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Article

The Late Permian araxoceratid ammonoids: a case of repetitive temporal and spatial unfolding of homoplastic conch characters

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With 9 figures

Abstract: The Wuchiapingian (early Late Permian) ammonoid family Araxoceratidae shows a morphological spectrum that is recurring in the three genera *Araxoceras* (early Wuchiapingian; Transcaucasus-Iran), *Vedioceras* (late Wuchiapingian; Transcaucasus-Iran) and *Konglingites* plus *Kiangsiceras* (late Wuchiapingian; South China). All three display a range of conch morphology from millstone-shaped to reel-shaped; they also repeatedly show the formation of a tricarinate venter. When the suture line is regarded as the main character for phylogenetic relationships in this group, these conch characters must be seen homoplastic because they iteratively formed in time and space. From the Wuchiapingian sedimentary rocks of NW Iran, three new species of araxoceratid ammonoids are described herein: *Araxoceras truncatum* n. sp. and *Araxoceras insolens* n. sp. (both early Wuchiapingian) as well as *Vedioceras fusiforme* n. sp. (late Wuchiapingian). With these new taxa, the taxonomic diversity and particularly the morphological disparity of the Late Permian ammonoids from the Transcaucasus-NW Iran region is extended.

Key words: Permian, Wuchiapingian, Ammonoidea, Iran, conch morphology.

1. Introduction

Late Permian ammonoids are principally known from only two regions, (1) the Transcaucasus-Iran region (e.g., Abich 1878; Stoyanow 1910; Ruzhencev 1959; Ruzhencev 1962; Ruzhencev 1963; Ruzhencev & Shevyrev 1965; Shevyrev 1965, 1968; Stepanov et al. 1969; Teichert et al. 1973; Bando 1979; Kotlyar et al. 1983; Zakharov et al. 2010; Ghaderi et al. 2014; Korn et al. 2016; Kiessling et al. 2018) and (2) South China (e.g., Sun 1939; Zhao 1965; Zhao 1966; Zhao et al. 1978; Zheng 1981; Zheng 1984; Liang & Guo 1982; Qin 1986; Yang 1987a; Yang 1987b; Guo 1988; Wang 1990; Yang & Xiong 1990; Yang & Yang 1992). These two regions show very different assemblage compositions; while in the Wuchiapingian, the differences are mainly expressed by different genera and species within the same families (e.g., the Araxoceratidae), the Changhsingian shows major differences even in the composition of families (Zhao et al. 1978; Korn et al. 2016). The reason for this conspicuous provincialism is not found yet.

It has been shown that the diversity of the Late Permian ammonoids from the Transcaucasus-Iran region is higher than expected after the publication of the assemblages from Armenia and Azerbaijan at the northern side of the Araxes (= Aras) river in the 1960s. For the late Changhsingian *Paratirolites* Limestone, a number of new taxa could be described from a section east of the town of Julfa (East Azerbaijan, Iran) (Ghaderi et al. 2014; Korn et al. 2016). In the following, we describe further previously unknown Wuchiapingian species in order to complement the diversity already known by the studies of earlier authors. We

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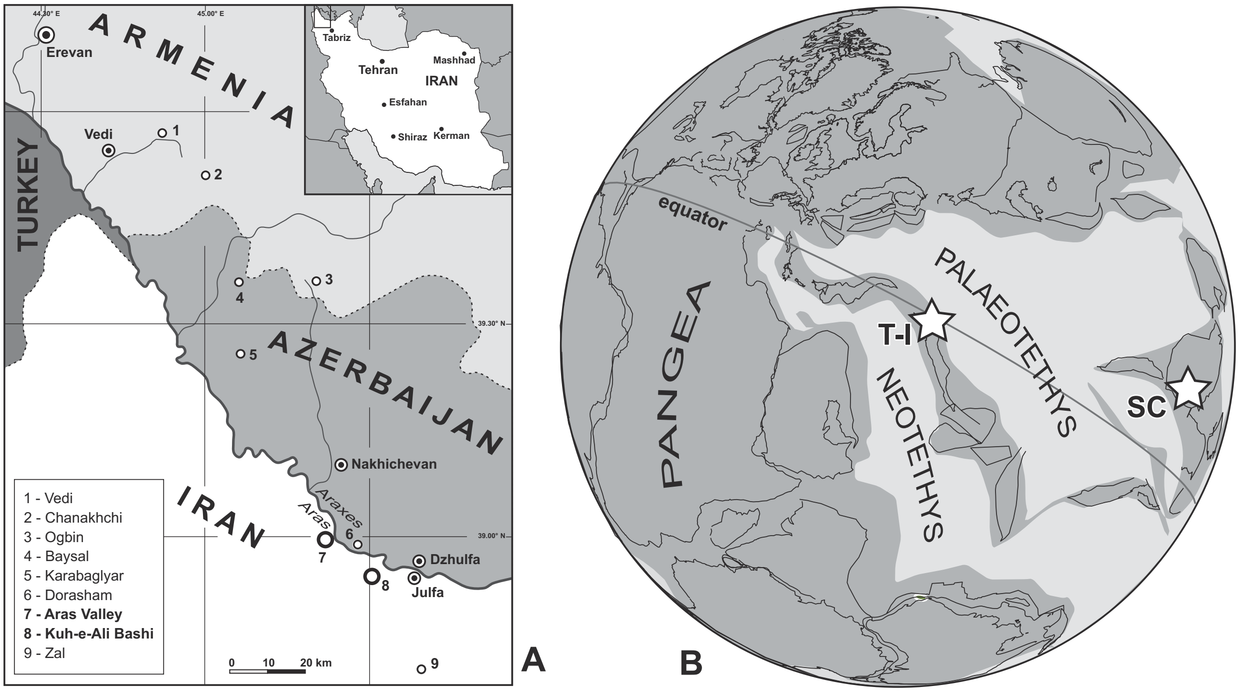


Fig. 1. A – Geographic position of Permian–Triassic boundary sections in the Transcaucasus and in NW Iran; mentioned sections highlighted. **B** – Palaeogeographic position of the Transcaucasus-Iran and South Chinese occurrences (globe after Stampfli & Borel 2002).

aim to contribute to the investigations of the demise of the biota and particularly the Ammonoidea in the dusk of the Late Palaeozoic.

The material described here come from two localities (Fig. 1A):

– Aras Valley section. The section is exposed on the southern side of the Aras Valley (West Azerbaijan, NW Iran; 39.0154° N, 45.4345° E) (Ghaderi et al. 2014). It is located about 19 km WNW of the towns of Dzhulfa (or Culfa; Azerbaijan) and Julfa (or Jolfa; NW Iran) in a dry small side valley beginning 200 metres west of the Aras (Araxes) River. The section has a position approximately 2 km north-west of the Dorasham I section of Ruzhencev et al. (1965). It exposes a complete Wuchiapingian and Changhsingian succession with considerably good outcrop conditions of the upper part of the Wuchiapingian Julfa Formation, the lower, shale-dominated part of the Changhsingian Ali Bashi Formation and an excellent outcrop of the Late Changhsingian *Paratirolites* Limestone.

– Kuh-e-Ali Bashi N section. The section is also new (Ghaderi et al. 2014) and exposes, in several neighbouring places (East Azerbaijan, NW Iran; 38.9456° N, 45.5137° E), the interval from the lower Ali Bashi Formation (which is poorly exposed) to the Early Triassic Elikah Formation. Specimens from the Wuchiapingian Julfa Formation are only available from float material.

2. Araxoceratid ammonoids in time and space

Araxoceratid ammonoids are practically known from only two regions worldwide (Fig. 1B):

1. The Transcaucasian-Iranian region: Already in the first ammonoid descriptions by Abich (1878), some araxoceratids were described such as "*Ceratites trochoides*", "*C. pessoides*", "*C. tropitus*", "*C. intermedius*", and "*C. Djoulfensis*", which can be attributed to *Prototoceras* (the first three species) and *Pseudotoceras* (the last two species). However, it took more than eighty years until Ruzhencev, in a se-

ries of articles (RUZHENCEV 1959; RUZHENCEV 1962; RUZHENCEV 1963) provided an excellent overview on the morphological range and taxonomic richness of the group. He regarded ten genera with about 30 species as belonging to the newly introduced family Araxoceratidae. All material came from a number of localities between Vedi (now Armenia) in the North and Dorasham (now belonging to Azerbaijan) at the Araxes River in the South. It was particularly the Dorasham sections that provided most of the material. Subsequently, some araxoceratids were described by ZAKHAROV (in KOTLYAR et al. 1983).

Araxoceratids were also described from the southern side of the Araxes River in NW Iran. Among these the enigmatic "*Julfotoceras tarazi*", introduced by BANDO (1973), was putatively collected from the *Paratirolites* Limestone of Julfa. However, very intensive field studies of this rock unit (KORN et al. 2016) did not provide any trace of this species and it may be argued that the single specimen under discussion comes in fact from the upper part of the Julfa Formation, which also contains red nodular limestones and lithologically closely resembles the *Paratirolites* Limestone.

From the Abadeh region in Central Iran, BANDO (1979) described a number of species of araxoceratids, some of which were new. Principally, a similar species spectrum like in the Transcaucasus was recorded. Finally, ZAKHAROV & MOUSAVI ABNAVI (in ZAKHAROV et al. 2010) added two species of *Araxoceras* from Abadeh.

2. South China: After the first record of "*Glyphioceras* (*Anderssonoceras*) *anfuense*" by GRABAU (1924), it took also a long time until detailed studies of the ammonoid group were published. Beginning with ZHAO (1965; 1966), numerous species had been established, summarized in the voluminous monograph by ZHAO et al. (1978), in which more than 40 species belonging to 16 genera in the two otoceratoid families Anderssonoceratidae (with the subfamilies Planodiscoceratinae and Anderssonoceratinae) and Araxoceratidae (with the subfamilies Araxoceratidae and Konglingitinae) were outlined. ZHENG & MA (1982) described a number of additional species particularly of the genus *Sanyangites*, LIANG (1983) outlined the new genera *Geermuceras* as well as *Lijiangoceras*, and later YANG & XIONG (1990) added the poorly known family Etoushanoceratidae.

Apart from the two main regions, araxoceratids are known from Coahuila in Mexico (KING & MILLER 1944; SPINOSA et al. 1970; SPINOSA & GLENISTER 2000), South Primorye, Russia (ZAKHAROV & PAVLOV 1986), Japan (EHIRO & BANDO 1985), and Thailand (FUJIKAWA & ISHIBASHI 1999).

3. Conch characters in the Araxoceratidae

The araxoceratid ammonoids are usually very easily recognizable because of their raised umbilical margin. Most of the species show a discoidal general shape but some possess the form of a wheel or a reel. The venter is usually flattened or tectiform with a keel, but may also be concave or additional keels and furrows. The shell surface is nearly smooth and decorated with faint growth lines, but ribs or notes are absent. Constrictions are also not known. The suture line of all species in the araxoceratids possesses similar characters:

External lobe: It may be either large and as deep as the adventive lobe (e.g., *Araxoceras*) or small and much shorter than the adventive lobe (e.g., *Vedioceras*, *Konglingites*), subdivided, usually the prongs are simple but they may be subdivided into two or, more rarely, numerous small notches.

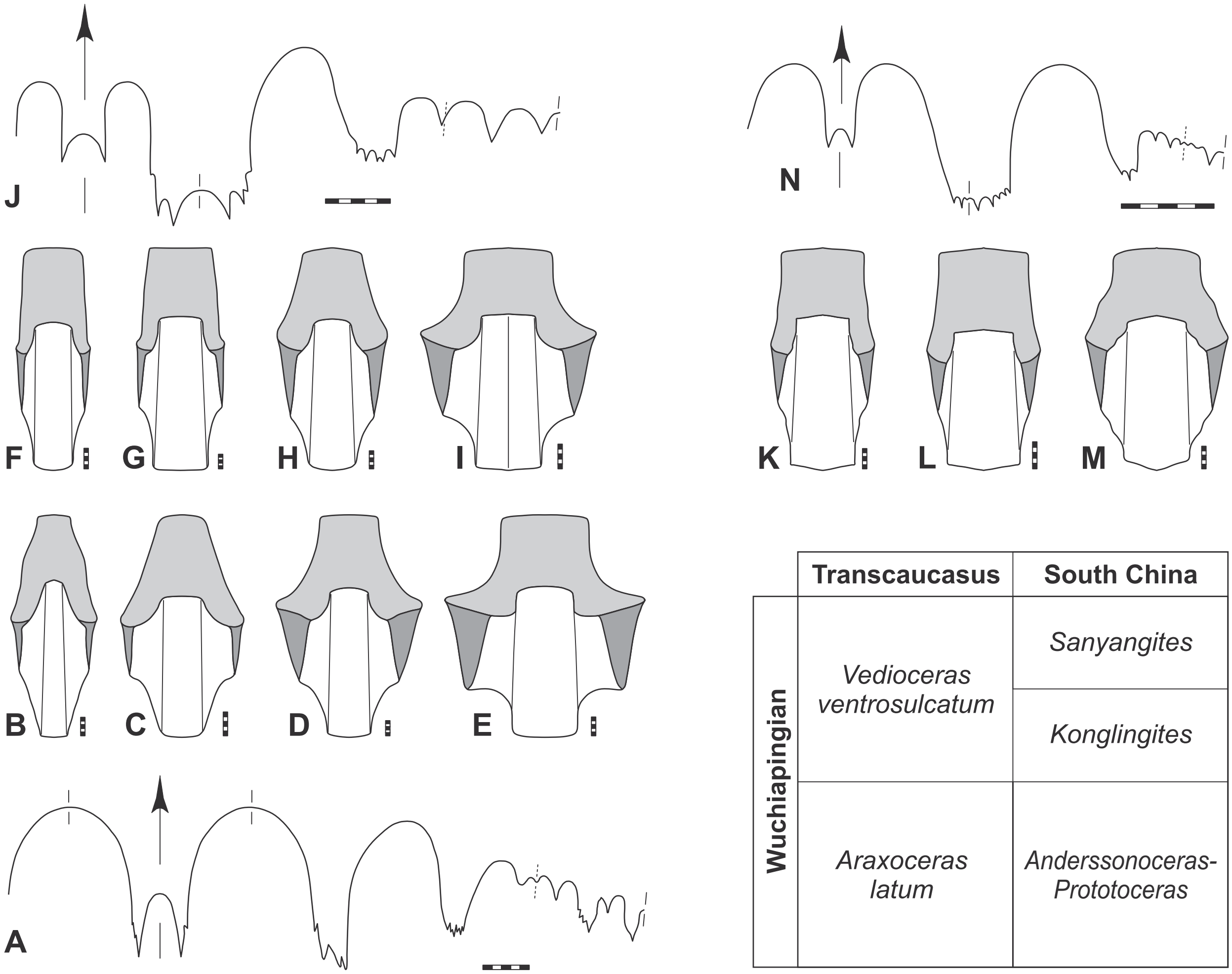
Ventrolateral saddle: It is broadly rounded and usually nearly symmetric, positioned of the half on the flank and half on the venter (e.g., *Araxoceras*) but in other genera entirely on the venter (e.g., *Vedioceras*, *Konglingites*).

Adventive lobe: Its general shape can be narrow (as wide as the external lobe) with nearly parallel flanks with small notches and positioned on the flank (e.g., *Araxoceras*), rather wide with converging flanks and numerous very small notches of similar size (e.g. *Konglingites*) or wide (twice the width of the external lobe) with notches of different size (e.g., *Vedioceras*); the adventive lobe can be positioned on the flank (e.g., *Araxoceras*) or subdivided by the ventrolateral shoulder in a ventral and lateral portion (e.g., *Vedioceras*, *Konglingites*).

Lateral saddle: It is usually rounded and asymmetric by some inclination towards the umbilicus.

Lateral lobe: It is, at least in most cases, well-defined usually smaller than the adventive lobe with fewer notches. In some cases (e.g., *Vescotoceras*, *Dzhulfoceras*) it may be tightly connected with the secondary lobes developed on the umbilical margin and inner flank area.

The list shows that there are indeed two clearly separable groups when the suture line is regarded. ZHAO et al. (1978) used this for the separation of the two subfamilies Araxoceratinae and Konglingitinae.



		Transcaucasus	South China
Wuchiapingian		*Vedioceras ventrosulcatum*	*Sanyangites*
			Konglingites
		Araxoceras latum	*Anderssonoceras-Prototoceras*

Fig. 2. Morphological range of conch geometry in the three Wuchiapingian genera *Araxoceras*, *Vedioceras* and *Konglingites*; suture lines and reconstructed dorsal views. A, C–H, J after RUZHENCEV (1962, 1963); K–N after ZHAO et al. (1978). **A** – *Araxoceras latum* RUZHENCEV, 1962, specimen PIN 1425/50; at 46 mm ww, 32 mm wh. **B** – *Araxoceras truncatum* n. sp., specimen MB.C.29132. **C** – *Araxoceras glenisteri* RUZHENCEV, 1962, specimen PIN 1425/63. **D** – *Araxoceras latum* RUZHENCEV, 1962, specimen PIN 1425/50. **E** – *Araxoceras latissimum* RUZHENCEV, 1959, specimen PIN 1425/1. **F** – *Vedioceras ogbinense* RUZHENCEV, 1962, specimen PIN 1425/165. **G** – *Vedioceras ventroplanum* RUZHENCEV, 1962, specimen PIN 1425/159. **H** – *Vedioceras umbonavarum* RUZHENCEV, 1962, specimen PIN 1425/173. **I** – *Vedioceras fusiforme* n. sp., specimen MB.C.29134. **J** – *Vedioceras umbonavarum* RUZHENCEV, 1962, specimen PIN 1425/173; at 27 mm ww, 22.5 mm wh. **K** – *Konglingites striatus* ZHAO, LIANG & ZHENG, 1978, specimen NIGP 14910. **L** – *Konglingites latisellatus* ZHAO & LIANG, 1966, specimen NIGP 14913. **M** – *Konglingites sinensis* ZHAO & LIANG, 1966, specimen NIGP 14897. **N** – *Konglingites striatus* ZHAO, LIANG & ZHENG, 1978, specimen NIGP 14910; at 33 mm dm. Scale bar units = 1 mm.

But they presented a phylogenetic tree in which the family Araxoceratidae as well the subfamily Konglingitinae are polyphyletic. They related their genera *Kiangsiceras* and *Konglingites* directly from *Araxoceras*, while they saw in *Vedioceras* a descendent of *Pericarinoceras* (Anderssonoceratidae).

To sum up, based on the suture line it can be said that there is a trend from a small adventive lobe positioned on the flank towards a wider adventive lobe that has a position in part on the venter and in part on the flanks. However, it cannot be stated with certainty if this is a phylogenetic trend.

It is interesting that a similar range of conch morphology occurs independently in time and space in the three genera *Araxoceras* (early Wuchiapingian; Transcaucasus–Iran), *Vedioceras* (late Wuchiapingian;

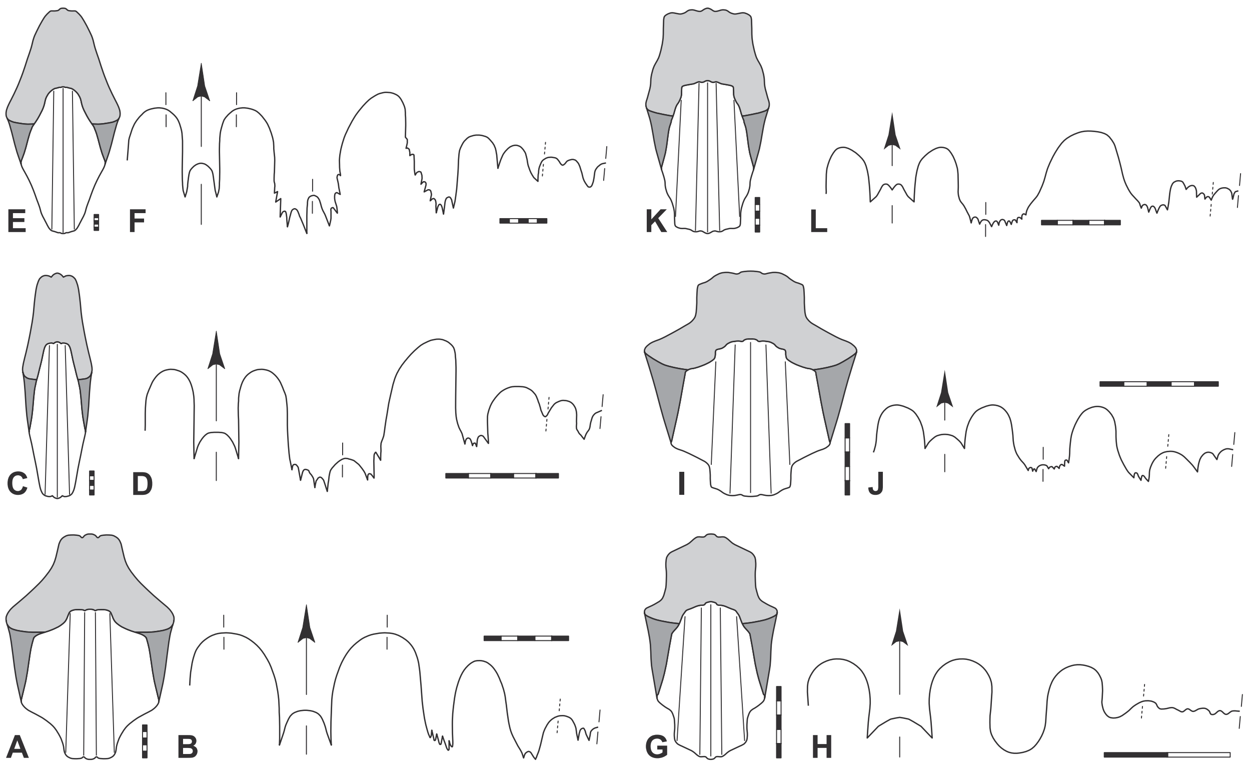


Fig. 3. Examples of iterative recurring conch, *Vedioceras* and *Konglingites*; reconstructed dorsal views and suture lines. A–F after RUZHENCEV (1962, 1963); G–L after ZHAO et al. (1978). **A, B** – *Araxoceras varicatum* RUZHENCEV, 1962, specimen PIN 1425/61; suture line at 23.5 mm ww, 11.0 mm wh. **C, D** – *Vedioceras ventrosulcatum* RUZHENCEV, 1963, specimen PIN 1425/175; suture line at 11.0 mm ww, 13.0 mm wh. **E, F** – *Avushoceras yakowlewi* RUZHENCEV, 1962, specimen PIN 1425/191; suture line at 31.0 mm ww, 32.5 mm wh. **G, H** – *Pericarinoceras robustum* ZHAO & LIANG, 1966, specimen NIGP 14893; suture line at 9.0 mm dm. **I, J** – *Kiangsiceras rotule* ZHAO & LIANG, 1965, specimen NIGP 14900; suture line at 15.0 mm dm. **K, L** – *Sanyangites tricarinatus* ZHAO, LIANG & ZHENG, 1978, specimen NIGP 34299; suture line at 28.0 mm dm. Scale bar units = 1 mm.

Transcaucasus–Iran) and *Konglingites* plus *Kiangsiceras* (probably late Wuchiapingian; South China):

– General conch shape: In the tree genera; conch shapes range from millstone-shaped to reel-shaped in a rather continuous succession (Fig. 2).

– Shape of the venter: In the three genera, most of the species possess a flattened venter. But in all of them, also species with tricarinatre venter occur: *Araxoceras varicatum*, *Vedioceras ventrosulcatum*, and *Konglingites rotule* (which was placed by ZHAO et al. 1978 in the separate genus *Kiangsiceras*). Differences, however, occur in the general shape of these three species: *A. varicatum* and *K. rotule* are reel-shaped, while *V.ventrosulcatum* has the shape of a millstone. It should be noted that the presence of ventral furrows and keels is a repeated theme in the Anderssonoceratidae and the Araxoceratidae (Fig. 3).

There are good reasons to assume that the suture line is a character better suitable for the phylogenetic analysis of the araxoceratids, simply because the main suture characters are stable within the genera despite of differences in conch shape between the species. Under this assumption, however, it can only be assumed that the possible late Wuchiapingian descendants of *Araxoceras*, i.e. *Vedioceras* and *Konglingites*, acquired their range of conch geometry independently. The very strange conch morphologies (raised umbilical ridge, tricarinate venter) must be regarded as homoplasies. The phylogenetic relationship between the two advanced late Wuchiapingian genera *Vedioceras* and *Konglingites* remain unclear. Based on the suture line, a phylogenetic lineage from *Araxoceras* to *Konglingites* and then to *Vedioceras* may be proposed because of the development of the external and adventive lobes, but this does not explain the clear geographic separation of the latter two genera.

The fact that there are no intermediates known, for instance, between *Araxoceras* and *Vedioceras* in the Transcaucasus-Iran region and between *Araxoceras* and *Konglingites* in South China speaks for immigration events from another yet unknown region.

4. Systematic descriptions

The description of the material follows the procedure outlined by Korn (2010) and Korn et al. (2016); the suture line terminology is according to Korn et al. (2003). The new material is stored in the collection of the Museum für Naturkunde, Berlin, under the catalogue numbers MB.C.29132 to MB.C.29134. Other cited material is stored in the collection of the Paleontological Institute, Russian Academy of Sciences (PIN prefix) and the Nanjing Institute of Geology and Palaeontology (NIGP prefix).

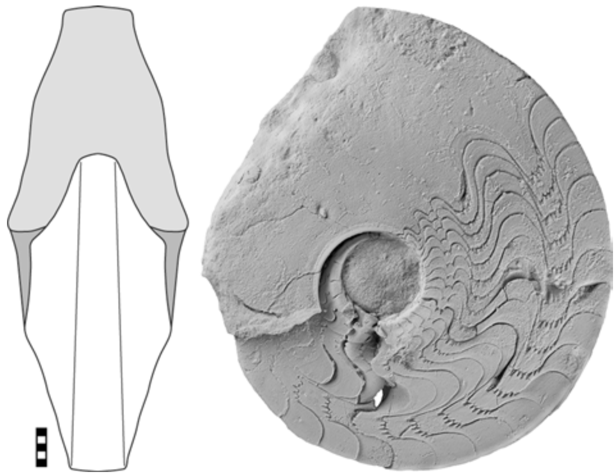


Fig. 4. *Araxoceras truncatum* n. sp., holotype MB.C.29132, from the Ali Bashi N section (float of the lower Julfa Formation; early Wuchiapingian), lateral view and reconstruction of dorsal view. Scale bar units = 1 mm.

Order Ceratitida Hyatt, 1884
Suborder Otoceratina Shevyrev & Ermakova, 1979
Superfamily Otoceratoidea Hyatt, 1900
Family Araxoceratidae Ruzhencev, 1959
Subfamily Araxoceratinae Ruzhencev, 1959

Genus *Araxoceras* Ruzhencev, 1959

Type species: *Araxoceras latissimum* Ruzhencev, 1959; by original designation.

Genus diagnosis: Genus of the family Araxoceratidae with wheel- or spindle-shaped conch, with narrow to very wide whorls (ww/dm = 0.50–0.90), venter flat or convex, sometimes with two grooves. Umbilicus rather narrow to moderately wide (uw/dm = 0.20–0.40), with slightly protruding or very conspicuous rim. External lobe deep; ventrolateral saddle wide, situated half on venter and half on flank. Adventive lobe very narrow with a position on the flank. Lateral lobe well-developed.

Included species:

latissimum: *Araxoceras latissimum* Ruzhencev, 1959; Transcaucasus.
rotoides: *Araxoceras rotoides* Ruzhencev, 1959; Transcaucasus.
latum: *Araxoceras latum* Ruzhencev, 1962; Transcaucasus.
glenisteri: *Araxoceras glenisteri* Ruzhencev, 1962; Transcaucasus.
tectum: *Araxoceras tectum* Ruzhencev, 1959; Transcaucasus.
varicatum: *Araxoceras varicatum* Ruzhencev, 1962; Transcaucasus.
abarquense: *Araxoceras abarquense* Zakharov & Mousavi Abnavi (in Zakharov et al. 2010); Central Iran.
iranense: *Araxoceras iranense* Zakharov & Mousavi Abnavi (in Zakharov et al. 2010); Central Iran.
insolens: Araxoceras insolens n. sp.; NW Iran.
truncatum: Araxoceras truncatum n. sp.; NW Iran.
simplex: *Araxoceras simplex* Qin, 1986; South China.

Discussion: *Araxoceras* is a rather species-rich genus that is mainly known from the Transcaucasus-Iran region (e.g., Ruzhencev 1959; Ruzhencev 1962) and from South China (e.g., Zhao et al. 1978). Here, in contrast to Shevyrev (1986) and Leonova (2002), we follow the genus concept expressed by Ruzhencev (1962), meaning that the genus contains only those araxoceratid species with the adventive lobe positioned on the flank and with a wheel-shaped or spindle-shaped conch with more or less flattened venter.

Zhao et al. (1978) described the species "*Araxoceras kiangsiense* Chao & Liang" from South China. According to the suture line with the adventive lobe positioned on the ventrolateral shoulder, it should be assigned to *Konglingites*. "*Araxoceras kiangsiense*" described by Qin (1986) requires confirmation.

Araxoceras truncatum n. sp.
Figs. 4, 5

Etymology: From the Latin truncatum = truncated, because the whorl profile has the shape of a truncated arrow.

Holotype: Specimen MB.C.29132; illustrated in Fig. 4.

Type locality and horizon: Ali Bashi N section (NW Iran); float from the lower Julfa Formation, (Wuchiapingian).

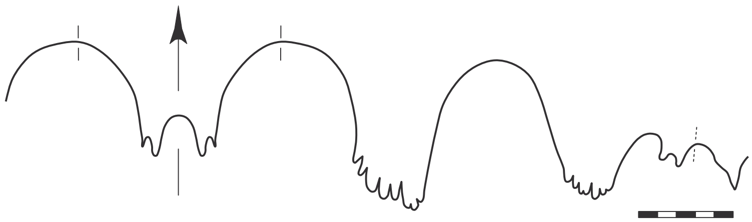


Fig. 5. *Araxoceras truncatum* n. sp., suture line of holotype MB.C.29132, from float of the Ali Bashi N section (lower Julfa Formation; early Wuchiapingian), at 21.8 mm ww, 21.4 mm wh. Scale bar units = 1 mm.

Material: Only the holotype.

Diagnosis: *Araxoceras* with a conch reaching 80 mm dm. Conch in the adult stage thinly discoidal (ww/dm ~ 0.40) and subinvolute (uw/dm ~ 0.17), whorl profile compressed (ww/wh ~ 0.80). Venter flattened; ventrolateral shoulders angular, flanks concave and sinuous in section, umbilical rim weakly raised. Altogether around 17 notches of the E, A and L lobes.

Description: Holotype MB.C.29132 is a rather well-preserved internal mould, in which parts of the bodychamber are preserved (Fig. 4). The maximum measurable diameter is 60 mm and the diameter of the phragmocone is 55 mm. Conspicuous septal crowding at the end of the phragmocone speaks for the adulthood of the specimen. At 60 mm diameter, the conch is thinly discoidal and subinvolute (ww/dm = 0.39; uw/dm = 0.17), with a compressed whorl profile (ww/wh = 0.80). The venter is nearly flat, the ventrolateral shoulders are angular and the flanks are curved in section, with two weakly concave areas separated by a convex midflank portion. The umbilical margin is pronounced and weakly raised, and the umbilical wall is curved towards the venter (Fig. 4).

The suture line has an external lobe that reaches only about 70 % of the depth of the adventive lobe (Fig. 4). Its prongs are subdivided and show two notches of unequal size; the symmetric ventrolateral saddle is broadly arched and symmetric. On the flank follows an asymmetric adventive lobe with nearly parallel flanks and an oblique base, which bears eight notches of slightly irregular size. It follows a parabolic lateral saddle and a V-shaped lateral lobe with seven small notches and finally some small secondary umbilical lobes. It is striking that the shape of the secondary notches of the adventive and lateral lobes is inverted, meaning that not the lobes are pointed and saddles rounded but vice versa.

Discussion: The new species has a marginal position within *Araxoceras* for three reasons. First, it possesses a comparatively short external lobe and, in respect, shows affinities to the closely related genus *Prototoceras* (which, however, possesses a tectiform venter with a keel). Second, it possesses a compressed whorl profile with sinuous flanks and shoes affinities to *Dzhulfoceras* (which has a suture line with few notches in the lobes and a conch with much narrower umbilicus).Third, it has a compressed conch that is slenderer than in any of the other *Araxoceras* species.

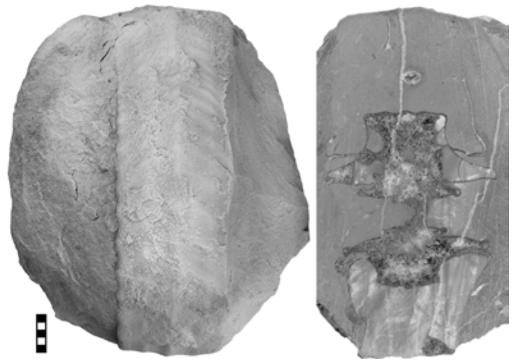


Fig. 6. *Araxoceras insolens* n. sp., holotype MB.C.29133, from the Aras Valley section (float of the lower Julfa Formation; early Wuchiapingian). **A** – Ventral view. **B** – Cross-section. Scale bar units = 1 mm.

Araxoceras insolens n. sp.
Figs. 6, 7

Etymology: From the Latin insolens = strange, because of the conch shape.

Holotype: Specimen MB.C.29133; illustrated in Fig. 6.

Type locality and horizon: Aras Valley section (NW Iran); float from lower the Julfa Formation, (Wuchiapingian).

Material: Only the holotype.

Diagnosis: *Araxoceras* with a conch reaching 50 mm dm. Conch ontogeny with conspicuous changes in the cross-section and particularly the whorl profile; ww/wh reaching a value of 3.00 in the middle growth stage and decreases to nearly 1.00 in the adult stage. Umbilical rim pronounced and hairneedle-shaped in section. Venter in the subadult stage flattened, with low mid-ventral keel and four longitudinal grooves.

Description: Holotype MB.C.29133 is a specimen with 46 mm conch diameter that is still surrounded by the matrix; only part of the venter ranges out of the embedding limestone nodule (Fig. 6). The venter is nearly flat on the last

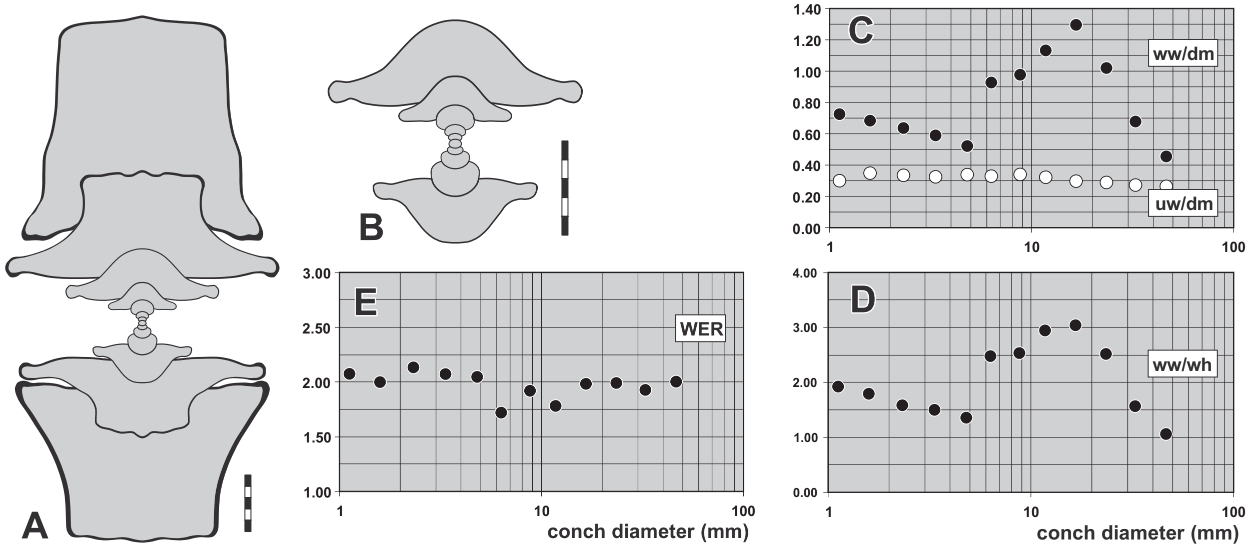


Fig. 7. *Araxoceras insolens* n. sp., holotype MB.C.29133, from (float of the lower Julfa Formation; early Wuchiapingian). **A, B** – Cross-section (partly reconstructed by re-deformation). **C–E** – Ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh) and whorl expansion rate (WER). Scale bar units = 1 mm.

volution, but shows a shallow midventral keel. The angular ventrolateral margin bears delicate tubercles spaced in distances of 2.5 mm; they initiate weak plications, which weaken out on the venter, where they protract forward to form a shallow rostrum. Half a volution earlier, the venter bears four shallow longitudinal grooves.

The cross-section shows the development beginning from the initial stage (Fig. 7). The inner three volutions up to a conch diameter of 5 mm show depressed oval to nearly circular whorl profiles. In the fourth whorl, a sudden change takes place in forming a very conspicuous umbilical rim, the wh/wh ratio reaches 2.50 (at 6.4 mm dm) and 3.00 (at 12 mm dm). The venter is broadly rounded for one and-a-half volutions, the flanks are concave and the conspicuously raised umbilical rim shows, in its section, a lateral projection in the form of a hair-needle shape. The following volutions show then a new whorl profile after the sudden flattening of the venter. This bears a low median keel and two rows of shallow longitudinal grooves on both sides. The ventrolateral shoulder is now angular, the flanks are concave and the umbilical rim is conspicuous with a hairneedle-shaped section. The whorl profile changes towards lower ww/wh ratios; while at 16.7 mm conch diameter the ratio is still exceeding 3.00, it is only 2.50 at 23.6 mm diameter. The last preserved whorl is then characterized by another change of the whorl profile; the umbilical rim becomes less important and the four groves on the venter disappear on the last half volution. At the largest diameter of 46 mm, the ww/wh ratio is only 1.07; the general whorl profile is nearly quadratic with flattened venter, nearly flattened curved flanks and angular, weakly raised umbilical margin.

Discussion: Although only present in a single specimen that is not even cleaned from the surrounding matrix, it is, because of its very particular conch geometry and conch ontogeny, described a new species. The conch ontogeny is very strange and justifies separation from the other species. The suture line is not discernible in the specimen, but the cross-section meeting septa allows the statement that it has a narrow adventive lobe with a position on the flank. An attribution to *Araxoceras* is thus justified.

Genus *Vedioceras* Ruzhencev, 1962

Type species: *Vedioceras ventroplanum* Ruzhencev, 1962; by original designation.

Genus diagnosis: Genus of the family Araxoceratidae with wheel- or spindle-shaped conch, with narrow to wide whorls (ww/dm = 0.30–0.75), venter flat or convex, sometimes with two grooves. Umbilicus rather narrow (uw/dm = 0.20–0.30), with slightly protruding or very conspicuous rim. External lobe extremely narrow and short; ventrolateral saddle also very narrow, situated completely on the venter. Adventive lobe very wide, divided by the ventrolateral shoulder into two parts. Lateral lobe much smaller than the adventive lobe.

Included species:

ventroplanum: *Vedioceras ventroplanum* Ruzhencev, 1962; Transcaucasus.

ogbinense: *Vedioceras ogbinense* Ruzhencev, 1962; Transcaucasus.

umbonavarum: *Vedioceras umbonavarum* Ruzhencev, 1963; Transcaucasus.

ventrosulcatum: Vedioceras ventrosulcatum Ruzhencev, 1963; Transcaucasus.

nakamurai: *Vedioceras nakamurai* Bando, 1979; Central Iran.

abadehense: Julfotoceras abadehense Bando, 1979; Central Iran.

fusiforme: Vedioceras fusiforme n. sp.; NW Iran.

Discussion: After its introduction by Ruzhencev (1962), *Vedioceras* has always been regarded as a valid genus based on its peculiarities of conch shape and particularly the suture line with the large adventive lobe located half on the flanks and half on the venter. Shevyrev (1986) and Leonova (2002) regarded *Vedioceras* as junior synonym of *Araxoceras*, but did not provide a discussion of reasons that may speak for a merging of the two genera. Here we follow the genus concept of the araxoceratids ammonoids expressed by Ruzhencev (1959, 1962, 1963) in separating the genera because of differences in conch shape and suture line. *Vedioceras* is well-defined by the small and short external lobe and the very large adventive lobe.

Shevyrev (1986) and Leonova (2002) also regarded *Konglingites* Zhao, Liang & Zheng, 1978 as synonymous with *Vedioceras*. This genus, which is mainly known only from Jiangxi (South China), has a suture line closely resembling *Vedioceras* with a small external lobe. It has also a wide adventive lobe that is located half on the venter and half on the flank, but this lobe has diverging flanks in contrast to *Vedioceras*, in which the adventive lobe has nearly parallel flanks.

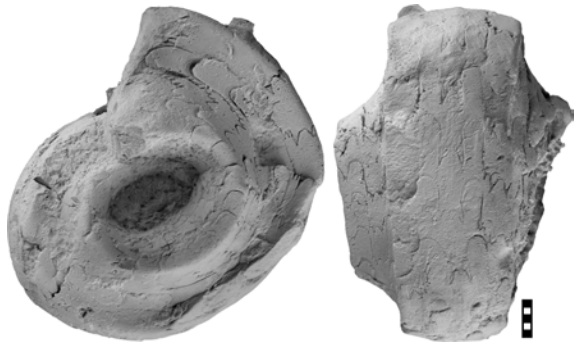


Fig. 8. *Vedioceras fusiforme* n. sp., holotype MB.C.29134, from the Aras Valley section, 22.40 m below the extinction horizon (upper Julfa Formation; late Wuchiapingian). Scale bar units = 1 mm.

Vedioceras fusiforme n. sp.
Figs. 8, 9

Etymology: From the Latin fusiforme = spindle-shaped, because of the conch shape.

Holotype: Specimen MB.C.29134; illustrated in Fig. 8.

Type locality and horizon: Aras Valley section (NW Iran); 22.40 m below the extinction horizon (= 8.45 m below the top of the Julfa Formation)), *Vedioceras ventrosulcatum* Zone (Wuchiapingian).

Material: Only the holotype.

Diagnosis: *Vedioceras* with a conch reaching 70 mm dm. Conch in the adult stage pachyconic (ww/dm ~ 0.75) and subinvolute (uw/dm ~ 0.25). Venter flattened, weakly tectiform; ventrolateral shoulders angular, flanks concave and umbilical rim conspicuously raised. Altogether around 22 notches of the E, A and L lobes.

Description: Holotype MB.C.29134 is a slightly distorted but otherwise rather well-preserved steinkern specimen with 45 mm diameter (Fig. 8). It is fully chambered with about 18 chambers of the last volution; the last septa are slightly crowded, which may speak for adulthood. Therefore, a maximum diameter including the bodychamber may have been 70 mm. The conch is pachyconic and subinvolute (ww/dm = 0.74; uw/dm = 0.25) with a depressed whorl section (ww/wh = 1.68) and a moderately high coiling rate (WER = 1.96). The very characteristic whorl profile shows a flattened tectiform venter with a very low and blunt median keel, from which weakly convex sides extend towards the rectangular ventrolateral shoulders. The flanks are concave and are laterally raised to form a strongly raised umbilical ridge, which is very narrow and borders the flanks from the steep and weakly convex umbilical wall (Fig. 9A).

The holotype has, at 44 mm conch diameter, a suture line characteristic for the genus *Vedioceras* (Fig. 9B). The external lobe with its subparallel flanks is weakly pouched and reaches a depth only a little bit deeper than half of the adventive lobe. One of the prongs is simple and the other has two small notches. The ventrolateral saddle, which has a position entirely on the venter, is narrower that the external lobe and slightly inflated. The adventive lobe is by far the dominant sutural element; it is almost exactly subdivided into a ventral portion situated on the venter and a dorsal portion situated on the outer flank. Both sides are slightly asymmetric; the centre of the lobe shows large notches and the sides show smaller and narrower notches. The lateral saddle is asymmetric and also the lateral lobe shows an asymmetry, being ventrally inclined, and possesses ten irregularly sized notches. Outside of the umbilical rim, another small bidentate lobe is placed.

Discussion: Regarding the conch geometry, the new species *Vedioceras fusiforme* has a morphological relationship to *V. umbonavarum* like *Araxoceras latissimum* Ruzhencev, 1959 has to *A. latum* Ruzhencev, 1962. It is, with a ww/dm ratio exceeding 0.70, the stoutest of all of *Vedioceras* species.

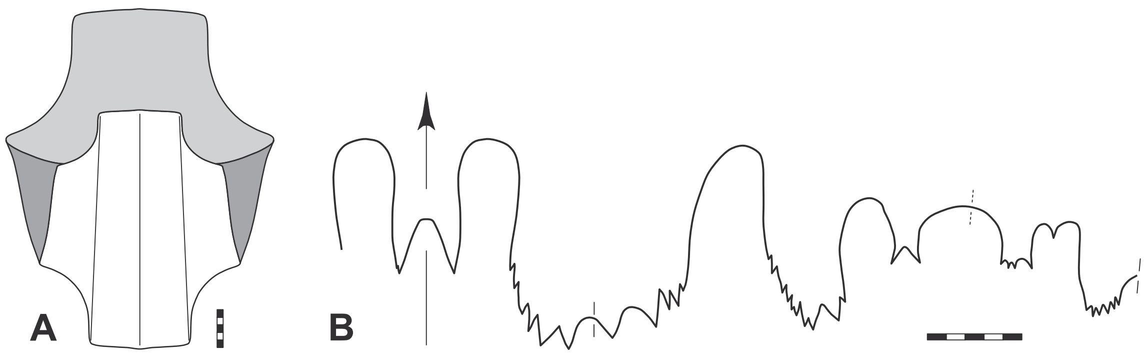


Fig. 9. *Vedioceras fusiforme* n. sp., holotype MB.C.29134, from the Aras Valley section, 22.40 m below the extinction horizon (upper Julfa Formation; late Wuchiapingian). **A** – Dorsal view. **B** – Suture line (reversed), at 44.5 mm dm, 29.5 mm ww, 19.0 mm wh. Scale bar units = 1 mm.

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