

# Sporadoceratid ammonoids from the Shotori Range (east-central Iran) – a case of putative gigantism caused by hydraulic sorting?

DIETER KORN<sup>1</sup>, ABBAS GHADERI<sup>2</sup>, LÉA DEVAERE<sup>1</sup>, VACHIK HAIRAPETIAN<sup>3</sup>,  
MOHAMMAD KHANEHBAD<sup>2</sup> and ZDZISŁAW BELKA<sup>4</sup>

<sup>1</sup> *Museum für Naturkunde Berlin, Invalidenstraße 43, 10115 Berlin, Germany.*

*E-mails: dieter.korn@mf-n-berlin.de; lea.devaere@mf-n-berlin.de*

<sup>2</sup> *Department of Geology, Faculty of Science, Ferdowsi University of Mashhad, Mashhad, Iran.*

*E-mails: aghaderi@um.ac.ir; mkhanehbad@um.ac.ir*

<sup>3</sup> *Department of Geology, Khorasgan (Esfahan) Branch, Islamic Azad University, P.O. Box 81595-158,  
Esfahan, Iran. E-mail: vachik@khuif.ac.ir*

<sup>4</sup> *Adam Mickiewicz University, Isotope Laboratory, Krygowskiego 10, PL 61-680 Poznań, Poland.  
E-mail: zbelka@amu.edu.pl*

## ABSTRACT:

Korn, D., Ghaderi, A., Devaere, L., Hairapetian, V., Khanehbad, M. and Belka, Z. 2019. Sporadoceratid ammonoids from the Shotori Range (east-central Iran) – a case of putative gigantism caused by hydraulic sorting? *Acta Geologica Polonica*, **69** (1), 27–49. Warszawa.

The Shotori Range of east-central Iran (east of Tabas) has yielded Famennian ammonoid assemblages dominated by the family Sporadoceratidae. Four genera *Maeneceras* Hyatt, 1884, *Iranoceras* Walliser, 1966, *Sporadoceras* Hyatt, 1884 and *Erfoudites* Korn, 1999 are represented. The conodont assemblage of one sample containing *Iranoceras* revealed an Upper *marginifera* Zone age. The ammonoid assemblages are characterised by comparatively large specimens; they reach conch diameters of 300 mm (including the body chamber) and the mean size is larger than 100 mm. The preservation of the material from the Shotori Range and size comparison with sporadoceratid assemblages from the Anti-Atlas of Morocco and the Rhenish Mountains of Germany suggest that hydraulic sorting has resulted in a bias towards large conchs, explaining the size distribution, rather than latitudinal differences. The new species *Maeneceras tabasense* is described; the genus *Iranoceras* is revised with a new description of the two species *Iranoceras pachydiscus* (Walliser, 1966) and *Iranoceras pingue* (Walliser, 1966).

**Key words:** Late Devonian; Famennian; Iran; Ammonoids; Body size; Conodonts.

## INTRODUCTION

The Famennian (Late Devonian) sporadoceratids are a long-living ammonoid lineage occurring from near the base of the stage up to the Hangenberg extinction event near the Devonian–Carboniferous boundary (Korn and Klug 2002). They are at their peak in terms of numbers and species diversity in the late early Famennian (*Maeneceras* Hyatt, 1884) and

the middle Famennian (particularly *Sporadoceras* Hyatt, 1884 and *Erfoudites* Korn, 1999) and play a subordinate role in the late Famennian. The sporadoceratids are a morphologically conservative group with only minor changes in conch morphology and suture line with time; only with respect to their shell ornament are they more variable and show a transition from simple growth lines with a convex course at the beginning towards biconvex growth lines in com-

bination with spiral lines later in their evolutionary history (e.g., Bogoslovsky 1971; Korn 1999).

Sporadoceratid ammonoids are known from numerous places worldwide; they are known from North America (e.g., Miller 1938) and South America (e.g., Kullmann 1993), Central Europe (e.g., Wedekind 1918; Lange 1929; Becker 1993), Eastern Europe (e.g., Nalivkina 1953; Bogoslovsky 1971), North Africa (e.g., Petter 1959; Korn 1999; Becker *et al.* 2002; Bockwinkel *et al.* 2002; Korn *et al.* 2015), southern Asia (e.g., Walliser 1966; Becker *et al.* 2004), eastern Asia (e.g., Ruan 1981) and Australia (e.g., Petersen 1975). In their wide geographical distribution, they differ from many other contemporaneous ammonoid groups, such as the clymeniids and the prionoceratid ammonoids. Sporadoceratids often occur in large numbers of specimens and dominate the ammonoid assemblages; this makes them interesting objects for studying intraspecific variation and survivorship patterns (e.g., Walton *et al.* 2010).

In the following, we discuss the size patterns of an assemblage containing sporadoceratid ammonoid species from the vicinity of Tabas (Shotori Range, East-Central Iran) in the context of body size; we compare them with two selected assemblages from the Rhenish Mountains of Germany and the Anti-Atlas of Morocco. These three regions differed in their latitude positions during the Devonian (Cocks and Torsvik 2006; Torsvik and Cocks 2013); while the Rhenish Mountains had a position about 20° S, the Anti-Atlas and the Shotori Range were located further south (about 45° S and about 40° S, respectively) with possible effects on sea water temperatures. However, a different opinion was presented by Golonka (2007) who suggested a position of central Iran at approximately 25° S latitude. A term frequently used in biogeographic research is ‘polar gigantism’, which describes the common phenomenon that invertebrates tend to grow exceptionally large at higher latitudes (e.g., Chapelle and Peck 1999; Moran and Woods 2012; Rosa *et al.* 2012). Such phenomena have also been described in the fossil record (Gutiérrez-Marco *et al.* 2009; Klug *et al.* 2015); therefore, it has to be considered if the assemblage containing large sporadoceratid specimens from Tabas may be a case of ‘polar gigantism’ due to its geographic position.

Variations in the body size of cephalopods have been studied in a number of cases using fossil and recent material, but often these studies were focused on extraordinarily large representatives of Palaeozoic nautiloids (e.g., Miller 1932; Teichert and Kummel 1960; Manger *et al.* 1999), Palaeozoic ammonoids (e.g., Clarke 1899; Korn and Klug 2007; Klug *et al.* 2015;

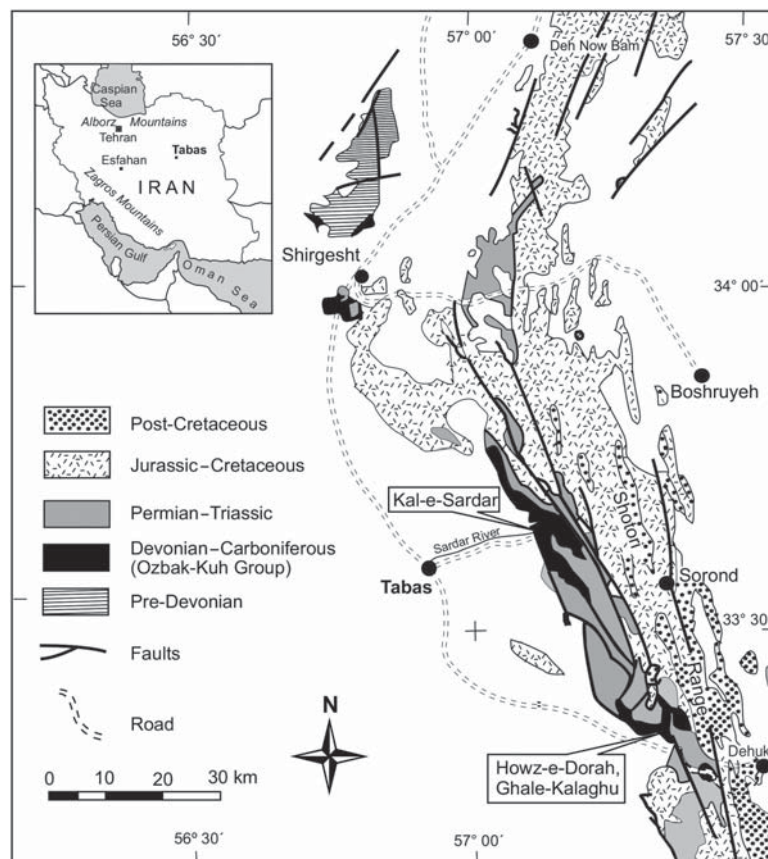
Korn 2017) and Mesozoic ammonoids (e.g., Landois 1895, but see Stevens 1988 for a thorough review on ammonoid gigantism) and coleoids (e.g., Kirk 1880; Kubodera and Mori 2005; Winkelmann *et al.* 2013). A review and discussion of size patterns in Palaeozoic invertebrates with respect to evolutionary and ecological aspects was given by Klug *et al.* (2015). In the following, we discuss the occurrence of an ammonoid assemblage composed of remarkably large specimens.

#### LOCALITIES WITH FAMENNIAN AMMONOIDS IN THE SHOTORI RANGE

Late Devonian ammonoid occurrences of the Shotori Range were discovered by Stöcklin and Ruttner in 1963 in the course of mapping the Tabas area (Stöcklin *et al.* 1965; Ruttner and Stöcklin 1966). These ‘Cephalopod Beds’ of Howz-e-Dorah and Kal-e-Sardar are a very fossiliferous rock member in the Devonian to Lower Carboniferous Shishtu Formation, which is mainly composed of shallow-water limestones (e.g., Stöcklin *et al.* 1965; Stöcklin and Nabavi 1971; Wendt *et al.* 1997, 2005). The cephalopod-bearing unit has a thickness between 20 and 28 m and is composed of shales with intercalated well-bedded detrital and oolitic limestone. The member is very fossiliferous and contains calcareous algae (Flügel 1961), brachiopods (Sartenaer 1966; Legrand-Blain 1999), ammonoids (Clapp 1940; Walliser 1966; Becker *et al.* 2004; Ashouri and Yamini 2006; Hairapetian and Korn 2011), trilobites (Morzadec *et al.* 2002; Feist *et al.* 2003) and fish remains (Schultze 1973; Hairapetian and Ginter 2010). Conodonts in particular have been used in several studies for the stratigraphic assignment of the sections (Yazdi 1996, 1999; Ashouri 1997, 2002, 2004; Gholamalian 2007; Gholamalian *et al.* 2009).

(1) Howz-e-Dorah. The section is located 48 km south-east of Tabas (Text-fig. 1) and exposes the whole ‘Cephalopod Beds’. Stöcklin *et al.* (1965) provided the first description of the Shishtu Formation that has a thickness of 543 m in this area. This includes the ‘Cephalopod Beds’ of 28 m thickness; the unit itself is subdivided into four parts represented by red oolitic limestone, sandy shales, calcareous sandstone and sandy hematitic limestone. Wendt *et al.* (1997, 2005) re-described the entire Devonian section of the area under the name Howz-e-Dorah and in the first article (Wendt *et al.* 1997) figured a rather detailed columnar section of the ‘Cephalopod Beds’.

Bahrami *et al.* (2011) provided a detailed conodont stratigraphy for the upper part of the ‘Cephalopod



Text-fig. 1. Geographic position of the studied outcrops at Howz-e-Dorah and Kal-e-Sardar in the vicinity of Tabas (Iran)

Beds' and the overlying Tournaisian 'Mush Horizon'. They reproduced the outcrop photograph published by Wendt *et al.* (1997) and used the name Ghale-kalaghu section for this outcrop. The conodont stratigraphy of the lower part of the 'Cephalopod Beds' was added by Bahrami *et al.* (2013).

According to Bahrami *et al.* (2011, 2013), the upper part of the 'Cephalopod Beds' shows a strong condensation; the Famennian conodont zones from the Uppermost *marginifera* Zone to the Lower *prae-sulcata* Zone have a thickness of only 3 m. This is in contrast to Wendt *et al.* (1997), who gave a conodont age from the Upper *marginifera* to the Lower *expansa* zones for a sample in the lower portion of the 'Cephalopod Beds'. Wendt *et al.* (1997) recognised strong reworking at various levels in the section and postulated the occurrence of stratigraphic gaps, while Bahrami *et al.* (2011, 2013) considered the Famennian succession as largely complete.

(2) Kal-e-Sardar. North of the Sardar river in the vicinity of Niaz and 22 km east-northeast of Tabas

(Text-fig. 1), the 'Cephalopod Beds' are exposed in a number of disconnected outcrops at the western margin of the Shotori Range. Caused by intensive folding and faulting in the western thrust zone of the Shotori Range, these sections are usually incomplete and difficult to interpret stratigraphically (Stöcklin *et al.* 1965; Wendt *et al.* 1997, 2005). According to Gholamalian (2007), the upper half of the 'Cephalopod Beds' belongs to the Famennian Middle to Upper *expansa* zones.

In the region of the Sardar River, the 'Cephalopod Beds' have yielded numerous ammonoid species, of which the first were described by Walliser (1966), who had already concluded that the sporadoceratids are predominant in the assemblages. He introduced the new subgenus *Sporadoceras* (*Iranoceras*) based on the very narrow internal lobe of these forms. This taxon, which is now regarded as a genus, has not yet been discovered from any other region.

After this first description, ammonoids from Kal-e-Sardar were studied several times. Becker *et al.* (2004)



Text-fig. 2. Ammonoids from Kal-e-Sardar-NW, Iran, occurring in association with the sporadoceratids. **A** – *Manticoceras* sp., specimen MB.C.26853. **B** – *Protactoclymenia* sp., specimen MB.C.26854. Scale bar units = 1 mm

discovered an assemblage characterised by the genus *Platyclymenia*; Ashouri and Yamini (2006) described some species-rich Frasnian to middle Famennian material and Hairapetian and Korn (2011) introduced the new Frasnian species *Beloceras sardarensis*.

#### MATERIAL

(1) Howz-e-Dorah. Besides some small clymeniids, three sporadoceratid specimens were surface-collected from the lower part of the ‘Cephalopod Beds’ at the section Howz-e-Dorah 1 of Wendt *et al.* (1997), which is the Ghale-kalaghu section of Bahrami *et al.* (2011, 2013). These are steinkern specimens embedded in a red oolitic limestone.

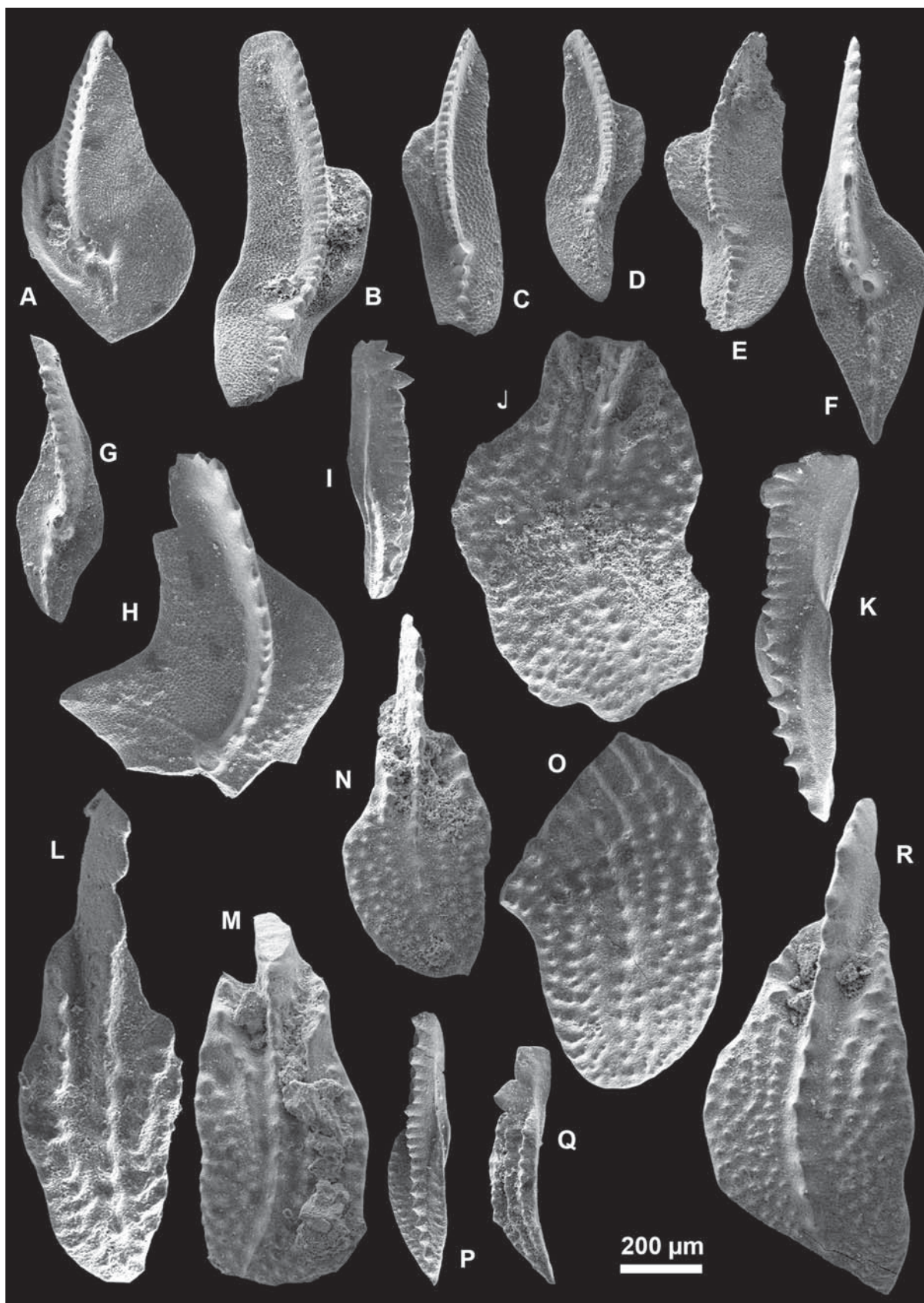
(2) Kal-e-Sardar-NW. Thirty ammonoid specimens were available for our study. All of them were surface-collected in the north-western area of the occurrence of the ‘Cephalopod Beds’. Nine of these

specimens were collected by us from a very small spot (about 20 m<sup>2</sup>) on top of a small hill, thus probably without mixing by distant horizons. However, this spot has yielded ammonoids of the genera *Manticoceras* Hyatt, 1884, *Sporadoceras* Hyatt, 1884, *Iranoceras* Walliser, 1966 and *Protactoclymenia* Wedekind, 1908, meaning that Frasnian to middle Famennian ammonoid faunas occur at the same place (Text-fig. 2). This phenomenon cannot be solved currently; reworking of material may have taken place in the section.

Almost all specimens are internal moulds and shell remains are only occasionally preserved. Even most of the specimens that were extracted from the surrounding rock do not show shell remains and were probably reworked. All sporadoceratids show phragmocones filled with coarse calcite cement. Body chambers are only occasionally preserved.

(3) Kal-e-Sardar-S. Four specimens (Hairapetian Coll.) come from the basal part of a small outcrop that is very close to the locality B6 of Walliser (1966), lo-

Text-fig. 3. Conodonts from the matrix attached to specimen 10 of *Iranoceras pachydiscus* (Walliser, 1966) from Kal-e-Sardar-NW, Iran. All are upper views except for I, K, P and Q, which are lateral views. **A** – *Palmatolepis marginifera marginifera* Helms, 1959; #NMG2. **B** – *Palmatolepis glabra pectinata* Ziegler, 1962; #NMG3. **C** – *Palmatolepis glabra glabra?* Ulrich and Bassler, 1926; #NMG4. **D** – *Palmatolepis glabra pectinata* Ziegler, 1962; #NMG6. **E** – *Palmatolepis glabra prima* Ziegler and Huddle, 1969; #NMG9. **F** – *Palmatolepis minuta minuta* Branson and Mehl, 1934; #NMG11. **G** – *Palmatolepis minuta minuta* Branson and Mehl, 1934; #NMG12. **H** – *Palmatolepis perlobata schindewolfi* Müller, 1956; #NMG13. **I** – *Polygnathus communis?* Branson and Mehl, 1934; #NMG16. **J** – *Polygnathus pennatuloideus* Holmes, 1928; #NMG19. **K** – *Polygnathus glaber medius* Helms and Wolska, 1967; #NMG20. **L** – *Polygnathus yazdii* Gholamalian, Ghorbani and Sajadi, 2009; #NMG29. **M** – *Polygnathus nodocostatus* → *Polygnathus pennatuloideus* Holmes, 1928; #NMG17. **N** – *Polygnathus nodocostatus* → *Polygnathus pennatuloideus* Holmes, 1928; #NMG27. **O** – *Polygnathus nodocostatus?* Branson and Mehl, 1934; #NMG30. **P** – *Polygnathus* aff. *P. procerus* Sannemann, 1955; #NMG18. **Q** – *Polygnathus communis dentatus* Druce, 1969; #NMG32. **R** – *Polygnathus pennatuloideus* Holmes, 1928; #NMG31



cated approximately 6 km east of Posha. *Maeneceras* sp. B was collected from a dark grey horizon rich in oncoids, a few metres away from the base of the outcrop.

CONODONT STRATIGRAPHY OF THE AMMONOID SAMPLES

(A. Gadheri, Z. Belka)

One of the ammonoid specimens (MB.C.26871) was found with about 700 g of attached carbonate sediment. This material has been dissolved for conodonts (processed with 8% formic acid). The sample yielded a moderately rich fauna with more than 80 conodont elements. Among these, more than a dozen palmatolepid and polygnathid taxa and some transitional forms were identified (Text-fig. 3). The assemblage is indicative of the Upper *marginifera* Zone (Text-fig. 4). It includes forms having a global distribution, within a low-latitude belt bounded north and south by the 40<sup>th</sup> parallels (Charpentier 1984), except the species *Polygnathus yazdii* Gholamalian, Ghorbani and Sajadi, 2009, which is so far known only from the Famennian of Iran (Gholamalian et al. 2009). In terms of palaeoecology, the fauna represents the palmatolepids-polygnathid biofacies characteristic for offshore pelagic settings (Sandberg 1976; Savoy and Harris 1993).

All conodont specimens are deposited in the col-

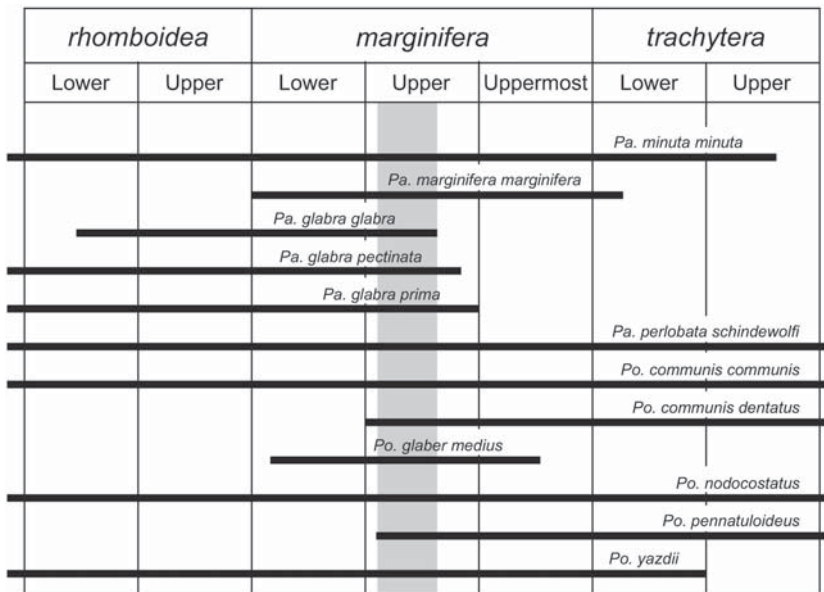
lection of the Department of Geology, Faculty of Science, Ferdowsi University of Mashhad, Iran.

PRESERVATION OF THE AMMONOID CONCHS

The carbonate facies with brachiopod-rich and oolitic limestone of the ‘Cephalopod Beds’ is not typical of ammonoid-bearing sediments; usually ammonoids are most common in outer shelf carbonates (‘cephalopod limestone’). The preservation of the ammonoids in the oolitic limestone shows some characteristics. The polished slab with one sporadoceratid specimen (Text-fig. 5) shows that the outer shell wall of the ammonoid is strongly damaged, while the shell wall of the earlier whorls and also the septa are much better preserved. The oolitic matrix, in which the conch is embedded, can also be seen in some of the phragmocone chambers. The shell wall was thus at least partly damaged before its burial.

Several preservation modes can be recognised in the ammonoid specimens under discussion:

(1) Septate specimens without remains of the body chambers. Nearly the entire phragmocone of the specimens is filled with white sparry cement; sometimes also the septa are only partially preserved. The shell itself is not preserved, instead some specimens are coated with a haematitic crust. – This preservation is the most common among the sporadoceratids and clymeniids.



Text-fig. 4. Stratigraphic ranges of the conodont taxa recovered from the matrix of the ammonoid specimen MB.C.26871 (ranges compiled from data provided by Ziegler 1962; Glenister and Klapper 1966; Ziegler and Sandberg 1984 and Gholamalian et al. 2009). The grey-shaded area is an interval considered to include the biostratigraphic position of the investigated fauna. Pa. = *Palmatolepis*; Po. = *Polygnathus*



Text-fig. 5. Polished slab with a sporadoceratid specimen embedded in oolitic limestone; Kal-e-Sardar-NW, Iran. Note the lack of the body chamber, the degree of damage of the outer shell wall, the rather well-preserved inner whorls and septa and the partial filling of phragmocone chambers by oolitic sediment

(2) Specimens embedded in dark-grey detrital limestone. Parts of the body chamber are preserved and the conchs are covered with a greenish-grey clayey coat. Shell details are not preserved. – This preservation is rather common among the sporadoceratids.

(3) Specimens embedded in micritic limestone with parts of the body chamber preserved; the shell ornament is also visible in some specimens. – This preservation is common among the Frasnian and a few Famennian ammonoids.

#### SIZE DISTRIBUTION OF THE AMMONOID CONCHS

During our field session in the Shotori Range, we found twenty-four specimens of sporadoceratids which are suitable for size analysis. All available specimens regardless of their size and preservation were collected. Precise taxonomic assignment was not possible for each of the specimens because of preservation limits, but it can be stated with certainty that at least four sporadoceratid genera (*Maeneceras*, *Sporadoceras*, *Iranoceras*, *Erfoudites*) are repre-

sented. These sporadoceratid specimens from the two localities Kal-e-Sardar-NW and Howz-e-Dorah show a size pattern that differs from material of other regions such as the Anti-Atlas of Morocco and the Rhenish Mountains of Germany (Text-fig. 6):

(1) The conchs attain a larger size; even one specimen of 160 mm diameter is still chambered (specimen AEU830; Text-fig. 7), this means that the conch diameter including body chamber would have been about 300 mm, a size extremely rare in sporadoceratid assemblages from Central Europe and North Africa. However, one has to take into account that from these regions, in contrast to the Shotori Range, large numbers of specimens have been collected.

(2) Various species of at least two sporadoceratid genera (*Maeneceras* and *Iranoceras*) reached very large sizes of more than 160 mm.

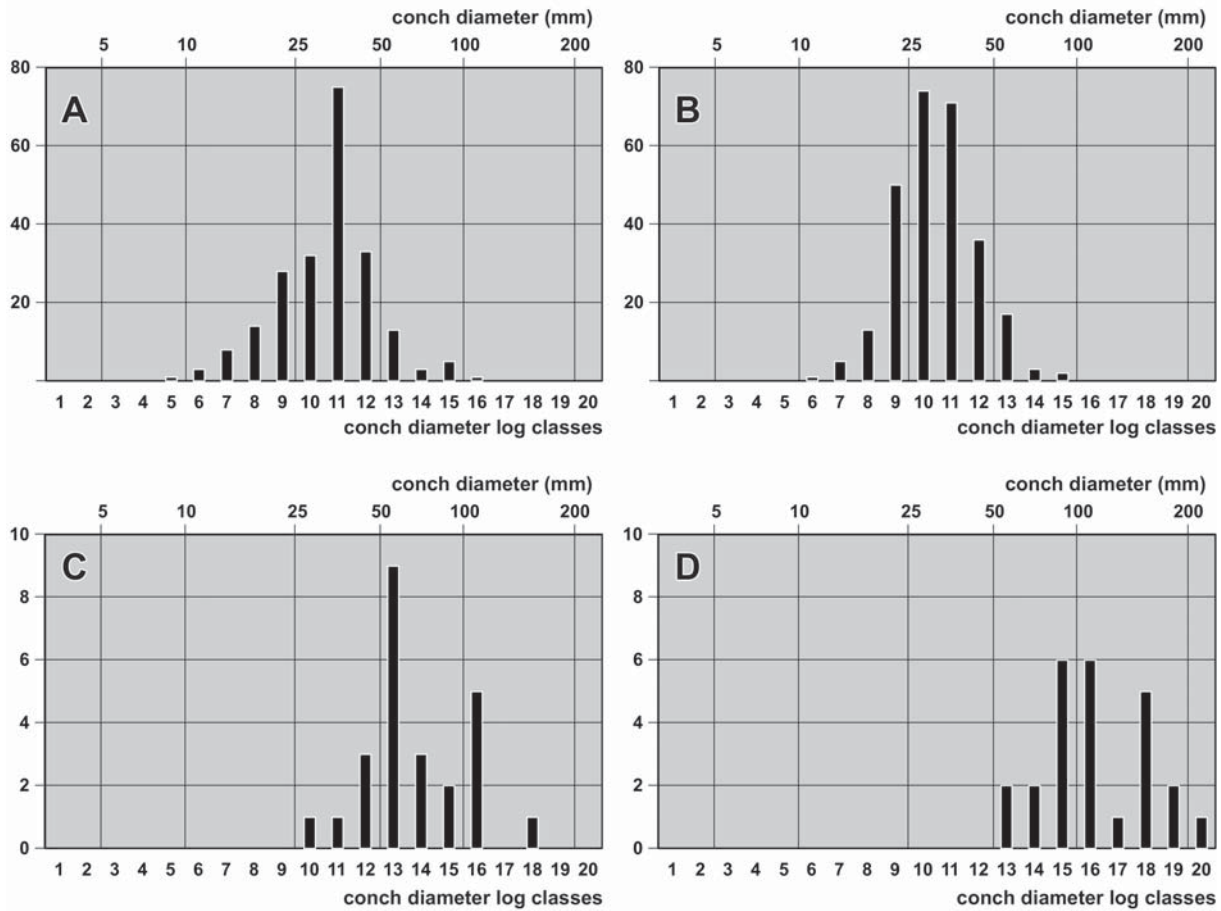
(3) The size distribution is asymmetric with a weakly skewed right side; small specimens are rare.

(4) The mean (130 mm) and median (116 mm) diameters (including the body chamber) of the sporadoceratids from the Shotori Range are much larger than those of the other regions. In the fauna of *Maeneceras meridionale* Frech, 1887 from Hassi Hebech (Anti-Atlas), these values are 35 mm (mean) and 34 mm (median) (Bockwinkel *et al.* 2002) and in the sample of *Sporadoceras bidens* (Sandberger and Sandberger, 1851) from the Rhenish Mountains they are 33 mm (mean) and 31 mm (median) (Walton *et al.* 2010).

The data presented above do not seem to support the hypothesis that the observed differences in size of sporadoceratid ammonoids are related to the different palaeogeographic position of the regions. Assemblages from the Rhenish Mountains and the Anti-Atlas of Morocco do not, despite their latitudinal differences, really differ in their size structures. At the same time, the assemblages from the Anti-Atlas and the Shotori Range differ strikingly despite their similar palaeolatitudinal positions.

The size distribution pattern of the sporadoceratid fauna from Tabas, with its predominance of large specimens, needs to be discussed in the light of the preservation of the specimens. In the specimens of *Maeneceras*, *Sporadoceras* and *Iranoceras*, traces of the shell are only rarely preserved in the outer whorl and even if so, the shell ornament is not preserved. It is likely for several reasons that most of the specimens have experienced some transport and scouring, which has destroyed the body chambers and possibly also portions of the phragmocones.

The preferential accumulation of large specimens can possibly be caused by two processes (for examples describing possible taphonomic causes for fos-



Text-fig. 6. Histograms showing the size distribution within assemblages of sporadoceratid ammonoids. **A** – *Maeneceras meridionale* (Frech, 1887) from Hassi Nebech, Anti-Atlas, Morocco (data from Bockwinkel *et al.* 2002). **B** – *Sporadoceras bidens* (Sandberger and Sandberger, 1851) from Enkenberg, Rhenish Mountains, Germany (data from Walton *et al.* 2010). **C** – Sporadoceratids from Kal-e-Sardar-NW and Howz-e-Dorah, Iran, after measurements of the phragmocone diameter. **D** – Sporadoceratids from Kal-e-Sardar-NW and Howz-e-Dorah, Iran, after calculation of the conch diameter with body chamber



sil and Recent nautilids, see Mapes *et al.* 2010a, b; Cichowolski *et al.* 2012; Hembree *et al.* 2014):

(1) Hydraulic sorting caused the transport of larger conchs from their original habitats (probably deeper shelf environments) to the shallower environment, in which the oolitic limestone was deposited. Studies by Chamberlain *et al.* (1981) and Wani *et al.* (2005) suggested that the floating potential of specimens of the Recent *Nautilus* Linnaeus, 1758 increases with the size of the conchs.

(2) When the conchs reached the shallow shelf, they were not immediately buried but possibly tum-

Text-fig. 7. The largest sporadoceratid specimen AEU830 (Hairpetian Coll.), probably *Maeneceras* sp., from Kal-e-Sardar, Iran. Note the characteristic preservation with lacking body chamber, lacking outer shell wall, haematitic crusts and white sparry calcite filling most of the phragmocone. Scale bar units = 1 mm



bled for some time on the sediment surface. The tumbling action may have caused the removal of body chambers and large parts of the outer shell wall. However, clear abrasion surfaces are missing (compare Fernández-López and Meléndez 1994).

## AMMONOID TAXONOMY

(D. Korn)

A total of 38 specimens were investigated in this study. The specimens are kept in the collection of the Museum für Naturkunde, Berlin (nos. MB.C.26853 to MB.C.26886) and the Azad University, Esfahan (nos. AEU830 to AEU833). The key for the description of Palaeozoic ammonoid species proposed by Korn (2010), including an explanation of the methods used, is followed here (Text-fig. 8).

Order Goniatitida Hyatt, 1884  
 Suborder Tornoceratina Wedekind, 1914  
 Superfamily Prionocerataceae Hyatt, 1884  
 Family Sporadoceratidae Miller and Furnish in  
 Miller *et al.*, 1957  
 Subfamily Sporadoceratinae Miller and Furnish in  
 Miller *et al.*, 1957

Genus *Maeneceras* Hyatt, 1884

TYPE SPECIES: *Goniatites acutolateralis* Sandberger and Sandberger, 1851, p. 98; by original designation.

DIAGNOSIS: Genus of the subfamily Sporadoceratinae with a V-shaped first adventive lobe, a deep and rounded or angular second adventive lobe and a deep, V-shaped internal lobe. Growth line course convex.

INCLUDED SPECIES: See Bogoslovsky (1971) and Korn and Klug (2002).

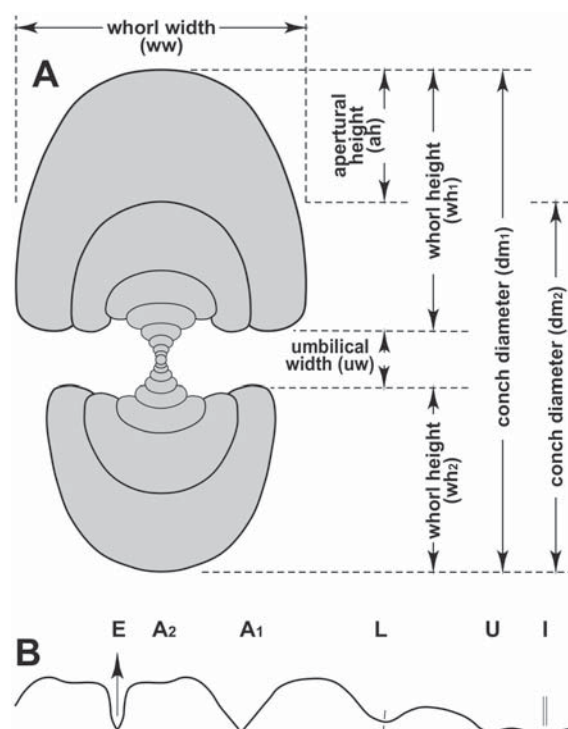
*Maeneceras subvaricatum* (Sobolew, 1914)  
 (Text-figs 9 and 10E, F)

1914.  $\beta$ -*Oma-dimeroceras* (*Sporadoceras*) *subvaricatum*; Sobolew, p. 35, pl. 6, fig. 5, text-fig. 26.

1966. *Sporadoceras* (*Sporadoceras*) sp., ex aff. gr. *Biferum*; Walliser, p. 12, pl. 2, figs 3, 4, text-fig. 3a-c.

1993. *Maeneceras* (*Maeneceras*) *biferum biferum*; Becker, p. 308, pl. 26, figs 3, 4, text-fig. 95c.

2002. *Maeneceras subvaricatum subvaricatum*; Bockwinkel *et al.*, pl. 1, figs 7-14, pl. 2, figs 1, 2, 9, text-fig. 2c.



Text-fig. 8. Conch dimensions obtained from ammonoid conch cross-sections and terminology of the sutural elements used in the systematic descriptions

2016. *Maeneceras subvaricatum subvaricatum*.; Becker in Hartenfels and Becker, p. 334, text-fig. 6.8. (with synonymy)

MATERIAL: Seven specimens from Kal-e-Sardar-NW, Tabas Basin, Iran.

DESCRIPTION: Specimen MB.C.26862 has a diameter of 55 mm and is fully chambered with weak septal crowding at the end of the phragmocone (see Table 1 for conch measurements). The thickly discoidal conch ( $ww/dm = 0.53$ ) has a nearly closed umbilicus ( $uw/dm = 0.05$ ) and a moderate coiling rate ( $WER = 1.88$ ). The conch is thickest at the umbilicus, from where the flanks converge towards the broadly rounded venter (Text-fig. 9B). The suture line has a V-shaped first adventive lobe with weakly convex flanks. The second adventive lobe is very shallow and rounded; the external lobe is very narrow and shallower than the first adventive lobe (Text-fig. 10F). The inner suture line is difficult to follow but it is clear that there is a deep and probably V-shaped internal lobe.

The larger specimen MB.C.26855 (Text-fig. 9A) has very similar conch proportions ( $ww/dm = 0.48$ ;



Text-fig. 9. *Maeneceras subvaricatum* (Sobolew, 1914) from Kal-e-Sardar-NW, Iran. A – Specimen MB.C.26855; B – Specimen MB.C.26862. Scale bar units = 1 mm

uw/dm = 0.01). It is fully septate at 72 mm conch diameter and is partly covered by a haematitic crust. At 68 mm phragmocone diameter, the suture line has a very narrow lanceolate external lobe. The second adventive lobe is symmetric and broadly rounded; it has a quarter the depth of the V-shaped and nearly symmetric fist adventive lobe (Text-fig. 10E).

**DISCUSSION:** The material belonging to this taxon has been attributed to various species (see a summary by Becker in Hartenfels and Becker 2016). Unfortunately, the type material of “ $\beta$ -*Oma-dimero-ceras* (*Sporadoceras*) *subvaricatum* Sobolew, 1914” has not been revised and the ontogeny of the conch shape, for instance, is not known. Material possibly belonging to this species is known from many regions, of which the Rhenish Mountains (e.g., Wedekind 1908) and the Anti-Atlas of Morocco (e.g., Petter 1959; Bockwinkel *et al.* 2002; Hartenfels and Becker 2016) are most important. However, the conch ontogeny of specimens from these regions has not yet been published. Material from the Anti-Atlas of Morocco was studied by Bockwinkel *et al.* (2002) with focus on size distribution, depth of the second adventive

lobe and number of steinkern constrictions. Based on the depth of the second adventive lobe, these authors distinguished three taxa: *Maeneceras subvaricatum nuntio* Becker, 1993, *Maeneceras subvaricatum subvaricatum* (Sobolew, 1914) and *Maeneceras latilobatum* (Schindewolf, 1923).

“*Sporadoceras subbilobatum* var. *meridionalis* Frech, 1902” is a species that was regarded by Korn (in Korn and Ziegler 2002) as a senior synonym of *Maeneceras subvaricatum*. As pointed out by Becker (in Hartenfels and Becker 2016), this is probably incorrect and *meridionalis* has to be placed in *Erfoudites*. Indeed, the cross-sections published by Korn (in Korn and Ziegler 2002) show that the whorl expansion rate decreases during the preadult and adult stages as in *Erfoudites rherisensis* Korn, 1999 (e.g., Korn *et al.* 2015); this is not the case in the genera *Maeneceras* and *Sporadoceras* where there is an adult increase.

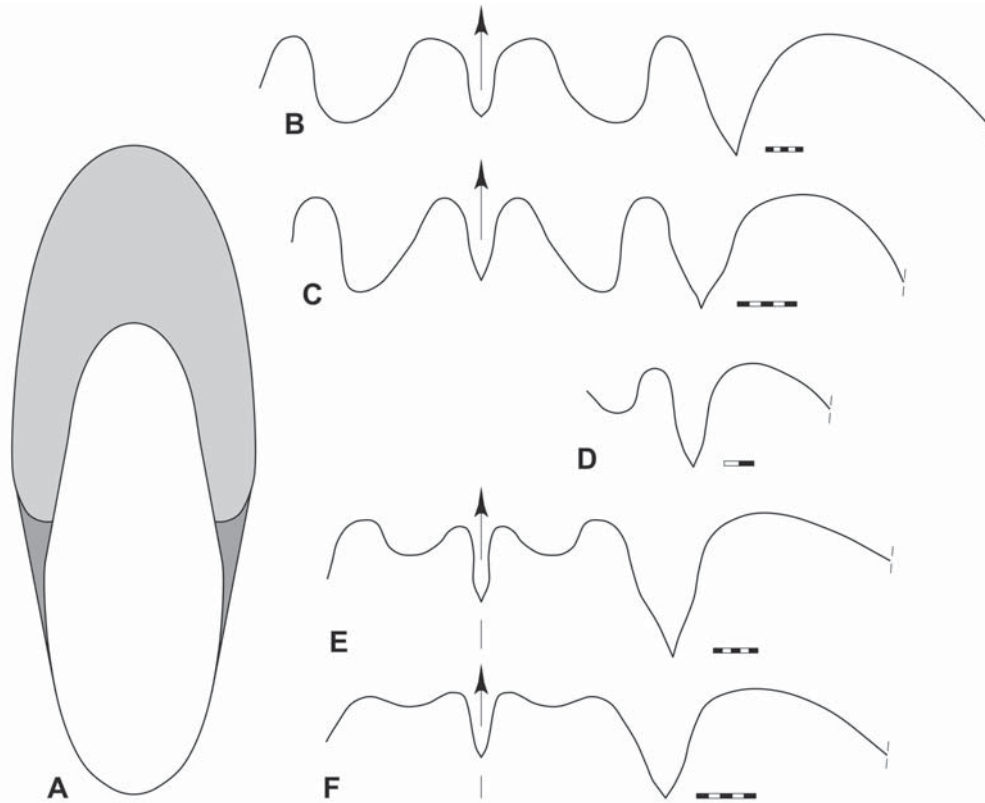
*Maeneceras tabasense* sp. nov.

(Text-figs 10A–C and 11)

1966. *Sporadoceras* (*Sporadoceras*) sp., ex aff. gr. *Sedg-*

No.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZ
MB.C.26855	71.8	34.7	40.9	0.7	21.8	0.48	0.85	0.01	2.06	0.47
MB.C.26857	63.5	33.0	36.5	1.0	16.8	0.52	0.90	0.02	1.85	0.54
MB.C.26864	61.2	28.7	34.5	2.6	17.0	0.47	0.83	0.04	1.92	0.51
MB.C.26862	54.9	29.0	29.9	2.7	14.9	0.53	0.97	0.05	1.88	0.50
MB.C.26856	50.5	25.2	29.0	1.4	13.5	0.50	0.87	0.03	1.86	0.53

Table 1. Conch dimensions (in mm) and ratios of specimens of *Maeneceras subvaricatum* (Sobolew, 1914) from Kal-e-Sardar, Iran



Text-fig. 10. Dorsal view and suture lines of *Maeneceras* spp. **A-C** – *Maeneceras tabasense* sp. nov. **A** – dorsal view of specimen MB.C.26883 from?; **B** – suture line of specimen MB.C.26883 from?, at 104.0 mm dm, 40.0 mm ww, 60.0 mm wh; **C** – specimen MB.C.26869 from Kal-e-Sardar-NW, Iran, at 58.0 mm dm, 24.5 mm ww, 33.5 mm wh. **D** – *Maeneceras* sp. A, suture line of specimen MB.C.26866 from Kal-e-Sardar-NW, Iran, at 39.0 mm dm, 20.5 mm ww, 21.5 mm wh. **E, F** – *Maeneceras subvaricatum* (Sobolew, 1914). **E** – suture line of specimen MB.C.26855 from Kal-e-Sardar-NW, Iran, at 68.0 mm dm, 33.5 mm ww, 41.0 mm wh; **F** – suture line of specimen MB.C.26862 from Kal-e-Sardar-NW, Iran, at 49.5 mm dm, 8.0 mm ww, 29.0 mm wh. Scale bar units = 1 mm

*wicki*; Walliser, p. 14, pl. 1, fig. 14, pl. 2, figs 1, 2, text-fig. 3f–k.

**ETYMOLOGY:** Named after the town of Tabas.

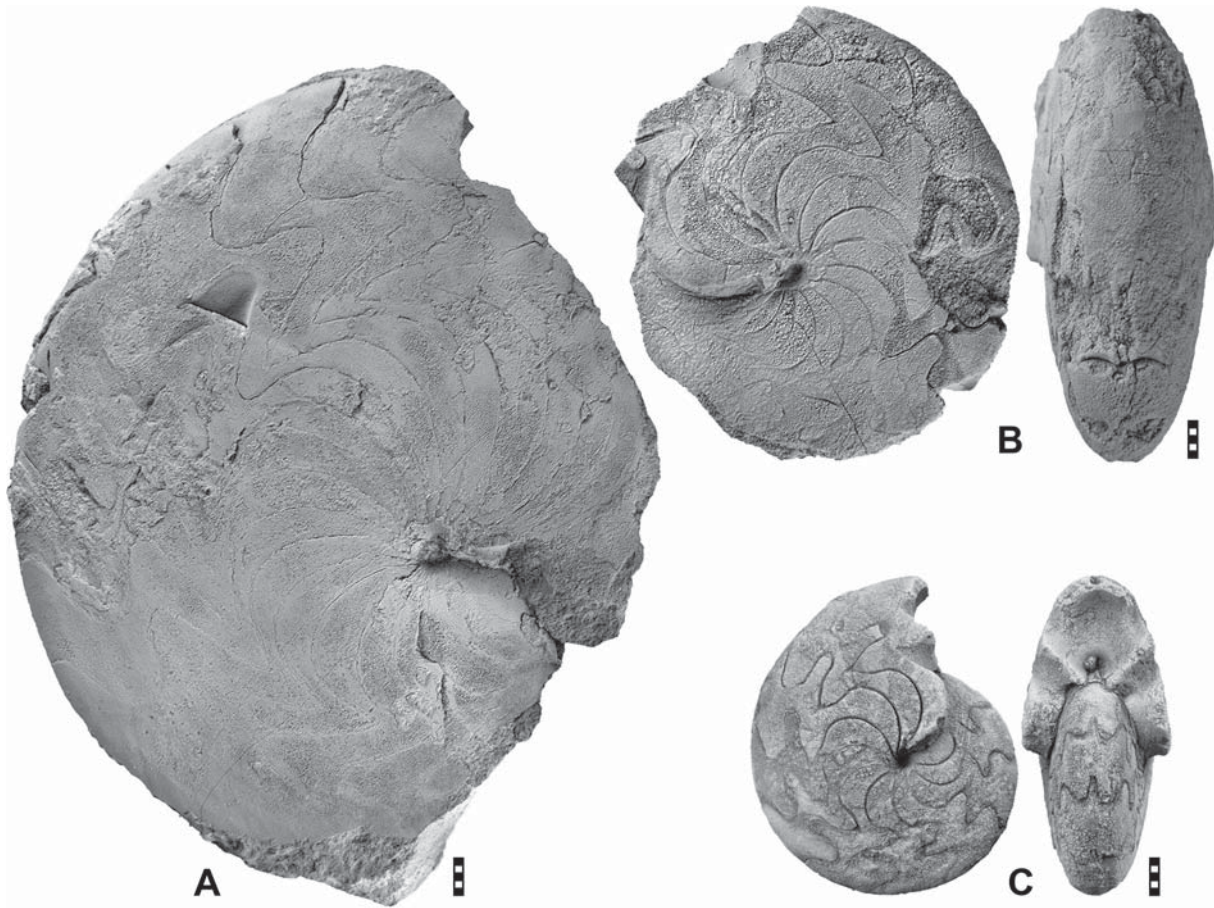
**HOLOTYPE:** Specimen MB.C.26883.

**TYPE LOCALITY AND HORIZON:** Howz-e-Dorah (Shotori Range, Eastern Iran); probably late early Famennian.

**DIAGNOSIS:** Species of *Maeneceras* with thinly discoidal conch ( $ww/dm = 0.40$  at 60 mm dm and  $0.35$  at 120 mm dm); flanks convex and converging, venter continuously rounded. Suture line with weakly asymmetric, broadly rounded second adventive lobe that has three quarters of the depth of the V-shaped first adventive lobe. The saddle between the adventive lobes is narrowly rounded.

**MATERIAL:** Six specimens; two are from Howz-e-Dorah, embedded in red oolitic limestone, another three specimens are from Kal-e-Sardar-NW and one is from Kal-e-Sardar-S, Tabas Basin, Iran.

**DESCRIPTION:** The large holotype MB.C.26883 is completely chambered; the phragmocone is incomplete at the end but its diameter can be estimated at 120 mm (Text-fig. 11A; see Table 2 for conch measurements). The specimen is, at 110 mm dm, thinly discoidal ( $ww/dm = 0.36$ ) with a nearly closed umbilicus. Its flanks are convex and the whorl profile is widest at some distance from the umbilicus. The venter is rather narrow but continuously rounded (Text-fig. 10A). The suture line has a weakly asymmetric first adventive lobe, of which the dorsal flank is concave and the ventral flank weakly convex. The secondary adventive lobe is three quarters of the depth of the first adventive lobe; it is U-shaped and weakly



Text-fig. 11. Specimens of *Maeneceras tabasense* sp. nov. from the Tabas Basin, Iran. A – Specimen MB.C.26883 from Howz-e-Dorah; B – Specimen MB.C.26869 from Kal-e-Sardar-NW; C – Specimen AEU832 from Kal-e-Sardar-S. Scale bar units = 1 mm

asymmetric (Text-fig. 10B). Both adventive lobes are separated by an asymmetric, narrowly rounded saddle that is continuously rounded at its top.

The incomplete phragmocone paratype MB.C. 26869 has a diameter of 60 mm and is thinly discoidal ( $ww/dm = 0.41$ ) with an almost closed umbilicus. The conch is widest near the umbilicus, from where the convex flanks converge towards the rather narrow, rounded venter (Text-fig. 11B). Shell remains are not preserved, but the internal mould shows, though corroded, a series of constrictions that extend with a deep sinus across the venter. The suture line

of this paratype has, at 58 mm phragmocone diameter, a narrow V-shaped external lobe that is nearly as deep as the second adventive lobe. Both lobes are separated by a narrow asymmetric saddle. The second adventive lobe has a broadly rounded base and is asymmetric with a much steeper dorsal flank. It is separated from the nearly symmetric, V-shaped first adventive lobe by a rounded and nearly symmetric saddle (Text-fig. 10C).

**DISCUSSION:** The material from Tabas differs from the Central European species *M. acutolaterale*

No.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZ
MB.C.26883	110.0	39.5	63.5	2.6	29.5	0.36	0.62	0.02	1.87	0.54
MB.C.26883	80.8	33.6	44.5	2.2	–	0.42	0.76	0.03	–	–
MB.C.26869	60.1	24.7	35.2	2.4	–	0.41	0.70	0.04	–	–
AEU832	42.2	19.8	23.8	0.9	13.0	0.47	0.83	0.02	2.09	0.45

Table 2. Conch dimensions (in mm) and ratios of specimens of *Maeneceras tabasense* sp. nov.

(Sandberger and Sandberger, 1851) and *M. sedgwicki* (Wedekind, 1908), which are possibly synonyms, in the well-rounded saddle between the first and second adventive lobe (subacute in the latter two species). *Maeneceras acutolaterale* has at least in a large growth stage of about 120 mm diameter a very narrow venter, which is continuously rounded in *M. tabasense*.

*Maeneceras latilobatum* (Schindewolf, 1923) has a similar conch shape and suture line, but the second adventive lobe has only half the depth of the first adventive lobe. In the new species, the second adventive lobe is almost as deep as the first adventive lobe.

*Maeneceras* sp. A  
(Text-figs 10D and 12)

**MATERIAL:** Two specimens from Kal-e-Sardar-NW, Tabas Basin, Iran.

**DESCRIPTION:** Specimen MB.C.26866 is a fairly well-preserved specimen with 53 mm conch diameter, of which the last quarter of the final whorl belongs to the body chamber (Text-fig. 12; see Table 3 for conch dimensions). Parts of the shell are preserved, but there is no ornament visible. The conch is discoidal (ww/dm = 0.45) with a closed umbilicus and weakly convex flanks that converge towards the rounded venter. The coiling rate is rather high (WER = 2.02). The suture line has a V-shaped first adventive lobe, in which both flanks are weakly convex. The second adventive lobe is short (one third of the first adventive lobe) and is broadly rounded (Text-fig. 10D).

*Maeneceras* sp. B  
(Text-fig. 13)

**MATERIAL:** One specimen from Kal-e-Sardar-S, Tabas Basin, Iran.

**DESCRIPTION:** Specimen AEU833 is a rather well-preserved fully chambered internal mould with



Text-fig. 12. *Maeneceras* sp. A from Kal-e-Sardar-NW, Iran, specimen MB.C.26866. Scale bar units = 1 mm



Text-fig. 13. *Maeneceras* sp. B from Kal-e-Sardar-S, Iran, specimen AEU833. Scale bar units = 1 mm

43 mm conch diameter (Text-fig. 13; see Table 4 for conch dimensions). It is thickly discoidal (ww/dm = 0.58) with a nearly closed umbilicus and a moderate coiling rate (WER = 1.90). The whorl profile is widest at the margin of the funnel-shaped umbilicus; the flanks converge strongly, and the venter is broadly

No.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZ
MB.C.26866	52.6	23.7	32.3	0.5	15.6	0.45	0.73	0.01	2.02	0.52
	38.2	19.4	21.6	0.4	–	0.51	0.90	0.01	–	–

Table 3. Conch dimensions (in mm) and ratios of the specimen of *Maeneceras* sp. A

No.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZ
AEU833	43.1	25.2	24.7	2.0	11.8	0.58	1.02	0.05	1.90	0.52
	31.3	18.4	15.9	1.8	–	0.59	1.16	0.06	–	–

Table 4. Conch dimensions (in mm) and ratios of the specimen of *Maeneceras* sp. B

rounded. The suture line has a V-shaped first adventive lobe with convex flanks. The second adventive lobe is short (less than one quarter of the first adventive lobe) and is broadly rounded.

**DISCUSSION:** The single specimen differs from the other specimens of the genus from the Shotori Range in the presence of the funnel-shaped umbilicus. Interestingly, one small specimen of *Iranoceras pingue* shows this type of umbilicus, but that specimen differs in its very shallow umbilical and internal lobes from the *Maeneceras* specimen.

#### Genus *Sporadoceras* Hyatt, 1884

**TYPE SPECIES:** *Goniatites bidens* Sandberger and Sandberger, 1851, p. 71; by original designation.

**DIAGNOSIS:** Genus of the subfamily Sporadoceratinae with a V-shaped first adventive lobe, a deep and rounded or angular second adventive lobe and a deep, V-shaped internal lobe. Growth line course convex.

**INCLUDED SPECIES:** See Bogolslovsky (1971) and Korn and Klug (2002).

#### *Sporadoceras* sp. A (Text-fig. 14)

**MATERIAL:** One incomplete phragmocone specimen from Kal-e-Sardar-NW, Tabas Basin, Iran.

**DESCRIPTION:** Specimen MB.C.26859 is an incomplete phragmocone with 56 mm diameter. It is cor-

roded and thus does not show any shell remains. The whorl profile appears to be triangular; it is widest at the closed umbilicus, from where the weakly convex flanks converge towards the rather narrow, rounded venter (Text-fig. 14A, B). The suture line was drawn at a phragmocone diameter of 57 mm. It has a small, narrowly V-shaped external lobe. Towards the umbilicus follow a broadly rounded, weakly asymmetric ventrolateral saddle and then the narrow and very conspicuous, asymmetric secondary adventive lobe. This has parallel flanks in the middle part, but its base is pointed on the ventral side. The midflank saddle is asymmetric with a strongly sinuous ventral flank and almost straight dorsal flank. The V-shaped first adventive lobe is weakly asymmetric (Text-fig. 14C).

#### Genus *Iranoceras* Walliser, 1966

**TYPE SPECIES:** *Sporadoceras (Iranoceras) pachydiscus* Walliser, 1966; by original designation.

**DIAGNOSIS:** Genus of the subfamily Sporadoceratinae with a very shallow, rounded internal lobe.

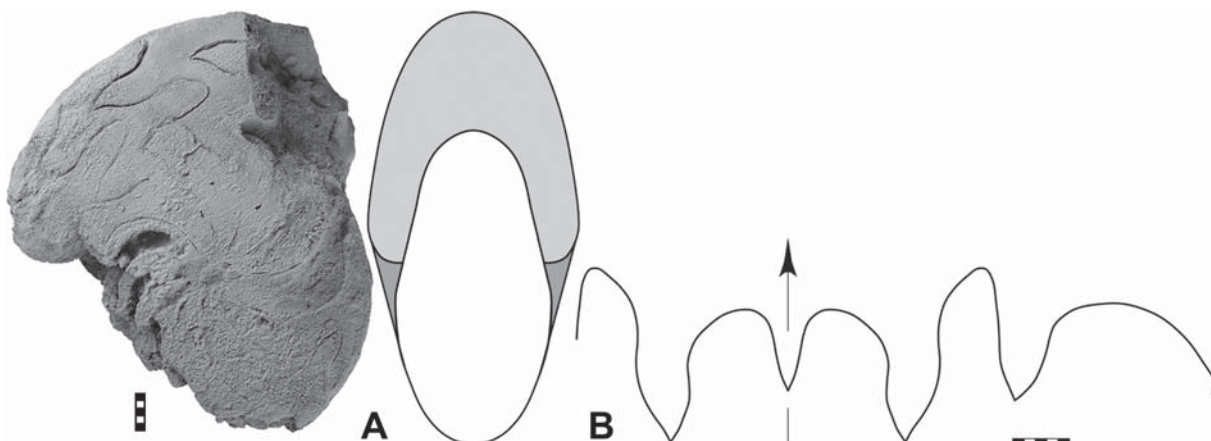
**INCLUDED SPECIES:**

*pachydiscus:* *Sporadoceras (Iranoceras) pachydiscus* Walliser, 1966, p. 16.

*pingue:* *Sporadoceras (Iranoceras) pingue* Walliser, 1966, p. 16.

*sphaericum:* *Sporadoceras (Iranoceras) sphaericum* Walliser, 1966, p. 16. (synonym of *Sporadoceras pingue*)

**DISCUSSION:** Walliser (1966) had only three specimens from two localities at Kal-e-Sardar (Ruttner



Text-fig. 14. *Sporadoceras* sp. A, specimen MB.C.26859 from Kal-e-Sardar-NW, Iran. A – Lateral and dorsal views; B – Suture line at 57.0 mm dm, 28.5 mm ww, 32.5 mm wh. Scale bar units = 1 mm

and Stöcklin 1966); he described each specimen as a new species. Further to this description, only one poorly preserved specimen of *Iranoceras* sp. has been figured by Ashouri and Yamini (2006). With only four specimens, it is difficult to say if the three species are justified. The new material is therefore important for helping to shed light on this problematic and apparently endemic genus.

Unfortunately, the type material appears to be lost and the descriptions of the three species are not really precise. There is no clear indication about the size of the specimens and the conch cross sections given by Walliser (1966, text-fig. 3) lack a scale, it is therefore hard to attribute a correct conch diameter for the cross sections. Additionally, the plates lack a scale and hence it can only be assumed that the specimens are figured in the original size.

*Iranoceras pachydiscus* (Walliser, 1966)  
(Text-figs 15 and 16)

1966. *Sporadoceras (Iranoceras) pachydiscus* Walliser, p. 16, pl. 3, fig. 1, text-fig. 3l, m.

**DIAGNOSIS:** Species of *Iranoceras* with thinly pachyconic conch at 8 mm dm ( $ww/dm = 0.70$ ), thereafter occurs a continuous transformation to a discoidal conch at 130 mm dm ( $ww/dm = 0.40$ ). Moderate coiling rate ( $WER = 1.70-1.80$ ) in the adult stage. Whorl profile with weakly converging flanks, conch widest in the umbilical area.

**MATERIAL:** Three specimens between 50 and 130 mm conch diameter from Kal-e-Sardar-NW; the smallest fragmentary specimen was used for a conch cross section. Additionally, one phragmocone specimen with a diameter of 100 mm from Howz-e-Dorah, Tabas Basin, Iran.

**DESCRIPTION:** The cross section of specimen MB.C.26872 is incomplete and had to be reconstructed because of some dissolution of the specimen (Text-fig. 16A; see Table 5 for conch measurements). The ontogenetic trajectory of the conch width index ( $ww/dm$ ) is very simple between 7 and 133 mm conch



Text-fig. 15. *Iranoceras pachydiscus* (Walliser, 1966), specimen MB.C.26870 from Kal-e-Sardar-NW, Iran. Scale bar units = 1 mm

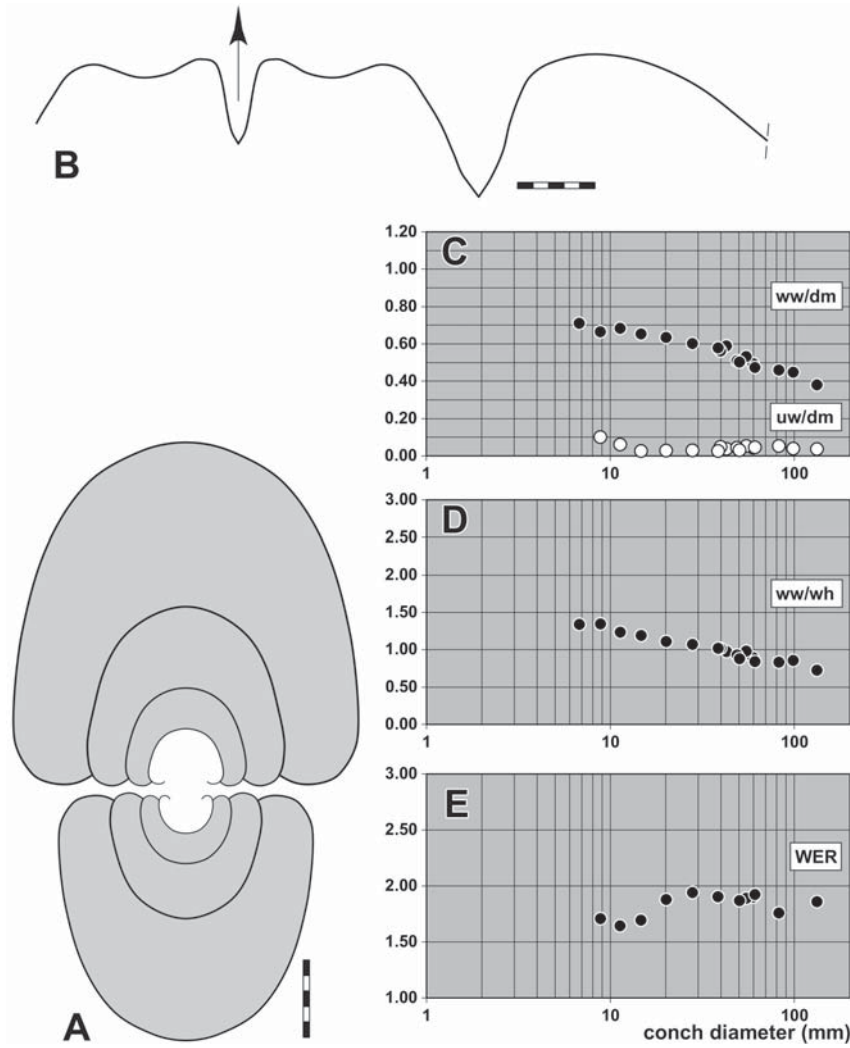
diameter; during this interval it decreases continuously from 0.70 to 0.38. The umbilicus is very narrow at a conch diameter larger than 14 mm and the whorl expansion rate changes from about 1.70 at 14 mm dm to 1.90 at 38 mm dm.

Specimen MB.C.26870 has a diameter of 60 mm and is fairly well-preserved. In this specimen, part of the body chamber ( $240^\circ$ ) is preserved, but no shell ornament can be seen. Instead, the entire specimen is coated by a clayey cover with mica crystals (Text-fig. 15). The conch is thickly discoidal ( $ww/dm = 0.49$ ) with a moderate coiling rate ( $WER = 1.89$ ). In both parameters, it closely resembles specimen MB.C.26862. However, in specimen MB.C.26870, the flanks do not converge as strongly.

The large specimen MB.C.26871 is, with 133 mm conch diameter, somewhat corroded without shell remains. Parts of the body chamber are preserved and the phragmocone has a diameter of 100 mm. The conch is discoidal ( $ww/dm = 0.35$ ) with a whorl profile that is widest near the midflank and shows only weakly converging flanks. The coiling rate is moderate ( $WER = 1.85$ ). The suture line shows, at a phragmocone whorl height of 39 mm (corresponding to a diameter of about 90 mm), a moderately wide first

No.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZ
MB.C.26871	133.0	50.0	70.0	4.5	35.3	0.38	0.71	0.03	1.85	0.50
MB.C.26870	59.7	29.3	33.2	2.4	16.3	0.49	0.88	0.04	1.89	0.51
MB.C.26872	38.61	22.18	21.97	0.88	10.58	0.57	1.01	0.02	1.90	0.52
	20.16	12.70	11.55	0.51	5.42	0.63	1.10	0.03	1.87	0.53
	11.34	7.70	6.30	0.65	2.48	0.68	1.22	0.06	1.64	0.61

Table 5. Conch dimensions (in mm) and ratios of specimens of *Iranoceras pachydiscus* (Walliser, 1966)



Text-fig. 16. *Iranoceras pachydiscus* (Walliser, 1966) from Kal-e-Sardar-NW, Iran. A – Specimen MB.C.26872; x 2.0; cross-section; B – Specimen MB.C.26871, at 37.0 mm ww, 40.0 mm wh; suture line; 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) of sectioned and other selected specimens. Scale bar units = 1 mm

adventive lobe with weakly convex flanks, a very shallow second adventive lobe and a small, V-shaped external lobe (Text-fig. 16B).

DISCUSSION: *Iranoceras pachydiscus* differs from *I. pingue* in the ontogenetic trajectory of the conch width index, which in *I. pachydiscus* decreases from 0.65 at 25 mm dm to 0.45 at 60 mm dm, while *I. pingue* has a stout conch at 60 mm dm (ww/dm = 0.60).

*Iranoceras pachydiscus* can be confused with the species *Maeneceras subvaricatum* when the internal suture line is not visible. However, the flanks do not converge as strongly in *I. pachydiscus* and the second adventive lobe is shallower.

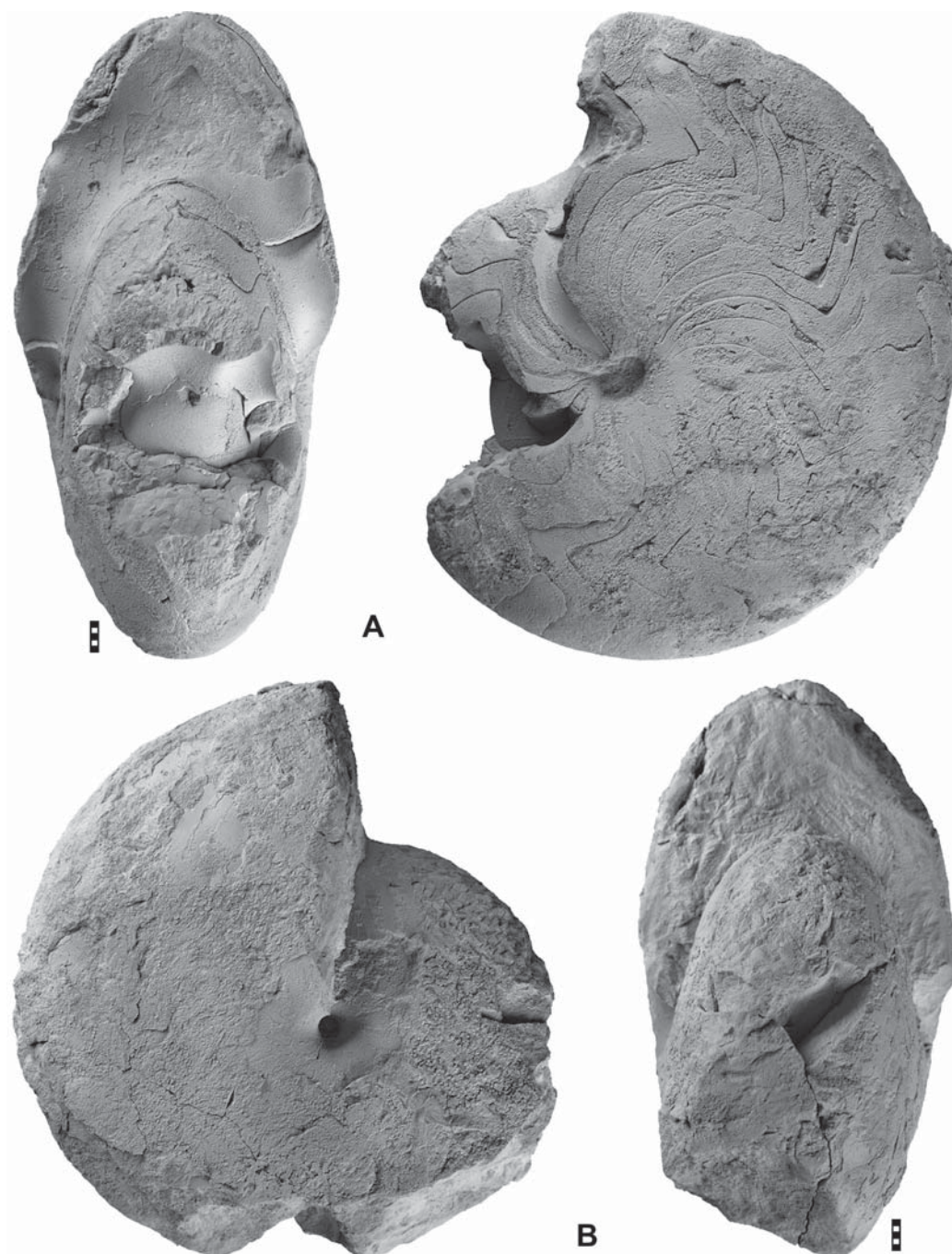
*Iranoceras pingue* (Walliser, 1966)  
(Text-figs 17–19)

1966. *Sporadoceras (Iranoceras) pingue* Walliser, p. 16, pl. 3, fig. 2, text-fig. 3n, o.

1966. *Sporadoceras (Iranoceras) sphaericum* Walliser, p. 16, pl. 2, fig. 7, text-fig. 3p, q.

DIAGNOSIS: Species of *Iranoceras* with thinly pachyconic conch at 25 mm conch diameter (ww/dm = 0.70) and thickly discoidal conch at 60 mm dm (ww/dm = 0.60). Low to moderate coiling rate (WER = 1.70–1.90) in the adult stage. Whorl profile with converging flanks, conch widest near the umbilicus.





Text-fig. 17. *Iranoceras pingue* (Walliser, 1966) from Kal-e-Sardar-NW, Iran. A – Specimen MB.C.26860; B – Specimen MB.C.26873. Scale bar units = 1 mm

**MATERIAL:** Two more or less complete phragmocone specimens and one incomplete specimen from Kal-e-Sardar-NW, with conch diameters ranging from 93 to 105 mm. In addition, there are three fragments, one from Kal-e-Sardar-NW, one from Howz-

e-Dorah and, one small specimen of 38 mm diameter from Kal-e-Sardar-S, Tabas Basin, Iran.

**DESCRIPTION:** The cross section of specimen MB.C.26874 is imperfect because of some dissolu-



Text-fig. 18. *Iranoceras pingue* (Walliser, 1966) from Kal-e-Sardar-S, Iran, specimen AEU831. Scale bar units = 1 mm

tion and recrystallization, but it allows for the study of conch ontogeny between 2 and 105 mm diameter (see Table 6 for conch measurements). During this interval the ontogeny of the conch width index is simple with a nearly continuous decrease from a value of 0.95 down to 0.50. The whorl profile has a simple outline during most of the interval; it is widest at the umbilicus with converging flanks and a continuously rounded venter (Text-fig. 19A).

Specimen MB.C.26860 is a somewhat corroded phragmocone specimen with 104 mm diameter (Text-fig. 17A); it possesses only small, strongly corroded shell remains. The specimen displays conspicuous septal crowding at the end of the phragmocone, while the first half volution of the terminal phragmocone has 13 septa, there are 17 septa in the second half. The conch is thickly discoidal with a weakly opened umbilicus ( $ww/dm = 0.50$ ;  $uw/dm = 0.05$ , but the umbilicus is smaller on the left side of the specimen). The whorl profile is rounded triangular and widest at the rounded umbilical margin, from where the flanks strongly converge towards the rounded but rather

narrow venter. The coiling rate is rather low ( $WER = 1.72$ ). The suture line has, at the end of the terminal phragmocone at 100 mm diameter, a rather small and shallow, V-shaped first adventive lobe with nearly rectangularly arranged flanks. The second adventive lobe is very shallow, and the narrow external lobe has about half of the depth of the first adventive lobe (Text-fig. 19B).

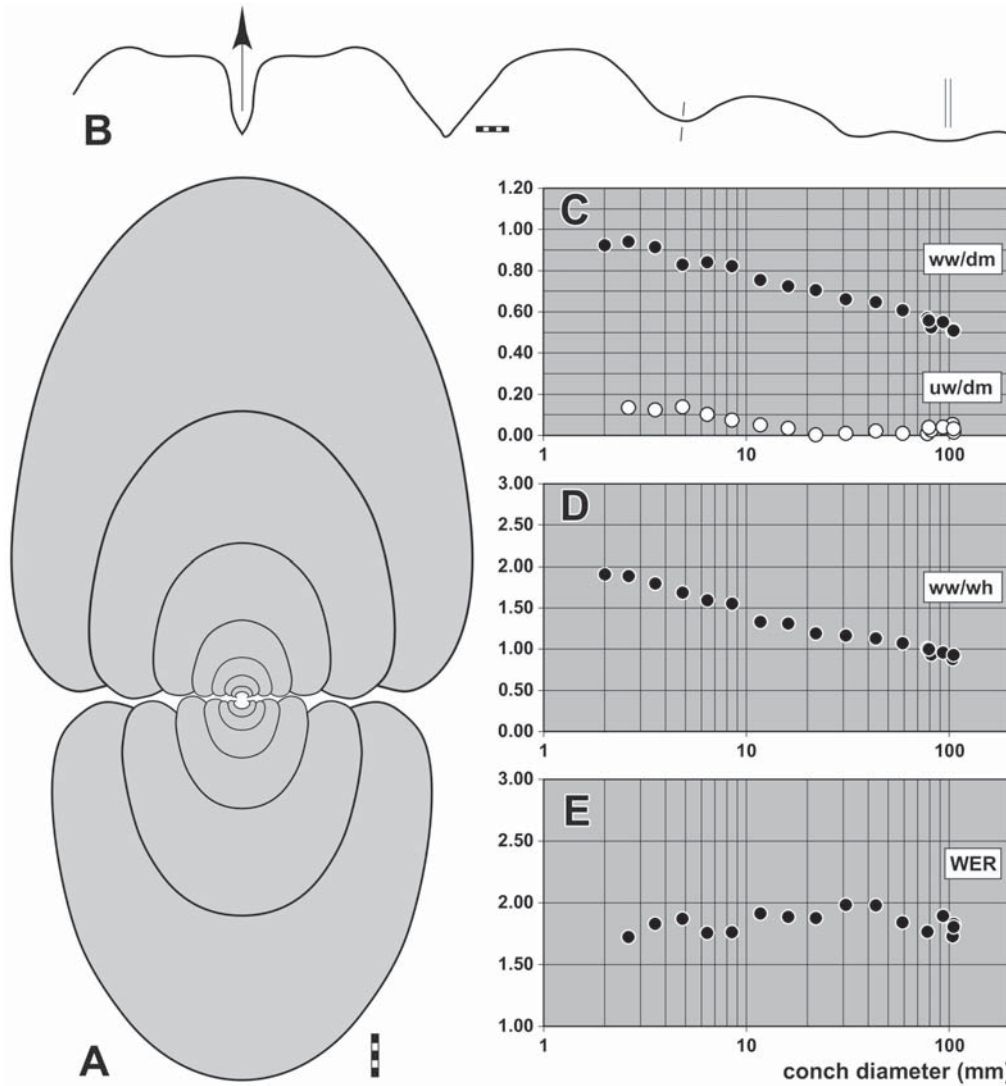
Specimen MB.C.26873 has a diameter of 93 mm and is nearly fully chambered (Text-fig. 17B). It is encrusted by a haematitic layer that does not show details of the shell surface. The conch is slightly stouter than specimen MB.C.26860 and differs also in the broader venter and in the higher coiling rate ( $WER = 1.89$ ). The suture line has a narrower first adventive lobe than specimen MB.C.26860.

The smaller, rather well-preserved specimen AEU831 has a conch diameter of 38 mm and is fully chambered (Text-fig. 18). It is pachyconic ( $ww/dm = 0.69$ ) with an almost closed umbilicus and a moderate coiling rate ( $WER = 1.92$ ). The umbilicus is funnel-shaped with a flattened oblique umbilical wall and a pronounced umbilical margin. The conch is widest at this place, from where the flanks converge towards the broadly rounded venter. The suture line is very similar to the large specimen MB.C.26860 with a V-shaped first adventive lobe and a very shallow second adventive lobe. Interestingly, the spacing of the septa is very irregular; sometimes two or more septa are crowded.

**DISCUSSION:** There is some variability within the material. The combination of a lower coiling rate with strongly converging flanks (specimen MB.C.26860) in contrast to the combination of a higher coiling rate with less strongly converging flanks (specimen MB.C.26873) cannot be confirmed by other specimens; the cross sections provided by Walliser (1966) demonstrate an opposite pattern.

No.	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZ
MB.C.26874	105.4	53.2	58	3.0	26.8	0.50	0.92	0.03	1.80	0.54
MB.C.26860	104.2	52.3	60.2	5.2	24.8	0.50	0.87	0.05	1.72	0.59
MB.C.26873	93.3	51.0	53.8	3.5	25.4	0.55	0.95	0.04	1.89	0.53
AEU831	38.2	26.2	22.2	1.3	10.6	0.69	1.18	0.03	1.92	0.52
MB.C.26874	105.70	53.68	60.09	1.33	27.38	0.51	0.89	0.01	1.82	0.54
	59.04	35.64	33.59	0.37	15.45	0.60	1.06	0.01	1.83	0.54
	31.04	20.40	17.71	0.20	8.96	0.66	1.15	0.01	1.98	0.49
	16.14	11.62	8.94	0.50	4.37	0.72	1.30	0.03	1.88	0.51
	8.53	6.97	4.52	0.60	2.09	0.82	1.54	0.07	1.76	0.54
	4.87	4.01	2.40	0.65	1.30	0.82	1.67	0.13	1.86	0.46
	2.64	2.47	1.32	0.35	0.63	0.94	1.87	0.13	1.72	0.53

Table 6. Conch dimensions (in mm) and ratios of specimens of *Iranoceras pingue* (Walliser, 1966)



Text-fig. 19. *Iranoceras pingue* (Walliser, 1966) from Kal-e-Sardar-NW, Iran. A – specimen MB.C.26874; cross-section; B – specimen MB.C.26860, at 104 mm dm, 52 mm ww, 60 mm wh; suture line; 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) of sectioned and other selected specimens. Scale bar units = 1 mm

Walliser (1966) stated that the two species under discussion differ in the width of the umbilicus, i.e., it should be completely closed in *Sporadoceras* (*Iranoceras*) *sphaericum*. However, the figures do not confirm this; in particular the cross sections show a very similar conch geometry. The second distinguishing character, i.e., the broader and more symmetric first adventive lobe, may fall within the intraspecific variation known from many sporadoceratid species. Therefore, the two species are synonymised here.

Subfamily Xenosporadoceratinae Korn in Korn and Klug, 2002

Genus *Erfoudites* Korn, 1999

TYPE SPECIES: *Erfoudites zizensis* Korn, 1999, p. 157; by original designation.

DIAGNOSIS: Genus of the subfamily Xenosporadoceratinae with a V-shaped first adventive lobe, a deep and rounded or angular second adventive lobe and

a deep, V-shaped internal lobe. Growth line course convex.

INCLUDED SPECIES: See Korn (1999) and Korn *et al.* (2015).

*Erfoudites* sp.  
(Text-fig. 20)

1966. *Sporadoceras* (*Sporadoceras*) sp., ex aff. gr. *descendens*; Walliser, p. 14, pl. 2, figs 5, 6, text-fig. 3d, e.

2004. *Erfoudites ungeri*; Becker *et al.*, p. 128, text-fig. 7.1–3.

MATERIAL: One specimen from Kal-e-Sardar-NW, Tabas Basin, Iran.

DESCRIPTION: The single specimen MB.C.26876 has a diameter of 38 mm and is embedded in a dark grey, partly black limestone. The final third of the last preserved volution belongs to the body chamber. The conch is discoidal ( $w/dm = 0.46$ ) with a completely closed umbilicus and a rather high coiling rate ( $WER = 2.21$ ). Portions of the shell are preserved; they show fine spiral lines (about 50 from umbilicus to midventer) which are wider than their interspaces. The weakly biconvex growth lines are much finer than the spirals (Text-fig. 20). The internal mould shows constrictions of various length; the last of these begins on the inner flank area where it is forwardly directed to form a low ventrolateral projection and a shallow ventral sinus. The suture line has a V-shaped, acute first adventive lobe with weakly convex flanks. The second adventive lobe is also V-shaped but rounded at its base. It is very small

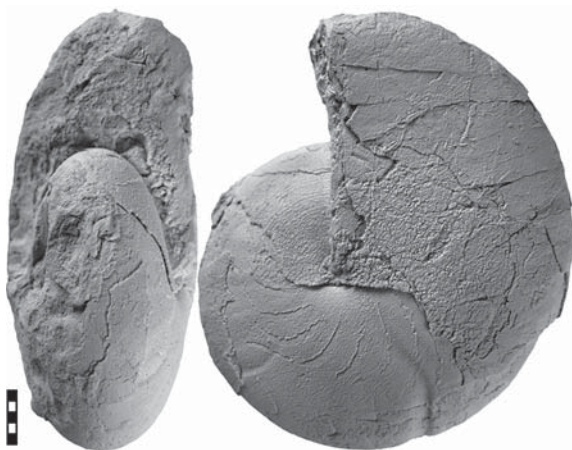
and reaches only 25 % of the depth of the  $A_1$  lobe. The V-shaped external lobe has nearly half the depth of the  $A_1$  lobe.

### Acknowledgements

We greatly acknowledge Markus Brinkmann (Berlin) for the mechanical preparation of the specimens, and Jasmin Hegert and Jan Schmidt (Berlin) for photography of the specimens. Thanks to H. Gholamalian (Esfahan) and Dieter Weyer (Berlin) for the discussion of the conodonts, and Sonny Walton (Bath) for a language check of an earlier version. Many thanks to Kenneth De Baets (Erlangen) for a critical review. LD was funded by the Alexander von Humboldt Foundation.

### REFERENCES

- Ashouri, A.R. 1997. Revision in stratigraphical position of the “Cephalopod Beds” and Devonian-Carboniferous boundary and introducing 5 conodont zones in Howz-e-Dorah (East Iran). *Geosciences*, **6**, 10–17.
- Ashouri, A.R. 2002. *Palmatolepis* (Conodonta, Late Devonian) from the Tabas region, Eastern Iran. *Iranian International Journal of Science*, **3**, 187–220.
- Ashouri, A.R. 2004. Late Devonian and Middle–Late Devonian conodonts from eastern and northern Iran. *Revista Española de Micropaleontología*, **36**, 355–365.
- Ashouri, A.R. and Yamini, A. 2006. Cephalopods and stratigraphical position of cephalopod bed of Shishtu Formation, Iran. *Geosciences Scientific Quarterly Journal*, **15**, 178–187.
- Bahrami, A., Corradini, C., Over, D.J. and Yazdi, M. 2013. Conodont biostratigraphy of the upper Frasnian–lower Famennian transitional deposits in the Shotori Range, Tabas area, Central-East Iran Microplate. *Bulletin of Geosciences*, **88**, 369–388.
- Bahrami, A., Corradini, C. and Yazdi, M. 2011. Upper Devonian–Lower Carboniferous conodont biostratigraphy in the Shotori Range, Tabas area, Central-East Iran Microplate. *Bollettino della Società Paleontologia Italiana*, **50**, 35–53.
- Becker, R.T. 1993. Stratigraphische Gliederung und Ammonoitiden-Faunen im Nehdenium (Oberdevon II) von Europa und Nord-Afrika. *Courier Forschungsinstitut Senckenberg*, **155**, 1–405.
- Becker, R.T., Ashouri, A.R. and Yazdi, M. 2004. The Upper Devonian *Annulata* Event in the Shotori Range (eastern Iran). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **231** (1), 119–143.
- Becker, R.T., House, M.R., Bockwinkel, J., Ebbighausen, V. and Aboussalam, Z.S. 2002. Famennian ammonoid zones of the eastern Anti-Atlas (southern Morocco). *Münstersche Forschungen zur Geologie und Paläontologie*, **93**, 159–205.



Text-fig. 20. *Erfoudites* sp., specimen MB.C.26876 from Kal-e-Sardar-NW, Iran. Scale bar units = 1 mm

- Bockwinkel, J., Becker, R.T. and Ebbighausen, V. 2002. Morphometry and Taxonomy of Lower Famennian Sporadoceratidae (Goniatitida) from Southern Morocco. *Abhandlungen der Geologischen Bundesanstalt*, **57**, 279–297.
- Bogoslovsky, B.I. 1971. Devonian ammonoids. II. Goniatites. *Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR*, **127**, 1–228. [In Russian]
- Branson, E.B. and Mehl, M.G. 1934. Conodonts from the Grassy Creek shale of Missouri. *Missouri University Studies*, **8** (3), 171–259.
- Chamberlain, J.A., Ward, P.D. and Weaver, J.S. 1981. Post-mortem ascent of *Nautilus* shells: implications for cephalopod paleobiogeography. *Paleobiology*, **7** (4), 494–509.
- Chapelle, G. and Peck, L.S. 1999. Polar gigantism dictated by oxygen availability. *Nature*, **399** (6732), 114–115.
- Charpentier, R.R. 1984. Conodonts through time and space: studies in conodont provincialism. *Geological Society of America Special Paper*, **196**, 11–32.
- Cichowolski, M., Pazos, P.J., Tunik, M.A. and Aguirre-Urreta, M.B. 2012. An exceptional storm accumulation of nautilids in the Lower Cretaceous of the Neuquén Basin, Argentina. *Lethaia*, **45**, 121–138.
- Clapp, F.G. 1940. Geology of eastern Iran. *Geological Society of America Bulletin*, **51** (1), 1–102.
- Clarke, J.M. 1899. The Naples fauna (fauna with *Manticoceras intumescens*) in Western New York. *New York State Museum Annual Report*, **5**, 31–161.
- Cocks, L.R.M. and Torsvik, T.H. 2006. European geography in a global context from the Vendian to the end of the Palaeozoic. In: Gee, D.G. and Stephenson, R.E. (Eds), European Lithosphere Dynamics. *Geological Society of London, Memoirs*, **32**, 83–95.
- Druce, E.C. 1969. Devonian and Carboniferous Conodonts from the Bonaparte Gulf Basin, Northern Australia and their use in international correlation. *Australia Bureau of Mineral Resources, Geology and Geophysics Bulletin*, **98**, 1–158.
- Feist, R., Yazdi, M. and Becker, R.T. 2003. Famennian trilobites from the Shotori range, E-Iran. *Annales de la Société géologique du Nord*, **10** (4), 285–294.
- Fernández-López, S. and Meléndez, G. 1994. Abrasion surfaces on internal moulds of ammonites as palaeobathymetric indicators. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **110**, 29–42.
- Flügel, H.W. 1961. *Receptaculites neptuni* Defr. 1827 from the Upper Devonian Kuh-i-Shotori, east Iran. *Bulletin of the Iranian Petroleum Institute*, **4**, 75–81.
- Frech, F. 1887. Die paläozoischen Bildungen von Cabrières (Languedoc). *Zeitschrift der Deutschen Geologischen Gesellschaft*, **39**, 360–488.
- Gholamalian, H. 2007. Conodont biostratigraphy of the Frasnian–Famennian boundary in the Esfahan and Tabas areas, Central Iran. *Geological Quarterly*, **51**, 453–476.
- Gholamalian, H., Ghorbani, M. and Sajadi, S.-H. 2009. Famennian conodonts from Kal-e-Sardar section, eastern Tabas, central Iran. *Rivista Italiana di Paleontologia e Stratigrafia*, **115** (2), 141–158.
- Glenister, B.F. and Klapper, G. 1966. Upper Devonian conodonts from the Canning Basin, Western Australia. *Journal of Paleontology*, **40**, 777–842.
- Golonka, J. 2007. Phanerozoic paleoenvironment and paleolithofacies maps. Late Palaeozoic. *Geologia*, **33**, 145–209.
- Gutiérrez-Marco, J.C., Sá, A.A., García-Bellido, D.C., Rábano, I. and Valério, M. 2009. Giant trilobites and trilobite clusters from the Ordovician of Portugal. *Geology*, **37**, 443–446.
- Hairapetian, V. and Ginter, M. 2010. Pelagic chondrichthyan microremains from the Upper Devonian of the Kale Sardar section, eastern Iran. *Acta Geologica Polonica*, **60**, 357–371.
- Hairapetian, V. and Korn, D. 2011. Phylogenetic analysis of the family Beloceratidae (Ammonoidea, Late Devonian) and a new *Beloceras* species from eastern Iran. *Bulletin of Geosciences*, **86**, 675–682.
- Hartenfels, S. and Becker, R.T. 2016. The global *Annulata* Events: review and new data from the Rheris Basin (northern Tafilalt) of SE Morocco. *Geological Society, London, Special Publications*, **423** (1), 291–354.
- Helms, J. 1959. Conodonten aus dem Saalfelder Oberdevon (Thüringen). *Geologie*, **8** (6), 634–677.
- Helms, J. and Wolska, Z. 1967. New Upper Devonian conodonts from Poland and Germany. *Acta Palaeontologica Polonica*, **12**, 227–238.
- Hembree, D.I., Mapes, R.H. and Goiran, C. 2014. The impact of high-energy storms on shallow-water *Nautilus* (Cephalopoda) taphonomy, Lifou (Loyalty Islands). *Palaios*, **29** (7), 348–362.
- Holmes, G.B. 1928. A bibliography of the conodonts with descriptions of Early Mississippian species. *Proceedings of the United States National Museum*, **72** (5), 1–38.
- Hyatt, A. 1883–1884. Genera of fossil cephalopods. *Proceedings of the Boston Society of Natural History*, **22**, 253–338.
- Kirk, T.W. 1880. On the occurrence of giant cuttlefish on the New Zealand coast. *Transactions of the New Zealand Institute*, **12**, 310–313.
- Klug, C., De Baets, K., Kröger, B., Bell, M.A., Korn, D. and Payne, J.L. 2015. Normal giants? Temporal and latitudinal shifts of Palaeozoic marine invertebrate gigantism and global change. *Lethaia*, **48**, 267–288.
- Korn, D. 1999. Famennian Ammonoid Stratigraphy of the Ma'der and Tafilalt (Eastern Anti-Atlas, Morocco). *Abhandlungen der Geologischen Bundesanstalt*, **54**, 147–179.
- Korn, D. 2010. A key for the description of Palaeozoic ammonoids. *Fossil Record*, **13**, 5–12.
- Korn, D. 2017. The genus *Gonioclymenia* (Ammonoidea; Late Devonian) in Central Europe. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **284**, 258–286.
- Korn, D., Bockwinkel, J. and Ebbighausen, V. 2015. Middle Famennian (Late Devonian) ammonoids from the Anti-At-

- las of Morocco. 2. Sporadoceratidae. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **278**, 47–77.
- Korn, D. and Klug, C. 2002. Ammonoae Devonicae. Fossilium Catalogus. I: Animalia, Pars 138, 375 p. Backhuys; Leiden.
- Korn, D. and Klug, C. 2007. Conch form analysis, variability, morphological disparity, and mode of life of the Frasnian (Late Devonian) ammonoid *Manticoceras* from Coumiac (Montagne Noire, France). In: Landman, N.H., Davis, R.A. and Mapes, R.H. (Eds), *Cephalopods Present and Past: New Insights and Fresh Perspectives*, pp. 57–85. Springer; New York.
- Korn, D. and Ziegler, W. 2002. The ammonoid and conodont zonation at Enkenberg (Famennian, Late Devonian; Rhenish Mountains). *Senckenbergiana lethaea*, **82**, 453–462.
- Kubodera, T. and Mori, K. 2005. First-ever observations of a live giant squid in the wild. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2583–2586.
- Kullmann, J. 1993. Paleozoic ammonoids of Mexico and South America. *Comptes Rendus XII ICC-P*, **1**, 557–562.
- Landois, H. 1895. Die Riesenammoniten von Seppenrade: *Pachydiscus Zittel seppenradensis* H. Landois. *Jahresberichte der Westfälischen Provinzialverwaltung, Wissenschaft und Kunst*, **23**, 99–108.
- Lange, W. 1929. Zur Kenntnis des Oberdevons am Enkeberg und bei Balve (Sauerland). *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge*, **119**, 1–132.
- Legrand-Blain, M. 1999. A Frasnian productid brachiopod fauna from Kale Sardar, Tabas region, eastern Iran. *Annales de la Société géologique du Nord*, **7**, 13–20.
- Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata, 824 p. Laurentius Salvius; Holmiae.
- Manger, W.L., Meeks, L.K. and Stephen, D.A. 1999. Pathologic gigantism in middle Carboniferous cephalopods, southern midcontinent, United States. In: Oloriz, F. and Rodriguez-Tovar, F.J. (Eds), *Advancing research on living and fossil cephalopods*, pp. 77–89. Kluwer Academic/Plenum Publishers; New York.
- Mapes, R.H., Landman, N.H., Cochran, K., Goiran, C., de Forges, B.R. and Renfro, A. 2010a. Early taphonomy and significance of naturally submerged *Nautilus* shells from the New Caledonia region. *Palaios*, **25** (9), 597–610.
- Mapes, R.H., Hembree, D.I., Rasor, B.A., Stigall, A., Goirand, C. and De Forges, B.R. 2010b. Modern *Nautilus* (Cephalopoda) taphonomy in a subtidal to backshore environment, Lifou (Loyalty Islands). *Palaios*, **25** (10), 656–670.
- Miller, A.K. 1932. The cephalopods of the Bighorn formation of the Wind River Mountains of Wyoming. *Transactions of the Connecticut Academy of Arts and Sciences*, **31**, 193–297.
- Miller, A.K. 1938. Devonian ammonoids of America. *Special papers of the Geological Society of America*, **14**, 1–262.
- Miller, A.K., Furnish, W.M. and Schindewolf, O.H. 1957. Paleozoic Ammonoidea. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Part L, Mollusca, Ammonoidea*, 4, L11–L79. Geological Society of America and University of Kansas Press; Kansas.
- Moran, A.L. and Woods, H.A. 2012. Why might they be giants? Towards an understanding of polar gigantism. *Journal of Experimental Biology*, **215** (12), 1995–2002.
- Morzadec, P., Dastanpour, M. and Wright, A.J. 2002. Asteroptygine trilobites from the Late Devonian of the Kerman region, Iran. *Alcheringa*, **26** (1), 143–149.
- Müller, K.J. 1956. Zur Kenntnis der Conodonten-Fauna des europäischen Devons, 1; die Gattung *Palmatolepis*. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **494**, 1–70.
- Nalivkina, A.K. 1953. Upper Devonian goniatites and clymenias of Mugodzary. *Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta (VNI-GR)*, novaya seriya, **72**, 60–125. [In Russian]
- Petersen, M.S. 1975. Upper Devonian (Famennian) ammonoids from the Canning Basin, Western Australia. *Journal of Paleontology, Memoirs*, **8**, 1–55.
- Petter, G. 1959. Goniatites dévoniennes du Sahara. *Publications du Service de la Carte géologique de l'Algérie (nouvelle série), Paléontologie*, **2**, 1–313.
- Rosa, R., Gonzalez, L., Dierssen, H.M. and Seibel, B.A. 2012. Environmental determinants of latitudinal size-trends in cephalopods. *Marine Ecology Progress Series*, **464**, 153–165.
- Ruan, Y.-P. 1981. Devonian and earliest Carboniferous Ammonoids from Guangxi and Guizhou. *Memoires of Nanjing Institute of Geology and Paleontology, Academia Sinica*, **15**, 1–152.
- Ruttner, A.W. and Stöcklin, J. 1966. Foreword. With key map, stratigraphic summary and description of fossil-localities. *Geological Survey of Iran Report*, **6**, 2–6.
- Sandberg, C.A. 1976. Conodont biofacies of Late Devonian *Polygnathus styriacus* Zone in western United States. *Geological Association of Canada, Special Paper*, **15**, 171–186.
- Sandberger, G. and Sandberger, F. 1850–1856. Die Versteinerungen des rheinischen Schichtensystems in Nassau. Mit einer kurzgefassten Geognosie dieses Gebietes und mit steter Berücksichtigung analoger Schichten anderer Länder, xiv + 564 p. Kreidel & Niedner; Wiesbaden.
- Sannemann, D. 1955. Oberdevonische Conodonten (to Ila). *Senckenbergiana lethaea*, **26** (1/2), 123–156.
- Sartenaer, P. 1966. Frasnian rhynchonellida from the ozbak-Kuh and tabas regions (east Iran). *Geological Survey of Iran, Report*, **6**, 25–53.
- Savoy, L.E. and Harris, A.G. 1993. Conodont biofacies and taphonomy along a carbonate ramp to black shale basin (latest Devonian and earliest Carboniferous), southernmost Canadian Cordillera and adjacent Montana. *Canadian Journal of Earth Sciences*, **30** (12), 2404–2422.
- Schindewolf, O.H. 1923. Beiträge zur Kenntnis des Paläo-

- zoikums in Oberfranken, Ostthüringen und dem Sächsischen Vogtlande. I. Stratigraphie und Ammonoitenfauna des Oberdevons von Hof a.S. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band*, **49**, 250–357, 393–509.
- Schultze, H.-P. 1973. Large Upper Devonian arthropods from Iran. *Fieldiana Geology*, **23**, 53–78.
- Sobolew, D. 1914. Comments on the phylogeny of goniatites. *Izvestiya Varshavskogo Politechnicheskogo Instituta*, **1914**, 1–191. [In Russian]
- Stevens, G. 1988. Giant ammonites: a review. In: Wiedmann, J. and Kullmann, J. (Eds), *Cephalopods: present and past*, pp. 141–166. E. Schweizerbart; Stuttgart.
- Stöcklin, J., Eftekhari-Nezhad, J. and Hushmand-Zadeh, A. 1965. Geology of the Shotori range (Tabas area, east Iran). *Geological Survey of Iran, Reports*, **3**, 1–69.
- Stöcklin, J. and Nabavi, M.H. 1971. Explanatory text of the Boshruyeh Quadrangle map 1: 250,000. *Geological Survey of Iran, Geological Quadrangle*, **17**, 1–50.
- Teichert, C. and Kummel, B. 1960. Size of endoceroid cephalopods. *Breviora Museum of Comparative Zoology*, **128**, 1–7.
- Torsvik, T.H. and Cocks, L.R.M. 2013. Gondwana from top to base in space and time. *Gondwana Research*, **24**, 999–1013.
- Ulrich, E.O. and Bassler, R.S. 1926. A classification of the toothlike fossils, conodonts, with descriptions of American Devonian and Mississippian species. *Proceedings of the United States National Museum*, **68**, 1–63.
- Walliser, O.H. 1966. Preliminary notes on Devonian, Lower and Upper Carboniferous goniatites in Iran. *Report, Geological Survey of Iran*, **6**, 7–24.
- Walton, S.A., Korn, D. and Klug, C. 2010. Size distribution of the Late Devonian ammonoid *Prolobites*: indication for possible mass spawning events. *Swiss Journal of Earth Sciences*, **103**, 474–494.
- Wani, R., Kase, T., Shigeta, Y. and De Ocampo, R. 2005. New look at ammonoid taphonomy, based on field experiments with modern chambered nautilus. *Geology*, **33**, 849–852.
- Wedekind, R. 1908. Die Cephalopodenfauna des höheren Oberdevon am Enkeberge. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band*, **26**, 565–633.
- Wedekind, R. 1914. Beiträge zur Kenntnis der Oberkarbonischen Goniatiten. *Mitteilungen aus dem Museum der Stadt Essen für Natur- und Völkerkunde*, **1**, 1–22.
- Wedekind, R. 1918. Die Genera der Palaeoammonoidea (Goniatiten). Mit Ausschluß der Mimoceratidae, Glyphioceratidae und Prolecanitidae. *Palaeontographica*, **62**, 85–184.
- Wendt, J., Hayer, J. and Karimi Bavandpur, A. 1997. Stratigraphy and depositional environment of Devonian sediments in northeast and east-central Iran. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **206**, 277–322.
- Wendt, J., Kaufmann, B., Belka, Z., Farsan, N. and Karimi Bavandpur, A. 2005. Devonian/Lower Carboniferous stratigraphy, facies patterns and palaeogeography of Iran – Part II. Northern and central Iran. *Acta Geologica Polonica*, **55**, 31–97.
- Winkelmann, I., Campos, P.F., Strugnell, J., Cherel, Y., Smith, P.J., Kubodera, T., Allcock, L., Kampmann, M.-L., Schroeder, H., Guerra, A., Norman, M., Finn, J., Ingrao, D., Clarke, M. and Gilbert, M.T.P. 2013. Mitochondrial genome diversity and population structure of the giant squid *Architeuthis*: genetics sheds new light on one of the most enigmatic marine species. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**, 1–9.
- Yazdi, M. 1996. Late Devonian–Carboniferous conodont biostratigraphy of the Tabas area, Eastern Iran, 221 p. Unpublished PhD Thesis, Macquarie University; Sydney.
- Yazdi, M. 1999. Late Devonian–Carboniferous conodonts from Eastern Iran. *Rivista Italiana di Paleontologia e Stratigrafia*, **105**, 167–200.
- Ziegler, W. 1962. Taxonomie und Phylogenie oberdevonischer Conodonten und ihre stratigraphische Bedeutung. *Abhandlungen des Hessisches Landesamtes für Bodenforschung*, **38**, 1–166.
- Ziegler, W. and Huddle, J.W. 1969. Die *Palmatolepis glabra*-Gruppe (Conodonta) nach der Revision der Typen von Ulrich & Bassler durch J. W. Huddle. *Fortschritte in der Geologie von Rheinland und Westfalen*, **16**, 377–386.
- Ziegler, W. and Sandberg, C.A. 1984. *Palmatolepis*-based revision of upper part of standard Late Devonian conodont zonation. *Geological Society of America, Special Paper*, **196**, 179–194.

Manuscript submitted: 14<sup>th</sup> February 2018

Revised version accepted: 14<sup>th</sup> June 2018