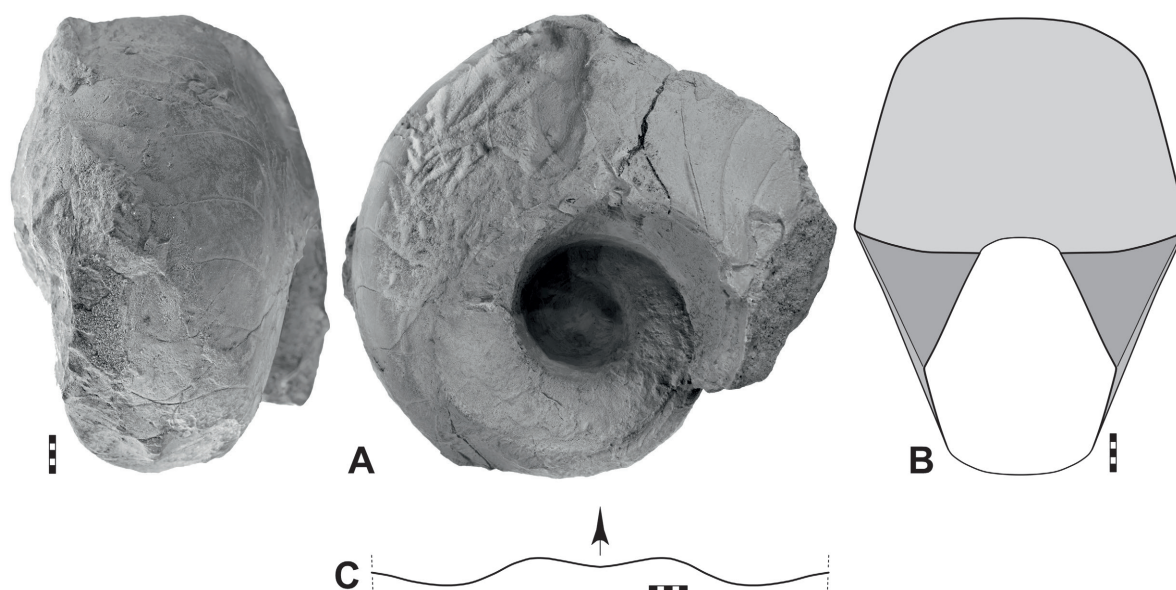
IRAN – **Esfahan Province** • 1 specimen; Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2011; Korn *et al.* leg.; MB.C.32149.

**Description**

Holotype MB.C.32148 is an incomplete, fully chambered specimen with a phragmocone diameter of at least 75 mm (Fig. 30A). It has been preserved without remains of the shell. The conch is, at 57 mm diameter, thinly pachyconic and subinvolute ( $ww/dm=0.68$ ;  $uw/dm=0.26$ ) with an extraordinarily high coiling rate ( $WER=3.38$ ) and a small whorl overlap zone ( $IZR=0.07$ ). The whorl profile is weakly depressed ( $ww/wh=1.39$ ) with a convex venter, a slightly pronounced by rounded ventrolateral shoulder and slightly flattened convergent flanks. The umbilical margin is very distinctive and subangular; it delimitates the broad and nearly flat, almost perpendicular umbilical wall (Fig. 30B). The suture line shows a shallow and broadly rounded external lobe and a twice as wide and deep, broadly rounded lateral lobe (Fig. 30C). The last volution of the phragmocone has slightly more than 20 septa ( $CLI=18$ ) and thus some indication for terminal septal crowding.

**Remarks**

*Shahrezanautilus weyeri* gen. et sp. nov. differs from *S. ghaderii* gen. et sp. nov. in having a much wider umbilicus; the  $uw/dm$  ratio is about 0.25 in *S. weyeri* gen. et sp. nov. but only about 0.15 in *S. ghaderii*. This difference parallels a difference in the whorl overlap rate, which is only about 0.07 in *S. weyeri*, but 0.25 in *S. ghaderii* and in the coiling rate, which is higher in *S. weyeri* ( $WER \sim 3.40$  compared to about 3.10 in *S. ghaderii*).



**Fig. 30.** *Shahrezanautilus weyeri* gen. et sp. nov., holotype MB.C.32148 (Weyer 2002 Coll.) from the *Vedioceras* beds of the Hambast Formation at Shahreza. **A.** Ventral and lateral views. **B.** Reconstruction of apertural view. **C.** Suture line at  $dm=50.2$  mm,  $ww=36.3$  mm,  $wh=26.5$  mm. Scale bar units = 1 mm.

*Shahrezanautilus weyeri* gen. et sp. nov. is difficult to confuse with any other Late Permian nautiloid species due to its specific morphology with a very high, flattened umbilical wall and an angular umbilical margin. The two species *Julfanautilus hairapetiani* Korn & Ghaderi, 2025 and especially *J. ashourii* Korn & Ghaderi, 2025 show a slight similarity, although they have a concave venter.

*Shahrezanautilus ghaderii* gen. et sp. nov.

[urn:lsid:zoobank.org:act:8FA187E3-F00F-44DE-A0FA-32A9E26A7B37](https://zoobank.org/act:8FA187E3-F00F-44DE-A0FA-32A9E26A7B37)

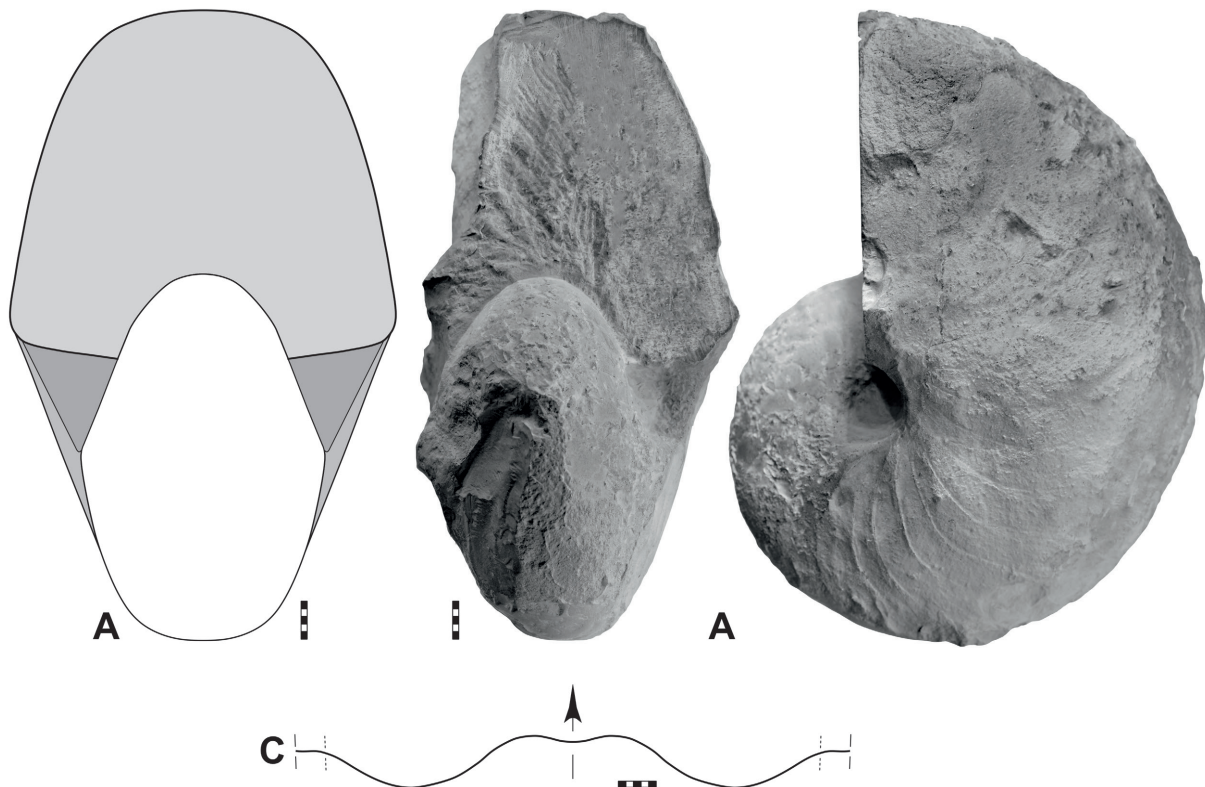
Fig. 31; Table 24

**Diagnosis**

Species of *Shahrezanautilus* gen. nov. with thinly pachyconic, involute conch (ww/dm  $\sim$ 0.62; uw/dm  $\sim$ 0.13), weakly depressed whorl profile (ww/wh  $\sim$ 1.10) and extraordinarily high coiling rate (WER  $\sim$ 3.10) at a conch diameter of 80 mm. Whorl profile with convex venter, convex and convergent flanks, a subangular umbilical margin, a steep umbilical wall and a moderately deep imprint zone (IZR  $\sim$ 0.25). Suture line with a very shallow external lobe and a weakly asymmetric, broadly rounded lateral lobe.

**Etymology**

Named after Abbas Ghaderi (Mashhad), in honour of his contribution in studying the Permian–Triassic boundary.



**Fig. 31.** *Shahrezanautilus ghaderii* gen. et sp. nov., holotype MB.C.32150 (Korn *et al.* 2011 Coll.) from the *Vedioceras* beds of the Hambast Formation at Baghuk Mountain. **A.** Reconstruction of apertural view. **B.** Dorsal and lateral views. **C.** Suture line at dm=48.5 mm, ww=32.5 mm, wh=29.5 mm. Scale bar units=1 mm.

**Table 24.** Conch dimensions (in mm) and ratios of *Shahrezanautilus ghaderii* gen. et sp. nov.; reconstructed values in italics.

Nr.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.32150	83.5	<i>52.0</i>	48.0	10.5	36.0	<i>0.62</i>	<i>1.08</i>	0.13	3.09	0.25
MB.C.32150	47.5	30.5	28.5	7.5	–	0.64	1.07	0.16	–	–

**Type material****Holotype**

IRAN – **Esfahan Province** • Baghuk Mountain; Hambast Formation, *Vedioceras* beds (late Wuchiapingian); 2011; Korn *et al.* leg.; illustrated in Fig. 31; MB.C.32150.

**Description**

Holotype MB.C.32150 is a largely chambered specimen with a conch diameter of 84 mm (Fig. 31B), which is heavily corroded on the last half volution. Some of the conch parameters on the last half volution can only be reconstructed. The conch is thinly pachyconic and involute ( $ww/dm \sim 0.62$ ;  $uw/dm = 0.13$ ) with an extraordinarily high coiling rate ( $WER = 3.09$ ) and a moderately deep whorl overlap ( $IZR = 0.25$ ). The whorl profile is weakly depressed ( $ww/wh \sim 1.08$ ) with a convex venter, convex convergent flanks, a narrowly rounded umbilical margin and a steep umbilical wall (Fig. 31A). The suture line shows a very shallow, rounded lobe on venter and a broadly rounded, nearly symmetric lateral lobe (Fig. 31C).

**Remarks**

*Shahrezanautilus ghaderii* gen. et sp. nov. differs from *S. weyeri* gen. et sp. nov. in having a much narrower umbilicus; the  $uw/dm$  ratio is about 0.15 in *S. ghaderii* but about 0.25 in *S. weyeri*. This difference parallels a difference in the whorl overlap rate, which is about 0.25 in *S. ghaderii*, but only 0.07 in *S. weyeri* and in the coiling rate, which is lower in *S. ghaderii* ( $WER \sim 3.00$  compared to about 3.40 in *S. weyeri*).

*Shahrezanautilus ghaderii* gen. et sp. nov. has some similarities with *Julfanautilus ashourii* Korn & Ghaderi, 2025 from Julfa. Like *S. ghaderii*, *J. apertum* has a stout, involute conch ( $ww/dm \sim 0.65$ ), which is more umbilicated in *J. apertum* ( $uw/dm \sim 0.25$  in *J. apertum*, but only 0.15 in *S. ghaderii*). The main difference between the two species is the shape of the venter, which is convex in *S. ghaderii* and concave in *J. apertum*.

**Discussion**

The Late Permian Hambast Formation of sections at Baghuk Mountain (Central Iran) has yielded diverse nautiloid assemblages. These species belong to 14 genera, six of which are new: *Lutonautilus* gen. nov., *Epitainoceras* gen. nov., *Ocunautilus* gen. nov., *Aifinautilus* gen. nov., *Baghuknautilus* gen. nov. and *Shahrezanautilus* gen. nov. Based on new material, a total of 24 new species is described. The material comes from four stratigraphic units, in ascending order:

- *Araxoceras* beds (early Wuchiapingian), nine species: *Epitainoceras lutense* gen. et sp. nov., *Serometacoceras pentagonum* sp. nov., *Domatoceras myloide* sp. nov., *Ocunautilus diplodocus* gen. et sp. nov., *Ocunautilus coelodesmus* gen. et sp. nov., *Ocunautilus tachytrepheus* gen. et sp. nov., *Aifinautilus icanus* gen. et sp. nov., *Paraliroceras macrogaster* sp. nov. and *Permonautilus adelphidus* sp. nov.
- *Prototoceras* beds (early Wuchiapingian), one species: *Tardunautilus aperimos* sp. nov.
- *Vedioceras* beds (late Wuchiapingian), 12 species: *Lutonautilus cratus* gen. et sp. nov., *Lutonautilus elachus* gen. et sp. nov., *Lutonautilus cymus* gen. et sp. nov., *Foordiceras eicosacanthum* sp. nov., *Foordiceras decacanthum* sp. nov., *Foordiceras ascetum* sp. nov., *Domatoceras canonium* sp. nov.,

- Domatoceras ocomphalum* sp. nov., *Liroceras leptum* sp. nov., *Baghuknautilus aplomorphus* gen. et sp. nov., *Shahrezanautilus weyeri* gen. et sp. nov. and *Shahrezanautilus ghaderii* gen. et sp. nov.
- *Paratirolites* beds (late Changhsingian), two species: *Tainoceras hystatum* sp. nov. and *Azarinautilus phorminx* sp. nov.

With 24 species, the assemblage from Baghuk is one of the most diverse Late Permian occurrences of coiled nautiloids. With 22 Wuchiapingian species alone, it is the second species-rich assemblage for this interval after the Transcaucasian region.

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## References

- Abich H. 1878. *Geologische Forschungen in den kaukasischen Ländern. Theil I. Eine Bergkalkfauna aus der Araxesenge bei Djoulfa in Armenien*. Hölder, Wien.
- Barskov I.S., Leonova T.B. & Shilovsky O.P. 2014. Middle Permian cephalopods of the Volga-Ural Region. *Paleontological Journal* 48: 1331–1414. <https://doi.org/10.1134/S0031030114130012>
- Chao K.-K. 1940. Upper Paleozoic cephalopods from central Hunan, China. *Journal of Paleontology* 14 (1): 68–73.
- Chao K.-K. 1954. Permian cephalopods from Tanchiashan, Hunan. *Acta Palaeontologica Sinica* 2: 1–58.
- de Koninck L. 1863. Descriptions of some fossils from India, discovered by Dr. A. Fleming, of Edinburgh. *Quarterly Journal of the Geological Society* 19: 1–19. <https://doi.org/10.1144/GSL.JGS.1863.019.01-02.05>
- Dernov V. 2024. *Tainoceras luxaeterna* sp. nov., a new Late Pennsylvanian nautiloid species (Cephalopoda) from the Donets Basin, eastern Ukraine. *Historical Biology*: 1–6. <https://doi.org/10.1080/08912963.2024.2427080>
- Dzik J. 1984. Phylogeny of the Nautiloidea. *Palaeontologia Polonica* 45: 1–219.
- Ehiro M. & Araki H. 1997. Permian cephalopods of Kurosawa, Kesenuma City in the Southern Kitakami Massif, Northeast Japan. *Paleontological Research* 1: 55–66. <https://doi.org/10.2517/prpsj.1.55>
- Ehiro M. & Takizawa F. 1989. *Foordiceras* and *Domatoceras* (nautiloid cephalopods) from the Upper Permian Toyoma Formation, southern Kitakami Massif, Northeast Japan. *Transactions and Proceedings of the Paleontological Society of Japan, New series* 155: 212–217.
- Eichwald C.E. von 1857. Beitrag zur geographischen Verbreitung der fossilen Thiere Russlands. Alte Periode. Klasse der Cephalopoden. *Moskovskoe obshchestvo lyubiteley prirody* 30: 192–212.
- Flower R.H. & Kummel B. 1950. A classification of the Nautiloidea. *Journal of Paleontology* 24: 604–616.

- Foord A.H. 1891. *Catalogue of the Fossil Cephalopoda in the British Museum, Part II. Containing the Remainder of the Suborder Nautiloidea, Consisting of the Families Lituitidae, Trochoceratidae, and Nautilidae, with a Supplement*. Order of the Trustees, London.
- Geinitz H.B. 1841. Über organische Reste im Zechstein bei Altenburg, Ronneburg und Gera. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde* 1841: 637–642.
- Gemmellaro G.G. 1889. La Fauna dei Calcari con *Fusulina* della Valle del Fiume Sosio nella Provincia di Palermo, Fascicolo II. Nautiloidea, Gastropoda. *Giornale di Scienze naturali ed economiche* 20: 97–182. <https://doi.org/10.5962/bhl.title.10774>
- Girty G.H. 1911. On some new genera and species of Pennsylvanian fossils from the Wewoka formation of Oklahoma. *New York Academy of Science, Annals* 21: 119–156. <https://doi.org/10.1111/j.1749-6632.1911.tb56931.x>
- Golovkinsky N.A. 1868. *O permskoi formatsii v tsentral'noi chasti Kamsko-Volzhskogo basseina [On the Permian Strata in the Central Part of the Kama-Volga Basin]*. Imperatorskaya Akademiya Nauk, St. Peterburg. [In Russian.]
- Gordon M.jr. 1965. Carboniferous Cephalopods of Arkansas. *Professional Papers, U.S. Geological Survey* 460: 1–322. <https://doi.org/10.3133/pp460>
- Gurley W.F.E. 1883. *New Carboniferous Fossils, Bulletin 2*. W.F.E. Gurley, Danville.
- Hampe O., Hairapetian V., Dorka M., Witzmann F., Akbari A.M. & Korn D. 2013. A first Late Permian fish fauna from Baghuk Mountain (Neo-Tethyan shelf, central Iran). *Bulletin of Geosciences* 88: 1–20. <https://doi.org/10.3140/bull.geosci.1357>
- Haniel C.A. 1915. Die Cephalopoden der Dyas von Timor. In: Wanner J. (ed.) *Paläontologie von Timor nebst kleineren Beiträgen zur Paläontologie einiger anderer Inseln des ostindischen Archipels*: 1–153. Schweizerbart, Stuttgart.
- Hayasaka I. 1957. Two Permian nautiloids from Takakura-yama near Yotsukura-machi, Fukushima Prefecture (Abukuma Plateau region). *Science Reports of the Yokohama National University. Section II, Biological and Geological Sciences* 6: 21–30.
- Hayasaka I. 1962. Two species of *Tainoceras* from the Permian of the Kitakami Mountains. *Bulletin of the National Science Museum* 6: 137–143.
- Heuer F., Leda L., Moradi Salimi H., Gliwa J., Hairapetian V. & Korn D. 2022. The Permian–Triassic boundary section at Baghuk Mountain, Central Iran: carbonate microfacies and depositional environment. *Palaeobiodiversity and Palaeoenvironments* 102: 331–350. <https://doi.org/10.1007/s12549-021-00511-1>
- Hind W. 1910. On four new Carboniferous nautiloids and a goniatite new to Great Britain. *Proceedings of the Yorkshire Geological Society* 17: 97–109. <https://doi.org/10.1144/pygs.17.2.97>
- Hyatt A. 1891. Carboniferous cephalopods. *Annual Report of the Geological Survey of Texas* 2: 327–356.
- Hyatt A. 1893. Carboniferous cephalopods. Second paper. *Annual Report of the Geological Survey of Texas* 4: 327–356, 379–474.
- Hyatt A. 1894. Phylogeny of an acquired characteristic. *Proceedings of the American Philosophical Society* 32: 349–647. <https://doi.org/10.5962/bhl.title.59826>
- Kayser E. 1883. Obercarbonische Fauna von Lo-ping. In: Richthofen F.v. (ed.) *China*: 160–208.
- King W. 1850. A monograph of the Permian fossils of England. *Monographs of the Palaeontographical Society* 3: 1–258. <https://doi.org/10.1080/02693445.1850.12088363>

- Klug C., Korn D., Landman N.H., Tanabe K., De Baets K. & Naglik C. 2015. Describing ammonoid conchs. In: Klug C., Korn D., De Baets K., Kruta I. & Mapes R.H. (eds) *Ammonoid Paleobiology: From Macroevolution to Paleogeography, Topics in Geobiology* 44: 3–24. Springer, Dordrecht. [https://doi.org/10.1007/978-94-017-9630-9\\_1](https://doi.org/10.1007/978-94-017-9630-9_1)
- Korn D. 2010. A key for the description of Palaeozoic ammonoids. *Fossil Record* 13: 5–12. <https://doi.org/10.1002/mmng.200900008>
- Korn D. 2025. A revised classification of the Carboniferous and Permian Nautilida. *European Journal of Taxonomy* 1017: 1–85. <https://doi.org/10.5852/ejt.2025.1017.3065>
- Korn D. & Bockwinkel J. 2022. Early Carboniferous nautiloids from the Central Sahara, southern Algeria. *European Journal of Taxonomy* 831: 67–108. <https://doi.org/10.5852/ejt.2022.831.1871>
- Korn D. & Ghaderi A. 2025. Late Permian nautiloids from Julfa. *European Journal of Taxonomy* 1018: 1–113. <https://doi.org/10.5852/ejt.2025.1018.3069>
- Korn D. & Klug C. 2023. Early Carboniferous coiled nautiloids from the Anti-Atlas (Morocco). *European Journal of Taxonomy* 885: 156–194. <https://doi.org/10.5852/ejt.2023.885.2199>
- Korn D., Ghaderi A., Ghanizadeh Tabrizi N. & Gliwa J. 2020. The morphospace of Late Permian coiled nautiloids. *Lethaia* 53: 154–165. <https://doi.org/10.1111/let.12348>
- Korn D., Hairapetian V., Ghaderi A., Leda L., Schobben M. & Akbari A. 2021a. The Changhsingian (Late Permian) ammonoids from Baghuk Mountain (Central Iran). *European Journal of Taxonomy* 776: 1–106. <https://doi.org/10.5852/ejt.2021.776.1559>
- Korn D., Leda L., Heuer F., Moradi Salimi H., Farshid E., Akbari A., Schobben M., Ghaderi A., Struck U., Gliwa J., Ware D. & Hairapetian V. 2021b. Baghuk Mountain (Central Iran): high-resolution stratigraphy of a continuous Central Tethyan Permian-Triassic boundary section. *Fossil Record* 24: 171–192. <https://doi.org/10.5194/fr-24-171-2021>
- Korn D., Miao L. & Bockwinkel J. 2022. The nautiloids from the Dalle à *Merocanites* of Timimoun (Tournaisian-Viséan boundary, Algeria). *European Journal of Taxonomy* 789: 104–129. <https://doi.org/10.5852/ejt.2022.789.1635>
- Kotlyar G.V., Zakharov Y.D., Kropatcheva G.S., Pronina G.P., Chedija I.O. & Burago V.I. 1989. *Pozdnepermiskii etap evolyutsii organicheskogo mira. Midiinskii yaruz SSSR*. Nauka, Leningrad. [In Russian.]
- Kruglov M.V. 1928. Verkhne-kamennougol'nye i artinskie nautilidy Urala. *Trudy Geologicheskogo Muzeya, Akademiya Nauk SSSR* 3: 63–206. [In Russian.]
- Kruglov M.V. 1933. Verkhnepermiskie nautilidy basseynov rek Pinegi i Kuloya [The Upper Permian Nautilida of the Pinega and Kuloi Rivers Basins]. *Trudy Geologicheskogo Instituta, Akademiya Nauk SSSR* 3: 185–208. [In Russian.]
- Kummel B. 1953. American Triassic coiled nautiloids. *Professional Papers, U.S. Geological Survey* 250: 1–104. <https://doi.org/10.3133/pp250>
- Kummel B. 1964. Nautiloidea-Nautilida. In: Moore R.C. (ed.) *Treatise on Invertebrate Paleontology*: K383–K466. The Geological Society of America and The University of Kansas Press, Lawrence, KS
- Leonova T.B. & Shchedukhin A.Y. 2020. Asselian–Sakmarian nautiloids of the Shakh-Tau Reef (Bashkortostan). *Paleontological Journal* 54: 1113–1134. <https://doi.org/10.1134/S0031030120100044>
- Liang X. 1984. Some nautiloids of Late Permian. *Acta Palaeontologica Sinica* 23: 699–704. [In Chinese.]

- Lintz J. 1958. The fauna of the Ames and Brush Creek shales of the Conemaugh Formation of western Maryland. *Journal of Paleontology* 32: 97–112.
- Ma J. 1997. Early Late Permian *Nautilus* in central Jiangxi. *Jiangxi Geology* 11: 27–32.
- McChesney J.H. 1860. Descriptions of new species of fossils from the Paleozoic rocks of the western states. *Transactions of the Chicago Academy of Science* 1: 1–76.
- Meek F.B. & Worthen A.H. 1865. Contributions to the Palaeontology of Illinois and other Western States. *Proceedings of the Academy of Natural Sciences of Philadelphia* 17: 245–273.
- Merla G. 1930. La fauna del Calcare a *Bellerophon* della regione dolomitica. *Memorie dell'Istituto Geologico della Regia Università di Padova* 9: 1–221.
- Miao L., Dai X., Korn D., Brayard A., Chen J., Liu X. & Song H. 2021. A Changhsingian (Late Permian) nautiloid assemblage from Gujiao, South China. *Papers in Palaeontology* 7: 329–351. <https://doi.org/10.1002/spp2.1275>
- Miller A.K. & Kemp A.H. 1947. A *Koninckioceras* from the Lower Permian of north-central Texas. *Journal of Paleontology* 21: 351–354.
- Miller A.K. & Owen J.B. 1934. Cherokee nautiloids of the northern Mid-Continent region. *University of Iowa Studies in Natural History* 16: 185–272.
- Miller A.K. & Thomas H.D. 1936. The Casper Formation (Pennsylvanian) of Wyoming and its cephalopod fauna. *Journal of Paleontology* 10: 715–738.
- Miller A.K. & Unklesbay A.G. 1942. Permian nautiloids from western United States. *Journal of Paleontology* 16: 719–738.
- Miller A.K. & Youngquist W.L. 1949. American Permian nautiloids. *Geological Society of America Memoires* 41: 1–28. <https://doi.org/10.1130/MEM41-p1>
- Miller A.K., Dunbar C.O. & Condra G.E. 1933. The nautiloid cephalopods of the Pennsylvanian system in the Mid-Continent region. *Nebraska Geological Survey Bulletin* 9: 1–240.
- Miller S.A. & Gurley W.F.E. 1897. New species of crinoids, cephalopods and other Palaeozoic fossils. *Bulletin of the Illinois State Museum of Natural History* 12.
- Mojsisovics E.v.M. 1869. Beiträge zur Kenntnis der Cephalopoden-Fauna des alpinen Muschelkalkes. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt, Wien* 19: 567–594.
- Mojsisovics E.v.M. 1902. Das Gebirge um Hallstatt. Die Cephalopoden der Hallstätter Kalke. 1. Band. *Abhandlungen der kaiserlichen und königlichen geologischen Reichsanstalt* 6: 175–356.
- Newell N.D. 1936. Some Mid-Pennsylvanian invertebrates from Kansas and Oklahoma: III. Cephalopoda. *Journal of Paleontology* 1: 481–489.
- Niko S. & Mapes R.H. 2016a. Coiled nautiloids from the lower Carboniferous Fayetteville Formation in Arkansas, Midcontinent North America. *Paleontological Research* 20: 7–17. <https://doi.org/10.2517/2015PR017>
- Niko S. & Mapes R.H. 2016b. Late Carboniferous coiled nautiloids from the Lost Branch Formation of Oklahoma, Midcontinent North America. *Paleontological Research* 20: 75–79. <https://doi.org/10.2517/2015PR020>
- Niko S., Mapes R.H. & Seuss B. 2022. Virgilian (Late Pennsylvanian) coiled nautiloids from the Finis Shale Member of the Graham Formation in Texas, southern Midcontinent North America. *Bulletin of the Tohoku University Museum* 21: 1–19.

- Prinoth H. & Posenato R. 2007. Late Permian nautiloids from the *Bellerophon* Formation of the Dolomites (Italy). *Palaeontographica Abteilung A* 282: 135–165. <https://doi.org/10.1127/pala/282/2007/135>
- Ramsbottom W.H.C. & Moore E.W.J. 1961. Coiled nautiloids from the Viséan of Ireland. *Geological Journal* 2: 630–644. <https://doi.org/10.1002/gj.3350020406>
- Reed F.R.C. 1931. New fossils from the *Productus* Limestones of the Salt Range, with notes on other species. *Memoirs of the Geological Survey of India, Palaeontologia Indica* 17: 1–56.
- Reed F.R.C. 1944. Brachiopoda and Mollusca from the *Productus* limestones of the Salt Range. *Palaeontologia Indica, New Series* 23: 1–768.
- Ruan Y & Zhou Z. 1987. Carboniferous cephalopods in Ningxia Hui Autonomous Region. In: *Namurian Strata and Fossils of Ningxia, China*: 55–177. Nanjing University Press, Nanjing. [In Chinese.]
- Ruzhencev V.E. & Shimansky V.N. 1954. Nizhneperskie svernutye i sognutie nautiloidei yuzhnogo Urala. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 50: 1–152. [In Russian.]
- Schmidt H. 1951. Nautiliden aus deutschem Unterkarbon. *Paläontologische Zeitschrift* 24: 23–57. <https://doi.org/10.1007/BF03044551>
- Schréter Z. 1974. Die Nautiloiden aus dem oberen Perm des Bükkgebirges. In: Sidó M., Zalányi B. & Schréter Z. (eds) *Neue paläontologische Ergebnisse aus dem Oberpaläozoikum des Bükkgebirges*: 253–311. Akadémia Kiadó, Budapest.
- Shimansky V.N. 1962a. Nadotryad Nautiloidea. Nautiloidei. Obshchaya chast. In: Orlov Y.A. (ed.) *Osnovy Paleontologii, Mollyuski - Golovonogie* 1: 33–72. Akademiya Nauk SSSR, Moskva. [In Russian.]
- Shimansky V.N. 1962b. Nadotryad Nautiloidea. Nautiloidei. Sistematicheskaya chast. Otryad Nautilida. In: Orlov Y.A. (ed.) *Osnovy Paleontologii, Mollyuski - Golovonogie* 1: 115–169. Akademiya Nauk SSSR, Moskva. [In Russian.]
- Shimansky V.N. 1965. Podotryad Nautiloidea. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 108: 157–165. [In Russian.]
- Shimansky V.N. 1967. Kamennougol'nie Nautilida. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 115: 1–258. [In Russian.]
- Shimansky V.N. 1979. Nautilida (izuchennost', stratigraficeskoe rasprostranenie, etapy razvitiya). *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 170: 1–67. [In Russian.]
- Shumard B.F. & Swallow G.C. 1858. Descriptions of new fossils from the Coal Measures of Missouri and Kansas. *Transactions of the St. Louis Academy of Science* 1: 198–227.
- Simić V. 1933. Gornji Perm u Zapadnoj Srbiji (Das Oberperm in Westserbien). *Rasprave Geološkog Instituta Kraljevine Jugoslavije [Mémoires du Service Géologique du Royaume de Yougoslavie]* 1: 1–130. [In Serbo-Croatian.]
- Sobolev E.S. 1989. Triasovye nautilidy severo-vostochnoy Azii. *Trudy Instituta Geologii I Geofiziki, Akademiya Nauk SSSR, Sibirskoe Otdelenie* 727: 1–193. [In Russian.]
- Stache G. 1877. Beitrage zur Fauna der Bellerophonkalke Südtirols. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt* 27: 271–318.
- Sturgeon M.T. & Miller A.K. 1948. Some additional cephalopods from the Pennsylvanian of Ohio. *Journal of Paleontology* 22: 75–80.
- Sturgeon M.T., Windle D.L., Mapes R.H. & Hoare R.D. 1982. New and revised taxa of Pennsylvanian cephalopods in Ohio and West Virginia. *Journal of Paleontology* 56: 1453–1479.

- Sturgeon M.T., Windle D.L., Mapes R.H. & Hoare R.D. 1997. Pennsylvanian Cephalopods of Ohio. Part 1. Nautiloid and Bactritoid Cephalopods. *Ohio Division of Geological Survey, Bulletin* 71: 1–191.
- Swallow G.C. 1860. Descriptions of new fossils from the Carboniferous and Devonian rocks of Missouri. *Transactions of the St. Louis Academy of Sciences* 1: 635–660.
- Taraz H., Golshani F., Nakazawa K., Shimuzu D., Bando Y., Ishi K., Murata M., Okimura Y., Sakagami S., Nakamura K. & Tokuoka T. 1981. The Permian and the Lower Triassic Systems in Abadeh Region, Central Iran. *Memoirs of the Faculty of Science, Kyoto University, Series of Geology and Mineralogy* 47: 61–133.
- Taschenberg E.O.W. 1882. Die Mallophagen mit besonderer Berücksichtigung der von Dr. Meyer gesammelten Arten. *Nova Acta der Kaiserlich Leopoldinisch-Carolinisch-Deutschen Akademie der Naturforscher* 44: 1–244. <https://doi.org/10.5962/bhl.title.82513>
- Teichert C. 1940. Contributions to nautiloid nomenclature. *Journal of Paleontology* 14 (6): 590–597.
- Teichert C. 1964. Morphology of hard parts. In: Moore R.C. (ed.) *Treatise on Invertebrate Paleontology*: K13–K53. The Geological Society of America and The University of Kansas Press, Lawrence, KS.
- Teichert C. & Kummel B. 1973. Nautiloid cephalopods from the Julfa Beds, Upper Permian, Northwest Iran. *Bulletin of the Museum of Comparative Zoology, Harvard University* 144: 409–434.
- Tichy G. 1975. Über das Erstauftreten von *Permonutilus* aus der Foldvik Creek Formation (Oberperm) von Ostgrönland. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1975: 693–703.
- Trenkner W. 1868. Palaeontologische Novitäten vom nordwestlichen Harze. I. Iberger Kalk und Kohlengengebirge von Grund. *Abhandlungen der Naturforschenden Gesellschaft zu Halle* 10: 123–182.
- Tucker J.K. 1976. A coiled nautiloid fauna from the Mattoon Formation (Pennsylvanian) of Illinois. *Transactions of the Illinois State Academy of Science* 69: 57–77.
- Tucker J.K. & Mapes R.H. 1978. Coiled nautiloid cephalopods from the Wolf Mountain Shale (Pennsylvanian), north-central Texas. *Journal of Paleontology* 52: 596–604.
- Turner J.S. 1954. New Carboniferous nautiloids from the North of England. *Transactions of Leeds Geologists Association* 6: 219–226.
- Tzwetaev M. 1888. Golovonogiya verkhnego yarusy srednerusskago kamenougol'nago izvestnyaka. *Trudy Geologicheskogo Komiteta* 5: 1–58. [In Russian.]
- Tzwetaev M. 1898. Nautilidy i ammoni nizhnyago otdela Srednerusskago kamennougol'nago izvestnyaka. *Trudy Geologicheskogo Komiteta* 8: 1–46. [In Russian.]
- Unklesbay A.G. 1962. Pennsylvanian Cephalopods of Oklahoma. *Bulletin of the Oklahoma Geological Survey* 96: 1–150.
- Vaillant-Couturier Treat I. 1933. Paléontologie de Madagascar. XIX. Le Permo-Trias marin. *Annales de Paléontologie* 22: 39–96.
- von Arthaber G. 1900. Das jüngere Paläozoicum aus der Araxes-Enge bei Djulfa. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 12: 209–302.
- Waagen W. 1879. Salt Range fossils, 1. *Productus* Limestone fossils. *Palaeontologia Indica* 1: 1–85.
- Worthen A.H. & Meek F.B. 1875. Descriptions and illustrations of invertebrate fossils from the Paleozoic formations. *Illinois Geological Survey* 6: 69–154.
- Wu S. & Kuang W. 1992. Study of nautiloids in the Upper Permian Changxingian reefs from Lichuan, west Hubei. *Journal of China University of Geosciences* 17: 289–294.

Xu G. 1977. Cephalopoda. *Fossil Atlas of South-Central China, Part 2*: 537–582. Geological Publishing House, Beijing.

Yakovlev N. 1899. Fauna nekotorykh verkhnepaleozoyskikh otlozheniy Rossii. 1. Golovonogie i brakhiopody. *Trudy Geologicheskoy Komiteta* 15: 1–150. [In Russian.]

Zhao J., Liang X. & Zheng Z. 1978. Late Permian cephalopods from South China. *Palaeontologia Sinica, Series B* 12: 1–194. [In Chinese.]

Zheng Z. 1984. Late Permian nautiloids from western Guizhou. *Acta Palaeontologica Sinica* 23: 239–253. [In Chinese.]

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