Phylogenetic analysis of the family Beloceratidae (Ammonoidea; Late Devonian) and a new *Beloceras* species from eastern Iran

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The cladistic analysis of the beloceratid ammonoids *Mesobeloceras* and *Beloceras* shows anagenetic development, by increasing number of sutural elements, in the stem group representatives and cladogenesis in the crown group. Crown group topology rules out vicariant evolution of the beloceratids and does not show palaeogeographic patterns. The widespread occurrences of multilobate species of *Beloceras* suggests connected low-latitude shelf areas between the regions of the Anti-Atlas, Montagne Noire, Rhenish Mountains, Shotori Range, Altay, and Canning Basin. A new species of *Beloceras*, *Beloceras sardarense* sp. nov., is described. • Key words: Ammonoidea, Devonian, Iran, phylogeny, biogeography.

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Beloceras is one of the most spectacular of the Palaeozoic ammonoids. It has the most multilobate suture line of all Devonian ammonoids; some of the species possessing up to 50 individual lobes and a conch shape that undergoes conspicuous ontogenetic changes (Korn *et al.* 2011). *Beloceras* is distributed in nearly all equatorial shelf areas of the middle and late Frasnian and regularly accompanies the genus *Manticoceras*.

The concept of species differentiation within the genus *Beloceras* has been discussed often during the last few decades (*e.g.* by Yatskov 1990, Korn & Klug 2002, and Korn *et al.* 2011). Conservative approaches have used only a few species names for the material assembled in the various regions (*e.g.* Rhenish Mountains, Montagne Noire, Anti-Atlas, Altay, and the Canning Basin). All records within these regions were usually attributed to only two species, *B. sagittarium* (*e.g.* by Bogoslovsky 1958, 1969; Glenister 1958) or *B. tenuistriatum* (*e.g.* by Korn & Klug 2002). Korn & Klug (2002) synonymised most of the species and only treated *B. tenuistriatum* and *B. stenumbilicatum* as valid.

An alternative concept has been expressed by Yatskov (1990), who interpreted every single occurrence as a different species and introduced several new genera and subgenera within the family Beloceratidae. Yatskov (1990, p. 38) proposed a phylogram with independent evolutionary lineages, each ending with extremely multilobate species. This hypothesis was not popular with ammonoid researchers, probably because it differed too much, in its radical splitting concept, from the existing taxonomic and phylogenetic concepts of the family Beloceratidae.

In a recent account, Korn *et al.* (2011) revised material of *Beloceras* from the Rhenish Mountains and the Anti-Atlas and reached the conclusion that in fact endemic species do occur in these regions. They partly supported the taxonomic concept proposed by Yatskov (1990) but did not reach a conclusion on whether the phylogenetic relationships that he outlined were likely or not. After submission of the manuscript, the second author became aware of material of *Beloceras* from the Kale Sardar section in the Shotori Range (eastern Iran). This occurrence is already known within the literature (Clapp 1940; Wendt *et al.* 1997, 2005; Yazdi 1999; Gholamalian 2007) but has not yet been described. In the following paper, another new endemic species of *Beloceras* will be introduced from this locality.

Geographic and stratigraphic setting

A number of scattered hills, representing Late Devonian "cephalopod beds" of the Shishtu Formation, are widely exposed on the northern bank of the Sardar River, west of

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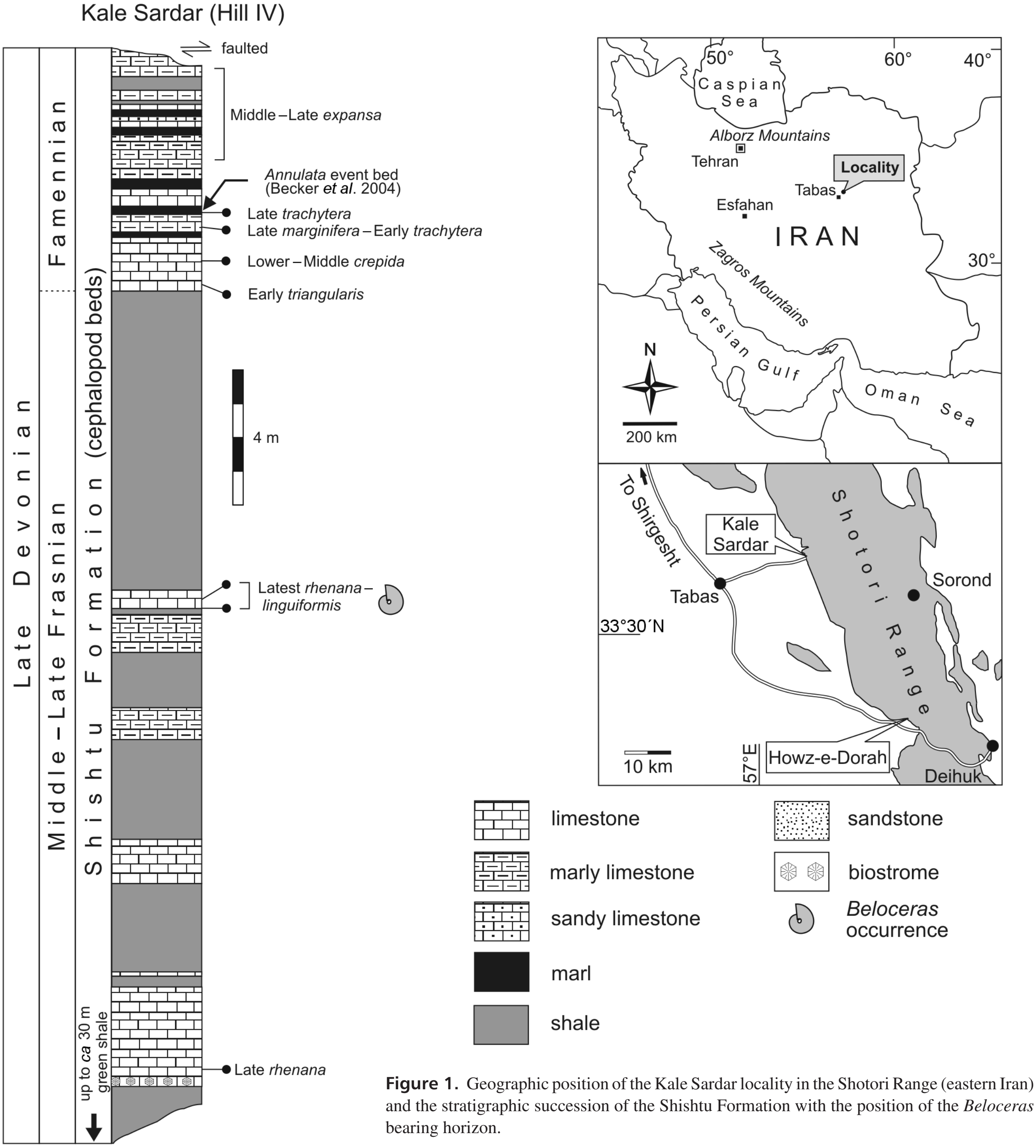

Figure 1. Geographic position of the Kale Sardar locality in the Shotori Range (eastern Iran) and the stratigraphic succession of the Shishtu Formation with the position of the *Beloceras* bearing horizon.

the Shotori Range, eastern Iran. After an early report by Clapp (1940), the outcrops in Kale Sardar were first studied in detail by Stöcklin *et al*. (1965). Thus far, this fossiliferous section was the most interesting locality in eastern Iran and has been featured in several works (Flügel 1961; Sartenaer 1966; Walliser 1966; Haas & Mensink 1970; Schultze 1973; Haas 1994; Legrand-Blain 1999; Yazdi 1999; Morzadec 2002; Feist *et al*. 2003; Becker *et al*. 2004; Ashouri 2002, 2004; Gholamalian 2007; Gholamalian *et al*. 2009; Webster *et al*. 2007; Hairapetian & Ginter 2010).

The new specimens of *Beloceras* were collected from a section (Hill IV in Becker *et al*. 2004), located approximately 22 km east of Tabas (N 33°39´ 26˝; E 57°8´ 38˝; Fig. 1). The lithology of the section commences with a series of oolitic limestones alternating with green shale grading into a condensed set of marls, marly limestones, and shales. The oolitic limestone, which contains *Beloceras* specimens changes laterally to a coeval red ferruginous ammonoid-bearing bed, in which *Manticoceras ammon* was found by Walliser (1966).

From the samples K5H and K5 in the oolitic limestone, very rich conodont assemblages including *Icriodus alternatus alternatus*, *I. alternatus helmsi*, *I. alternatus mawsonae*, *Ancyrodella buckeyensis*, *Ancyrognathus triangularis*, *Palmatolepis gigas gigas*, *Pa. winchelli*, *Polygnathus aequalis*, *P. evidens*, *P. politus*, *P. procerus*, *P. webbi*, and *P. vachiki* were collected (Gholamalian 2007, table 2). These species suggest an age interval from the Late *rhenana* to the *linguiformis* Zones (Gholamalian 2007) and this is entirely consistent with an earlier conodont dating (Yazdi 1999, p. 176).

Systematic palaeontology

Suborder Gephuroceratina Ruzhencev, 1957
Superfamily Belocerataceae Hyatt, 1884
Family Beloceratidae Hyatt, 1884

Genus *Beloceras* Hyatt, 1884

Type species. – *Goniatites sagittarius* Sandberger & Sandberger, 1851, p. 77.

***Beloceras sardarense* sp. nov.**
Figure 2

1999 *Beloceras tenuistriatum* – Yazdi, p. 171.
2005 *Beloceras tenuistriatum* – Wendt *et al*., p. 56.

Derivation of name. – After the Sardar River, where the material was collected.

Holotype. – Specimen MB.C.21997 (Hairapetian Coll.); illustrated in Fig. 2.

Type locality and horizon. – Northern bank of the Sardar River, 22 km east of Tabas (Shotori Range, Central Iran); Shishtu Formation (late Frasnian).

Material. – The holotype and a poorly preserved paratype from the type locality.

Diagnosis. – Species of *Beloceras* with extremely discoidal (ww/dm = 0.24) and involute conch (uw/dm = 0.14 in stages larger than 70 mm dm). Umbilical wall rather steep; shallow spiral groove in the midflank area. Suture line with six secondary prongs of the external lobe, a very narrow V-shaped lateral lobe, and eight umbilical lobes on the flanks at a conch diameter of 95 mm; formula of the ventral suture line in this growth stage (E_2 E_3 E_4 E_5 E_6 E_7 E_1 E_7 E_6 E_5 E_4 E_3 E_2) L U_2 U_4 U_6 U_8 U_{10} U_{12} U_{14} U_{16} U_{18}). Prongs of the external lobe are narrowly V-shaped to lanceolate; the saddles between the U_8 lobe and the E_4 lobe are tectiform.

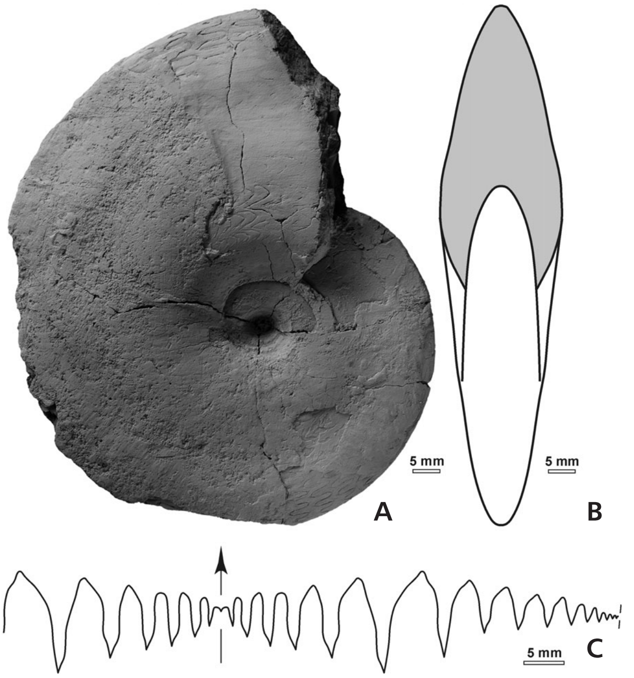

Figure 2. *Beloceras sardarense* sp. nov., holotype MB.C.21997 from Kale Sardar (Hairapetian Coll.). • A – lateral view; × 0.7. • B – dorsal view; × 0.7. • C – suture line at 96.1 mm dm, 22.5 mm ww, 49.5 mm wh; × 1.0.

Description. – Holotype MB.C.21997 is a fully septate specimen with a conch diameter measuring 97 mm (Fig. 2A, Table 1). It is extremely discoidal (ww/dm = 0.24) and involute (uw/dm = 0.14) with a narrowly rounded venter and an oblique, slightly incurved umbilical wall. The flanks converge towards the venter and possess a shallow midflank groove, which is very weak at the beginning of the last preserved whorl but becomes more prominent towards the end of the phragmocone (Fig. 2A, B).

The suture line of the holotype was drawn at a conch diameter of 96 mm (Fig. 2C). It shows six secondary prongs of the external lobe, all being very narrow and deep. These lobes differ in their outline; the E_2 lobe is Y-shaped with a very narrow base and converging flanks in the upper half, the E_3 lobe is lanceolate with slightly pouched flanks, the E_4 and E_5 lobes are asymmetric with slightly curved ventral flanks, and the E_6 lobe is small and narrowly V-shaped. The L lobe is Y-shaped with a very narrow base and flanks

Table 1. Conch dimensions (in mm) and proportions for the holotype of *Beloceras sardarense* sp. nov. from Kale Sardar.

	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.21997	97.0	23.0	51.3	13.7	35,8	0.24	0.45	0.14	2.51	0.30

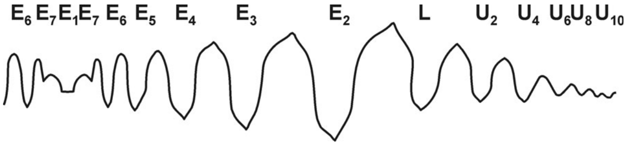

Figure 3. Suture line terminology used in this paper.

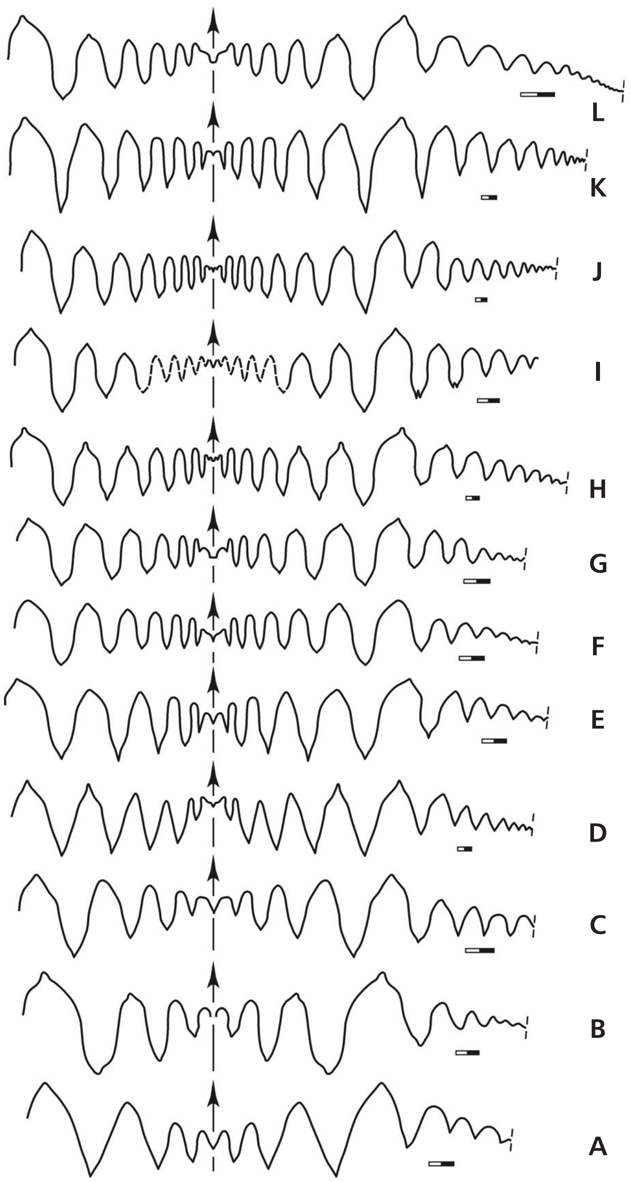

Figure 4. Suture lines of the beloceratid species included in the phylogenetic analysis. • A – *Mesobeloceras kayseri* (Holzapfel, 1882), specimen MB.C.22067 from the Beul in the Rhenish Mountains (Denckmann Coll.), at 11.1 mm ww, 28.6 mm wh. • B – *Mesobeloceras thomasi* Glenister, 1958, holotype after Glenister (1958, fig. 12b), at 35 mm dm. • C – *Beloceras webbelense* Korn *et al*., 2011, paratype MB.C.22026 (Paeckelmann 1920 Coll.) from the Martenberg near Adorf (Rhenish Mountains), at 8.4 mm ww, 23.6 mm wh (after Korn *et al*. 2011). • D – *Beloceras petterae* Yatskov, 1990, specimen MB.C.22033.1 (Bockwinkel Coll.) from Hassi Nebech (Anti-Atlas, Morocco), at 13.2 mm ww, *ca* 50 mm wh (after Korn *et al*. 2011). • E – *Beloceras jorfense* Korn *et al*., 2011, holotype MB.C.22047 (Wendt Coll.) from Tantana (Anti-Atlas, Morocco), at 61.1 mm dm, 10.7 mm ww, 30.0 mm wh (after Korn *et al*. 2011). • F – *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842), specimen MB.C.22007 (Denckmann 1893 Coll.) from the Martenberg near Adorf, at 37.0 mm dm, 9.0 mm ww, 19.0 mm wh (after Korn *et al*. 2011). • G – *Beloceras bogoslovskyi* (Yatskov, 1990), paratype after Bogoslovsky (1969, fig. 102zh), at 28.7 mm wh. • H – *Beloceras glenisteri* (Yatskov, 1990), holotype after Glenister (1958, fig. 14), at 126 mm dm. • I – *Beloceras schulzi* (House & Kirchgasser, 1985), holotype after House & Kirchgasser (in House *et al*. 1985, fig.10a). • J – *Beloceras sagittarium* (Sandberger & Sandberger, 1851), specimen MB.C.19183 (Schultz 1967 Coll.) from the Braunsberg near Tegau (Thuringian Mountains), at 128.5 mm dm, 26.5 mm ww, 67.5 mm wh (after Korn *et al*. 2011). • K – *Beloceras sardarense* sp. nov., holotype MB.C.21997 from Kale Sardar (Hairapetian Coll.), at 96.1 mm dm, 22.5 mm ww, 49.5 mm wh. • L – *Beloceras stenumbilicatum* Bogoslovsky, 1958, holotype after Bogoslovsky (1969, fig. 102z), at 20.7 mm wh. Scale bar = 2 mm.

diverging strongly in the uppermost part. The umbilical lobes are rather uniform in their outline, being V-shaped and becoming smaller towards the umbilicus. Seven of the saddles in the midflank area (between the U_8 lobe and the E_4 lobe) are tectiform at their top, with the saddle between the L and E_2 lobes being dominant and slightly mammiform.

Comparisons. – The new species cannot be confused with any of the other *Beloceras* species. It differs from all of the other known species of the genus in the presence of the midflank spiral groove, producing a slender pear-shaped whorl cross section. Furthermore, *B. sardarense* has a stouter conch than all of the other species (ww/dm = 0.24 in *B. sardarense* and less than 0.20 in the other species).

Species such as *B. sagittarium* and *B. sardarense* are similar in number and shape of their sutural elements, but in *B. sardarense*, seven saddles show a tectiform outline (only three or four saddles do this in the other species of the genus). Furthermore, the lobes (particularly the L and E_2 lobes) are narrower and deeper in *B. sardarense*.

Phylogenetic analysis of *Beloceras* species

Cladistic analyses of ammonoids have only rarely been done (for a summary, see Neige *et al*. 2007, Yacobucci in press). However, in some case studies (*e.g*. Landman 1989; Korn 1997, 2001; Monks 1999; Moyne & Neige 2004; McGowan & Smith 2007) it has been proven that the method can be successfully applied to this fossil group.

We analysed the beloceratid ammonoids (genera *Mesobeloceras* and *Beloceras*; Figs 3, 4) using the parsimonious cladistic method (Figs 5, 6) using the PAST software (Hammer *et al.* 2008), and the following preconditions formed its framework:

- Twelve taxa were included: two species of *Mesobeloceras* and ten species of *Beloceras*.

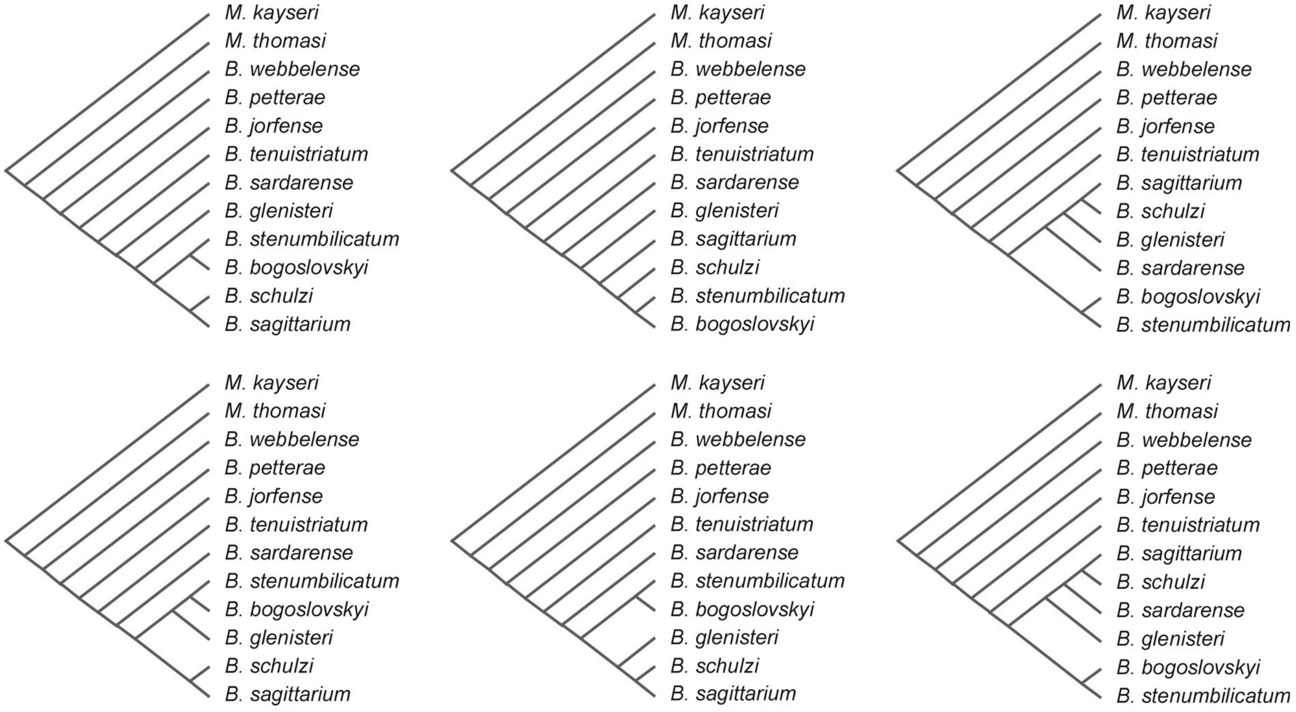

Figure 5. Phylogenetic analysis of the beloceratid ammonoids, six most parsimonious trees.

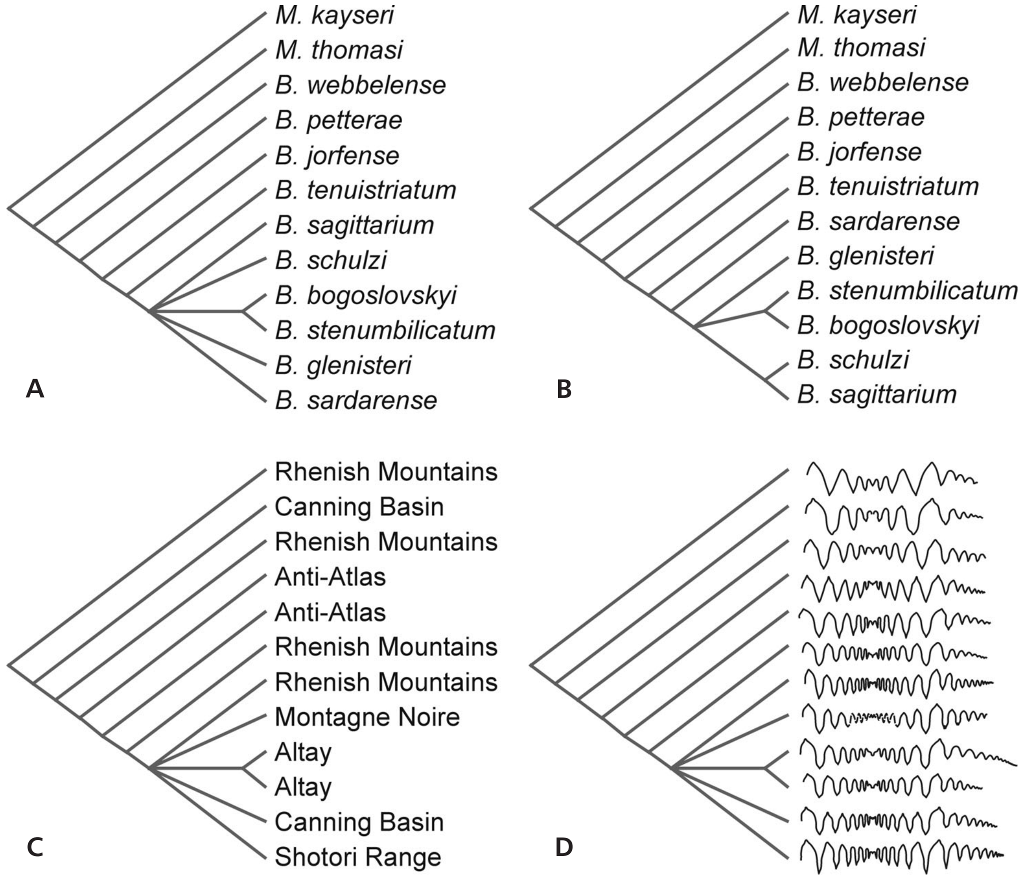

Figure 6. Phylogenetic analysis of the beloceratid ammonoids. • A – strict consensus tree. • B – 50% majority consensus tree. • C – strict consensus tree with the regions with the beloceratid species. • D – strict consensus tree with the suture lines of the beloceratid species.

Table 2. Character list used in the analysis of the beloceratid species.

No.	Character	Character state 0	Character state 1	Informative	CI in mp trees
1	uw/dm ratio	> 0.25	< 0.25	yes	1.00
2	uw/dm ratio	> 0.20	< 0.20	yes	1.00
3	uw/dm ratio	> 0.15	< 0.15	yes	0.50
4	umbilical rim	strong	moderate or weak	yes	1.00
5	umbilical rim	strong or moderate	weak	yes	0.25
6	lateral groove	no	yes	no	1.00
7	ventrolateral groove	no	yes	yes	0.50
8	E lobe prongs	< 3	> 3	yes	1.00
9	E lobe prongs	< 4	> 4	yes	1.00
10	E lobe prongs	< 5	> 5	yes	1.00
11	U lobes	< 3	> 3	yes	1.00
12	U lobes	< 4	> 4	yes	1.00
13	U lobes	< 5	> 5	yes	0.33
14	E4 lobe width	moderate	narrow	yes	0.50
15	E4 lobe shape	V-shaped	lanceolate	yes	1.00
16	E4-E3 saddle	rounded	not rounded	yes	1.00
17	E4-E3 saddle	not acute	acute	yes	0.50
18	E4-E3 saddle	not tectiform	tectiform	yes	1.00
19	E3 lobe width	moderate	narrow	yes	0.26
20	E3 lobe shape	V-shaped	lanceolate	yes	1.00
21	E3-E2 saddle	acute	tectiform	yes	0.50
22	E2 lobe width	moderate	narrow	yes	0.33
23	E2 lobe width	narrow	very narrow	no	1.00
24	E2 lobe shape	V-shaped	lanceolate	yes	0.50
25	E2-L saddle	acute	tectiform	yes	1.00
26	L lobe width	moderate	narrow	yes	0.67
27	L lobe width	narrow	very narrow	no	1.00
28	L lobe shape	V-shaped	lanceolate	yes	0.44
29	L lobe subdivided	no	yes	no	1.00
30	L-U2 saddle	rounded	tectiform	yes	0.33
31	U2 lobe width	wide	moderate or narrow	yes	1.00
32	U2 lobe width	wide or moderate	narrow	yes	0.53
33	U2 lobe shape	V-shaped	lanceolate	yes	0.32
34	U2 lobe subdivided	no	yes	no	1.00

- *Mesobeloceras kayseri* (Holzapfel, 1882) was chosen as the outgroup because it has the lowest number of sutural elements out of all of the analysed species.
- A total of 34 characters were included, all with the two character states 0 and 1. Therefore, some quantitative characters (*e.g.* the number of sutural elements) with more than two character states were split into singular characters.
- Seven characters refer to the conch shape and 27 characters to the suture line.

The analysis revealed the following results:

- Of the 34 characters, 29 of them are informative (Table 2) and 5 are autapomorhic characters (regarding only the species *Beloceras sardarense* and *B. schulzi*).
- The parsimony analysis led to six most parsimonious trees with a tree length of 57 steps.
- Differences between these six trees regard only the crown group (composed of the six most multilobate species).
- The consensus trees show two patterns, (1) anagenesis in the stem group representatives (*Mesobeloceras* and less multilobate species of *Beloceras*) and (2) cladogenesis in the crown group (multilobate species of *Beloceras*).

- The strict consensus tree (Fig. 6A) shows the crown group with five branches rooting in one node; these five branches represent the five regions (Montagne Noire, Rhenish Mountains, Altay, Shotori Range, Canning Basin) from which the six multilobate species of *Beloceras* (*B. sagittarium*, *B. schulzi*, *B. bogoslovskyi*, *B. stenumbilicatum*, *B. sardarense*, *B. glenisteri*) are known (Fig. 6C).
- The 50% majority tree (Fig. 6B) shows *B. sardarense* (Shotori Range) as the sister group of three separate branches, (1) *B. sagittarium* and *B. schulzi* (Rhenish Mountains, Montagne Noire), (2) *B. bogoslovskyi* and *B. stenumbilicatum* (Altay), and (3) *B. glenisteri* (Canning Basin).
- The consistency index of the analysis is 0.60.
- Of the 29 informative characters, 14 of them have a consistency index of 1 within the six most parsimonious trees.
- The consistency index of the informative characters in the six most parsimonious trees is 0.71.
- There is no visible general pattern in the quality of the characters. The consistency index of the characters referring to distinct sutural elements (width, shape) does not prove any of the characters to be of any particular value.
- Characters that are very stable are those that refer to the number of sutural elements (secondary prongs of the external lobe, umbilical lobes).

Results and discussion

The phylogenetic analysis of the beloceratid ammonoids allows for a number of interpretations:

1. The genus *Beloceras* is monophyletic. – The cladograms show that the distribution of characters rules out a polyphyletic origin of the genus (Figs 5, 6).

2. There are major trends in the phylogeny of the beloceratid ammonoids. – This result is not surprising because the tendency towards multilobate suture lines, as seen in the beloceratids, is also known from a number of Palaeozoic and Mesozoic ammonoid lineages, *e.g.* late Middle Devonian pharciceratids (Bogoslovsky 1969), Early Carboniferous acrocanitids (Korn *et al.* 2007), Carboniferous and Permian medlicottiids (Ruzhencev 1949), and Triassic pinacoceratids (Mojsisovics 1873). In these cases there occurs a covariation with the transformation of conch geometry; the multilobate taxa are also the ones with a narrow umbilicus.

3. There are no parallel lineages within *Beloceras* leading to multilobate species, as proposed by Yatskov (1990, p. 38). All multilobate species of the genus are rooted in a common node, and the multiplication of prongs of the external lobe as well as the umbilical lobe can be regarded as a synapomorphic character (Fig. 6D).

4. The cladograms can be interpreted in a way that suggests that there is no vicariance in the evolution of the beloceratid ammonoids. Species of different complexity within distinct regions (Rhenish Mountains, Anti-Atlas, Canning Basin) do not form monophyla, ruling out independent vicariant evolutionary lineages (Fig. 6C).

5. The cladograms do not allow the recognition of palaeogeographic patterns. In the species constituting the crown group (the multilobate species of *Beloceras*), all geographic regions are separate branches rooting in one node. The only exceptions may be the Rhenish Mountains and the Montagne Noire, which in five of the six most parsimonious trees form a monophyletic unit. However, this result may be caused by the incomplete data set for *B. schulzi* (question marks in characters 10 and 13) and its overall similarity to *B. sagittarium*.

6. The phylogenetic analysis of the beloceratid ammonoids suggests a correspondence of the faunas between the equatorial shelves (regions Anti-Atlas, Montagne Noire, Rhenish Mountains, Shotori Range, Altay, and the Canning Basin). In light of this result, the middle and late Frasnian can be seen as a time interval of pronounced cosmopolitism.

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