Beloceras, the most multilobate Late Devonian ammonoid

DIETER KORN, JÜRGEN BOCKWINKEL, VOLKER EBBIGHAUSEN & SONNY A. WALTON

Beloceras is the most multilobate among the Late Devonian ammonoids, with a suture line composing up to 50 or more singular lobes. Revision of the material from the Rhenish Mountains and Thuringian Mountains of Germany and the Anti-Atlas of Morocco led to the conclusion that endemic species can be identified mainly on the base of differences in the suture line. The species *Beloceras sagittarium* (Sandberger & Sandberger, 1851), *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842), and *Beloceras webbelense* sp. nov. are described from the Rhenish Mountains and *Beloceras petterae* Yatskov, 1990 as well as *Beloceras jorfense* sp. nov. from the Anti-Atlas. • Key words: Ammonoidea, Gephuroceratina, Beloceratidae, Frasnian, morphometrics, suture line.

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The Frasnian ammonoid assemblages are characterised by a wide spectrum of morphologies, in which species with simple conch morphology (*i.e.* with similar conch geometry throughout ontogeny) and also a simple suture line (*i.e.* with few sutural elements) co-occurred with species possessing highly complex multilobate suture lines and a rather complex conch ontogeny (*e.g.* Korn & Klug 2002). The ammonoid family with the highest number of sutural elements in the Frasnian is the Beloceratidae, with some species possessing conchs with up to 50 or even more lobes *Beloceras* specimens may be quite large, with conch diameters reaching up to 300 mm (*B. sagittarium*). The most advanced Late Devonian ammonoids belong to this genus, having the most complex suture line and an extremely discoidal conch, occupying a marginal position in the morphospace occupied by the Devonian ammonoids.

Beloceras or closely related genera have been reported from practically all regions in which Frasnian ammonoids have been found. An exception to this distribution is the Timan, but from this region young specimens of *Beloceras* were misinterpreted and described as *Nordiceras* (Bogoslovsky 1958, 1969).

Beloceras is a genus that urgently requires a revision based on the original material. Up to now, only a few of the occurrences have been described with sufficient material, but even for the type species a clear demarcation has not been drawn. For instance, it was not clear if all the specimens from the Rhenish Mountains belong to only one species, or if *B. tenuistriatum* has a global distribution, occurring in the Rhenish Mountains, the Anti-Atlas, the Canning Basin, *etc*. Yatskov (1990) has proposed a number of new species (see below) with the hypothesis that each regional occurrence has its own endemic species. The evidence for such a view was weak, and hence these names usually have been treated as synonyms. Although such endemism cannot be excluded, a thorough revision is necessary to support this hypothesis.

In this report, specimens from the Rhenish Mountains and the Anti-Atlas are revised based on previously unpublished material in order to outline the morphological spectrum of the Beloceratidae in the two regions.

Geographic and stratigraphic distribution of *Beloceras*

Specimens of *Beloceras* and closely related genera are known from a number of regions, reviewed below (Fig. 1).

Rhenish Mountains: Beyrich (1837) described a species under the name '*Ammonites multilobatus*' from the "rothen Goniatiten-Kalk von Oberscheld", but unfortunately it is not known where the type material has been stored. From the description and illustration of the suture line it is most likely a species of *Beloceras*. Anyway '*Ammonites multilobatus* Beyrich, 1837' is a junior homonym of '*Ammonites multilobatus* Bronn, 1832' and hence invalid.

D'Archiac & de Verneuil (1842) described '*Goniatites tenuistriatus*' from Oberscheld and their very accurate lithographic illustrations allow a rather clear characterisation of the conch geometry. Unfortunately, d'Archiac & de Verneuil (1842) did not illustrate suture lines of their species and the current whereabouts of this material is not known. Sandberger & Sandberger (1851) described '*Goniatites Sagittarius*' from Seßacker near Oberscheld, mainly based on a large septate specimen.

Occurrences of the genus *Beloceras* in the Rhenish Mountains (Fig. 2) were subsequently reported several times. Holzapfel (1882) listed '*Beloceras multilobatum* Beyrich, 1837' from the Martenberg and Webbel Mine near Adorf and the Charlottenzug Mine near Bredelar. This means that he did not separate between the three species described in this article; according to his illustrations we can infer that the most likely identity for his specimens is *B. webbelense* sp. nov. He also newly introduced '*Beloceras Kayseri*', which is now attributed to the genus *Mesobeloceras*.

Wedekind (1913, 1918) listed '*Beloceras multilobatum* Beyrich, 1837', '*Beloceras Kayseri* Holzapfel, 1882', and the new species '*Beloceras Denckmanni*' from the Martenberg near Adorf. The latter two are now attributed to *Mesobeloceras*. Matern (1931) gave faunal lists including '*Beloceras multilobatum* Beyrich, 1837' and '*Beloceras Kayseri* Holzapfel, 1882' from localities in the area of Oberscheld, but he did not describe or figure the material. Clausen (in Clausen *et al.* 1991) figured '*Beloceras* cf. *sagittarium* → *Beloceras subacutum*' from the Beringhausen Tunnel, including the first cross section of the genus from the Rhenish Mountains.

For a long time it was not clear which species names were valid for the material; most of the authors used the names '*B. multilobatum*' and '*B. sagittarium*'. Schindewolf (1940) then claimed that '*B. tenuistriatum* d'Archiac & de Verneuil (1842)' is the species name having priority over *B. sagittarium*, however, the two species are separated here.

Thuringian Mountains: Müller (1956) described '*Beloceras multilobatum* Beyrich, 1837' from the upper *Manticoceras* Stufe of the Geipel quarry near Schleiz.

Devonshire: Foord & Crick (1897) and House (1963) listed '*Beloceras sagittarium*' from the area of Chudley.

Cantabrian Mountains: Poorly preserved material of '*Beloceras* cf. *tenuistriatum*' was reported by Kullmann (1960) from the Arruz region of Palencia. From the León province, Kullmann (1963) figured '*Beloceras tenuistriatum*'.

Menorca: Hermite (1887) listed material from Santa Rita under the name '*Beloceras multilobatum*'. This material has not been revised.

Pyrenees: The occurrence of *Beloceras* was reported from the Pyrenees (*e.g.* Sanz-López 2002), but the specimens have not been described.

Montagne Noire: A well-preserved specimen from the 'Pic de Cabrières' of '*Beloceras multilobatum* Beyrich, 1837' has been figured by Frech (1897, pl. 32a, fig. 9). Frech (1897, p. 177f, text-fig. 1 and 1902, p. 60, text-fig. 19) figured the suture line of the specimen two times (once rotated by 180 degrees). The illustrated specimen is involute (uw/dm = 0.09) and in this respect closely resembles *Beloceras sagittarium* (Sandberger & Sandberger, 1851) and *Beloceras stenumbilicatum* Bogoslovsky, 1958. The suture line figured by Frech (1897, 1902) is obviously not correct, as Frech (1902, p. 60) stated himself. The figures show more or less triangular lobes and saddles, but the photograph (Frech 1897, pl. 32a, fig. 9) shows lanceolate secondary prongs of the external lobe.

Böhm (1935) described additional fragmentary specimens of '*Beloceras multilobatum* Beyrich, 1837' from Coumiac. Schulz (1967) described more and better-preserved material from this locality under the species name '*Beloceras sagittarium* (Sandberger & Sandberger, 1851)'. Schulz showed suture lines, which occasionally display serrated lobes (lateral lobe and outer umbilical lobe). On the basis of this observation House & Kirchgasser (in House et al. 1985) identified two species within the assemblage, attributed to different genera, namely '*Beloceras sagittarium* (Sandberger & Sandberger, 1851)' for the specimens lacking serration and '*Ceratobeloceras schulzi* House & Kirchgasser (1985)' for the specimens with 'ceratitic subdivision of the ventrad umbilical lobes'. Yatskov (1990) then renamed the specimens with non-serrated lobes and introduced the new species '*Beloceras* (*Beloceras*) *gallicum* Yatskov, 1990' and chose a holotype from the material described by Schulz (1967). Becker & House (1994) did not use this name and figured non-serrated specimens under the species name '*Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842)'. Further studies are required to show if the material from the Montagne Noire represents synonyms of other species or if they are endemic species.

Carnic Alps: Frech (1902, pl. 4, fig. 11) figured a fragment of a rather large specimen from the Valentintörl; according to his misinterpretation of the age of the specimen (Frech thought that it came from Early Devonian rocks), he introduced the new species '*Beloceras praecursor* Frech, 1902'. The fragment has a whorl height of about 50 mm and is multilobate with at least six secondary prongs on the external lobe. According to the figure, which shows rather

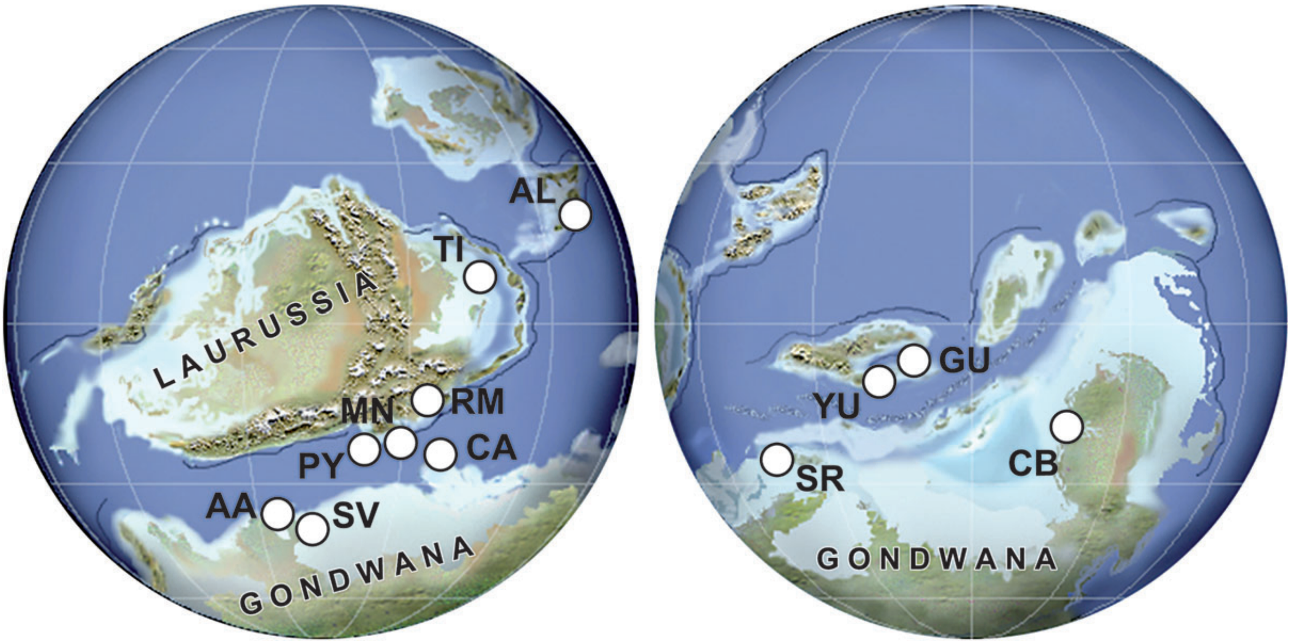


Figure 1. Palaeogeographic reconstruction of the Late Devonian (after Ron Blakey, http://jan.ucc.nau.edu/~rcb7/index.html) with the proposed positions of the occurrences of the genus *Beloceras*. Abbreviations: AA – Anti-Atlas, SV – Saoura Valley, PY – Pyrenees, MN – Montagne Noire, CA – Carnic Alps; RM – Rhenish Mountains, TI – Timan, AL – Altay, SR – Shotori Range, YU – Yunnan, GU – Guangxi, CB – Canning Basin.

symmetric V-shaped lobes and also triangular saddles, it can be assumed that the specimen was polished and that details of the suture line were erased.

Timan: The genus *Beloceras* was believed to be absent in the ammonoid-rich occurrences of the Timan. However, '*Prolecanites timanicus* Holzapfel, 1899', was based on small specimens with a maximum diameter of 20 mm. Bogoslovsky (1955, 1969) introduced the new genus name *Nordiceras* for this problematic species and placed it in the family Pharciceratidae. Becker & House (*in* Becker *et al.* 2000) revised some of the species, which are important for the Frasnian succession of the Timan, including *Nordiceras timanicum*. They illustrated newly collected material from this species, but this was also rather small (less than 13 mm in dm). The authors introduced the *Nordiceras timanicum* Zone for an interval in the middle Frasnian Domanik Formation and correlated this zone tentatively with the *Beloceras tenuistriatum* Zone. Korn & Klug (2002) introduced the new family Nordiceratidae for the genus *Nordiceras* and placed it in the Belocerataceae.

The *Beloceras* material from Büdesheim has a particularly close morphological resemblance with *Nordiceras timanicum* in all respects. The minor differences regard the ornament (with weak folds on the outer flank in *B. sagittarium*), and the suture line that shows a slightly faster ontogenetic development in the latter species. The consequence of this is that the genus *Nordiceras* has to be put into synonymy with *Beloceras* and the family Nordiceratidae into synonymy with the family Beloceratidae.

Altay: Bogoslovsky (1958, 1969) described two species, one of which he attributed to '*Beloceras sagittarium* (Sandberger & Sandberger, 1851)' and the other, *Beloceras stenumbilicatum* Bogoslovsky, 1958, was new. Bogoslovsky noticed narrowly and widely umbilicate conch forms within '*B. sagittarium*' and this material was later (Yatskov 1990) used for the description of a new species '*Mesobeloceras bogoslovskyi* Yatskov, 1990'.

Saoura Valley: Termier & Termier (1950, text-figs 25–27) figured a specimen of '*Beloceras sagittarium* (Sandberger & Sandberger, 1851)' from Béni Abbès in Algeria. The (possibly inaccurate) suture line figure shows an external lobe with just two secondary prongs, a lateral lobe and four umbilical lobes on the flank. Such a configuration is unlikely, but Yatskov (1990) used this figure for his new species '*Sinobeloceras termieri* Yatskov, 1990' to represent an evolutionary lineage in which the subdivision of the external lobe is decelerated.

Petter (1959) described the new species '*Beloceras subacutum*' based on a whorl fragment from Béni-Abbès. According to her figures (Petter 1959, pl. 10, fig. 4, text-fig. 44C), this specimen must belong to *Mesobeloceras*. However, Yatskov (1990) used this species as the type species of his new genus *Atopobeloceras*.

Anti-Atlas: Petter (1959) figured two specimens probably belonging to *Beloceras*. The best specimen (Petter 1959, pl. 10, fig. 1, text-fig. 44a), with a conch diameter of 75 mm, comes from 'Ride de l'Adrar' in the Tafilalt (Anti-Atlas) and was described as '*Beloceras tenuistriatum* (d'Archiac &

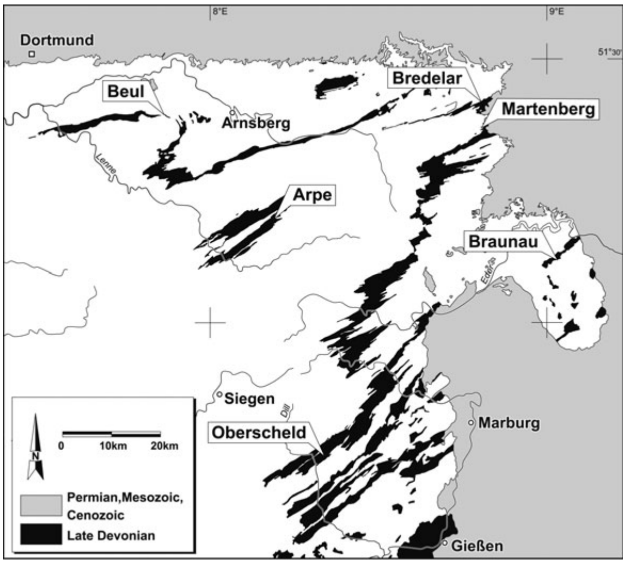


Figure 2. The main occurrences of *Beloceras* in the Rhenish Mountains.

	"standard zones" (Becker & House 2000)	Rhenish Mountains (Becker & House 2000)
FRASNIAN	*Crickites holzapfeli*	*Crickites holzapfeli* *Crickites rickardi*
	Archoceras varicosum	*Archoceras varicosum*
	Neomanticoceras paradoxum	*Neomanticoceras paradoxum* *Maternoceras sandbergeri*
	Playfordites tripartitus	*Playfordites tripartitus* *Costamanticoceras nodulosum*
	Beloceras tenuistriatum	*Beloceras tenuistriatum*
	Mesobeloceras kayseri	*Mesobeloceras kayseri*
	Prochorites alveolatus	
	Probeloceras lutheri	
	Sandbergeroceras syngonum	*Sandbergeroceras costatum*
	Timanites keyserlingi	*Koenenites lamellosus*
	Koenenites styliophilus	
	Petteroceras feisti	*Ponticeras* spp.

Beloceras

Figure 3. Frasnian ammonoid stratigraphy and the stratigraphic distribution of the genus *Beloceras*.

de Verneuil), 1837 var. ?' [sic!]. It was used by Yatskov (1990) to introduce the new species '*Beloceras* (*Beloceras*) *petterae* Yatskov, 1990' based on the probably inaccurate suture line drawing provided by Petter (1959, p. 185, text-fig. 44a). The second specimen described by Petter (1959, pl. 10, fig. 2) as '*Beloceras* cf. *tenuistriatum* (d'Archiac & de Verneuil), 1837' [sic!] is a whorl fragment, which is difficult to interpret.

Additionally, Petter (1959, pl. 10, figs 3, 5, 6, 9, 10, text-fig. 44b) described a specimen, with a conch diameter of 69 mm as '*Beloceras kayseri* (Holzapfel), 1882' from Themateni Znigui (Taouz region). This specimen belongs, according to its suture line and conch shape, to the genus *Mesobeloceras*.

Shotori Range: Yazdi (1999) as well as Wendt *et al.* (2005) reported '*Beloceras tenuistriatum*' from eastern Iran; however, this material has not yet been described.

Yunnan: Chao (1956, pl. 1, figs 12–16) figured three specimens of his new species '*Beloceras acutum*' from the Baoshan Block. They have a very narrow umbilicus and a suture line with four secondary prongs of the external lobe at 36 mm conch diameter. These characters put forward a strong case for its inclusion in the *Beloceras*; however, Yatskov (1990) used this species as the type species of his new genus *Sinobeloceras*.

Guangxi: Ruan (1981, pl. 9, figs 19, 22, text-fig. 20) published figures of poorly preserved specimens of a beloceratid, and the suture line can only be seen as a schematic representation. However, Yatskov (1990) based his new species '*Sinobeloceras ruani* Yatskov, 1990' on these illustrations. The material may belong to '*Beloceras acutum* Chao, 1956'.

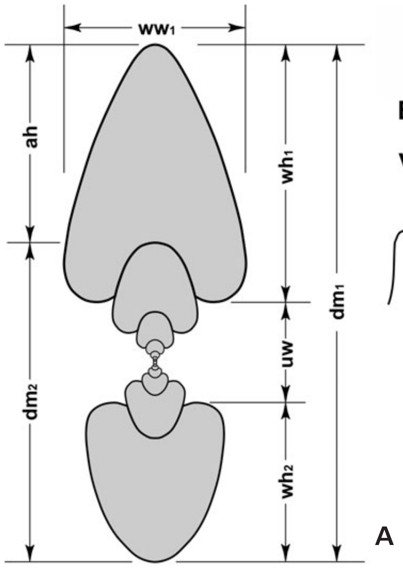
Canning Basin: Teichert (1941, 1943) reported the presence of the genus *Beloceras* in the Canning Basin. Glenister (1958), in his monograph described two species of the family Beloceratidae, '*Mesobeloceras thomasi* Glenister, 1958' and '*Beloceras sagittarium* (Sandberger & Sandberger, 1851)'. Yatskov (1990) identified the latter as his new species '*Mesobeloceras glenisteri* Yatskov, 1990'. House (1971) figured the wrinkle layer of this species.

All these occurrences show that *Beloceras* has a stratigraphic position in the upper part of the Frasnian (Fig. 3) of the ammonoid stratigraphy proposed by Becker & House (2000). The *Beloceras tenuistriatum* Zone was defined with the first entry of the genus. Occurrences of *Beloceras* in well-studied sections have been reported from the Martenberg near Adorf (House & Ziegler 1977) in the classic German ammonoid zones Iβ, Iγ, and Iδ (*i.e.* correlating with the *Beloceras tenuistriatum* Zone to the *Crickites holzapfeli* Zone of the revised Frasnian zonation (Becker & House 2000). *Beloceras* became extinct at the Frasnian-Famennian boundary.

Material of *B. sagittarium* from the Thuringian Mountains has been dated with conodonts. Poorly preserved specimens from Schleiz (see appendix) derive from a limestone bed immediately below the Upper Kellwasser Horizon and belong in the Upper *rhenana* or the *linguiformis* Zone (Weyer *et al.* 2003). Specimens of '*B. tenuistriatum*' (= *B. petterae*) from Ouidane Chebbi in the Anti-Atlas of Morocco have been dated and as a result of this they have been placed in Zone 6 (*primus* Zone) of the Frasnian composite standard (Belka *et al.* 1999).

Material

We studied material from four principal regions of Germany and Morocco, (1) the Eifel Mountains (locality Büdesheim), (2) the Rhenish Mountains (a number of localities including Beul, Bredelar, Martenberg, Oberscheld, Ense), (3) the Thuringian Mountains (localities Braunsberg and Vogelsberg), and (4) the Anti-Atlas. A total of 165 specimens have



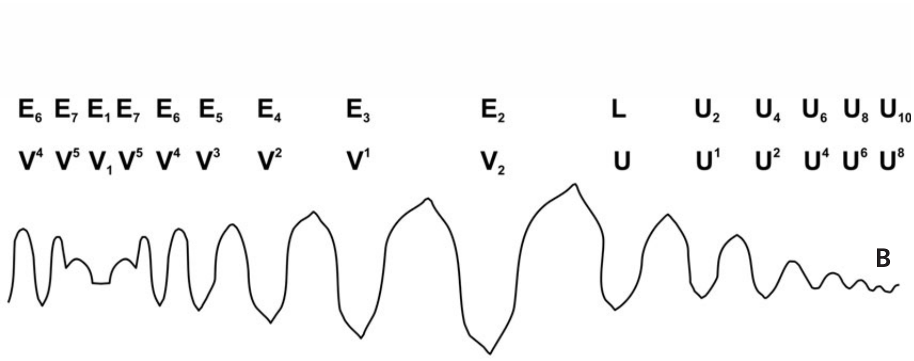


Figure 4. Terminology used in the descriptions. • A – conch dimensions (after Korn & Klug 2007). • B – comparison of the suture line terminologies used in this paper, upper line and the articles by Bogoslovsky (1971) as well as Yatskov (1990), lower line.

been studied, all of them are stored in the collection of the Museum für Naturkunde Berlin (see appendix).

Systematic palaeontology

The descriptions and illustrations follow the scheme proposed by Korn (2010) for Carboniferous ammonoids (Fig. 4). The terminology of the suture line was used according to Wedekind (1918) and Schindewolf (1929) but with some modifications (for a summary see Korn & Klug 2002). The terminology of the suture lines of gephuroceratid ammonoids is still debated and the naming of the distinct sutural elements can be varied according to which suture terminology is used. Therefore, Miller *et al*. (1957, p. L19) stated for sutural formulas that "… if they are not readily understandable they do not serve a good purpose". However, sutural formulas, despite their shortcomings, still help to understand differences between ontogenetic traits and are used here to characterise the species.

Bogoslovsky (1969) separated two principal developmental processes of the external lobe (his V lobe):

(1) The external lobe is subdivided by an incision of its flanks, becoming secondary prongs. The formula of the external lobe is (V_2 V_1 V_2), proposed for *Manticoceras*, *Beloceras*, *etc*. Translated to the concept of Schindewolf (1929) this would be (E_2 E_1 E_2); we use this (E_2 E_1 E_2) system in the present study (Fig. 4).

(2) The external lobe is subdivided by the raising of a median saddle causing secondary prongs. The formula is then (V_1 V_1), as proposed for *Timanoceras*. Bogoslovsky (1957, 1969) used this criterion for a separation of *Timanoceras* from the gephuroceratids and introduced the suborder Timanoceratina for this single genus. The validity of this taxon must be questioned; the putative difference in the development of the suture line is probably caused by different preservation and preparation techniques. As Clausen (1969) demonstrated, the pyritic phragmocones of *Manticoceras* specimens from Büdesheim would fall into this category.

Conch measurements, proportions, and growth rates are applied according to Korn & Klug (2007), as they were used there for gephuroceratid ammonoids (Fig. 4).

The abbreviations used in the text are: conch diameter (dm), whorl width (ww), whorl height (wh), umbilical width (uw) = $dm_1 - wh_1 - wh_2$, apertural height (ah) = $dm_1 - dm_2$. Conch proportions (growth rates) and expansion rates were calculated in the following way by using the three basic conch parameters: conch width index (CWI) = ww_1/dm_1, whorl width index (WWI) = ww_1/wh_1, umbilical width index (UWI) = uw/dm_1 or $(dm_1 - wh_1 - wh_2)/dm_1$, whorl expansion rate (WER) = $(dm_1/dm_2)^2$ or $[dm_1/(dm_1 - ah)]^2$, imprint zone rate (IZR) = $wh_1 - ah/wh_1$ or $[wh_1 - (dm_1 - dm_2)]/wh_1$.

Suborder Gephuroceratina Ruzhencev, 1957

Included superfamilies. –
Gephurocerataceae Frech, 1897
Timanocerataceae Ruzhencev, 1957 [synonym of Gephurocerataceae]
Belocerataceae Hyatt, 1884

Superfamily Belocerataceae Hyatt, 1884

Included families. –
Acanthoclymeniidae Schindewolf, 1955
Beloceratidae Hyatt, 1884

Eobeloceratidae Becker & House, 1994 [synonym of Beloceratidae]
Nordiceratidae Korn & Klug, 2002 [synonym of Beloceratidae]

Family Beloceratidae Hyatt, 1884

Included genera. – *Naplesites* Yatskov, 1990,
Anabeloceras Clarke, 1899 [nomen nudum; synonym of *Naplesites*],
Chaoceras Yatskov, 1990 [synonym of *Naplesites*],
Merzougites Korn & Klug, 2002,
Eobeloceras Schindewolf, 1936,
Mesobeloceras Glenister, 1958,
Atopobeloceras Yatskov, 1990 [probably a synonym of *Mesobeloceras*],
Sinobeloceras Yatskov, 1990 [probably a synonym of *Beloceras*],
Beloceras Hyatt, 1884,
Ceratobeloceras House & Kirchgasser, 1985 [synonym of *Beloceras*],
Idiobeloceras Yatskov, 1990 [synonym of *Beloceras*],
Nordiceras Bogoslovsky, 1955 [synonym of *Beloceras*].

Genus *Beloceras* Hyatt, 1884

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

Included species. –
acutum: *Beloceras acutum* Chao, 1956, p. 103; Yunnan.
bogoslovskyi: *Mesobeloceras bogoslovskyi* Yatskov, 1990, p. 47; Altay.
gallicum: *Beloceras* (*Beloceras*) *gallicum* Yatskov, 1990, p. 48; Montagne Noire.
glenisteri: *Mesobeloceras glenisteri* Yatskov, 1990, p. 47; Canning Basin.
jorfense: *Beloceras jorfense* sp. nov.; Anti-Atlas.
multilobatum: *Ammonites multilobatus* Beyrich, 1837, p. 33; Rhenish Mountains [non *Ammonites multilobatus* Bronn, 1832].
petterae: *Beloceras* (*Beloceras*) *petterae* Yatskov, 1990, p. 48; Saoura Valley.
praecursor: *Beloceras praecursor* Frech, 1902, p. 61; Carnic Alps.
ruani: *Sinobeloceras ruani* Yatskov, 1990, p. 45; Guangxi.
sagittarium: *Goniatites sagittarius* Sandberger & Sandberger, 1851, p. 77; Rhenish Mountains.
schulzi: *Ceratobeloceras schulzi* House & Kirchgasser, 1985, p. 9; Montagne Noire.
shidianense: *Beloceras shidianensis* Yang, 1984, p. 33; Yunnan.
stenumbilicatum: *Beloceras stenumbilicatum* Bogoslovsky, 1958, p. 121; Altay.
tenuistriatum: *Goniatites tenuistriatus* d'Archiac & de Verneuil, 1842, p. 343; Rhenish Mountains.
termieri: *Sinobeloceras termieri* Yatskov, 1990, p. 45; Anti-Atlas.
timanicum: *Prolecanites timanicus* Holzapfel, 1899, p. 47; Timan.
webbelense: *Beloceras webbelense* sp. nov.; Rhenish Mountains.

Discussion. – The genus *Beloceras* is understood here as including species with an extremely discoidal, subinvolute to involute conch and an adult suture line with at least four secondary prongs of the external lobe. *Mesobeloceras* has a wider umbilicus than *Beloceras*, but it is the latter character in particular that separates *Beloceras* from *Mesobeloceras*, which possesses only three secondary prongs.

There is an obvious morphological evolution within the family Beloceratidae; the closure of the umbilicus is paralleled by the increase of sutural elements. Another trend can be seen in the shape of the sutural elements, particularly in the secondary prongs of the external lobes. These are V-shaped and separated by triangular saddles in *Mesobeloceras*, producing a zigzag course of the suture line. The less advanced representatives of *Beloceras*, such as *B. webbelense* and *B. petterae* are similar in this respect, but those species with increasing numbers of lobes (*B. sagittarium*, *B. stenumbilicatum*) possess lanceolate lobes and tectiform saddles. Finally, weakening of the umbilical rim, which is very prominent within this genus, can be seen in species of *Beloceras*.

At the moment it cannot be fully verified if independent lineages are present in *Beloceras*, but the conch shape and configuration of the suture line suggest that the taxon is monophyletic. Further studies will show if the genus is represented by endemic species and if the morphological evolution within the genus reflects the stratigraphic occurrence of the species.

Beloceras sagittarium (Sandberger & Sandberger, 1851)

Figures 5C, D, 6–10

* 1851 *Goniatites sagittarius* Sandberger & Sandberger, p. 77, pl. 4, fig. 3.
non 1851 *Goniatites sagittarius* Sandberger & Sandberger, pl. 4, fig. 3c–e. [= *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842)]
1931 *Beloceras multilobatum*. – Matern, p. 76.
non 1958 *Beloceras sagittarium*. – Bogoslovsky, p. 119, pl. 6, figs 3, 4, pl. 7, fig. 1. [= *Beloceras bogoslovskyi* (Yatskov, 1990)]

non 1958 *Beloceras sagittarium*. – Glenister, p. 85, pl. 5, fig. 12, pl. 10, fig. 7, pl. 13, figs 1–5, pl. 14, figs 1–8. [= *Beloceras glenisteri* (Yatskov, 1990)]
non 1969 *Beloceras sagittarium*. – Bogoslovsky, p. 299, text-fig. 101d, 10a–zh, pl. 27, figs 7, 8, pl. 28. [= *Beloceras bogoslovskyi* (Yatskov, 1990)]
non 1971 *Beloceras sagittarium*. – House, p. 24, pl. 1, fig. 4. [= *Beloceras glenisteri* (Yatskov, 1990)]
1991 *Beloceras* cf. *sagittarium* → *Beloceras subacutum*. – Clausen *in* Clausen *et al.*, p. 32, text-fig. 5C, pl. 13, fig. 4, 5.

Holotype. – Specimen MB.C.4501 (Dannenberg Coll.); Museum für Naturkunde Berlin.

Type locality and horizon. – Sessacker near Oberscheld; red Frasnian cephalopod limestones.

Material. – Specimens from four principal areas in Germany are available for study:

(1) Ten pyritized specimens (7–25 mm in conch diameter) and one calcareous fragment of a phragmocone which is about 120 mm in diameter from the Eifel Mountains (Büdesheim). All the specimens are preserved as internal moulds with parts of the body chamber preserved.

(2) Two specimens (Denckmann 1900 and 1902 Coll.), with conch diameters of 46 and 117 mm, from the northern margin of the Rhenish Mountains (Beul near Eisborn). These specimens are embedded in grey or reddish cephalopod limestone; shell remains are preserved. One specimen (Mempel Coll.) with a conch diameter of 42 mm comes from Arpe.

(3) Twelve specimens from the eastern margin of the Rhenish Mountains besides the holotype: 5 specimens (Müller & Denckmann Coll.) which are between 37 and 86 mm in dm from the Charlottenzug Mine near Bredelar; three specimens (Dannenberg, Lotz 1901 Coll.) between 77 and 115 mm in dm from the Seßacker near Oberscheld; one specimen with a diameter of 50 mm from the Staatliche Grube near Oberscheld; two specimens (Denckmann 1888 Coll.) measuring 100 and 102 mm in dm from the Schmidt quarry near Braunau (Kellerwald). Most of the specimens were collected during the period when the ironstone mines in the Rhenish Mountains were still being worked. They are often preserved with shell remains in red cephalopod limestone or haematitic iron ore.

(4) Thirty-five specimens (ranging from 35–135 mm in conch diameter) from the Thuringian Mountains: 19 specimens from dark-grey limestones of the Braunsberg near Tegau (Schultz 1967 Coll.); 10 specimens up to 129 mm in diameter from red cephalopod limestones of the Vogelsberg quarry near Göschitz (Bartzsch & Weyer 1985 Coll.), and six fragments (Bartzsch & Weyer 1995 Coll.) from Schleiz.

Diagnosis. – Species of *Beloceras* with involute conch (uw/dm = 0.10 in stages larger than 50 mm diameter). Suture line with six or seven secondary prongs of the external lobe, a lanceolate lateral lobe, and six or more umbilical lobes on the flanks at a conch diameter of 60 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}. All external lobes are lanceolate, the E_4, E_5, and E_6 lobes are very narrow and deep; three or four of the larger saddles (between the L lobe and the E_4 lobe) are tectiform. The adult suture line has an increasing number of umbilical lobes.

Description of material from the Rhenish Mountains. – The type specimen (MB.C.4501; Dannenberg Collection) of '*Goniatites sagittarius* Sandberger & Sandberger, 1851' in the Museum für Naturkunde, Berlin has a conch diameter of approximately 120 mm and is fully septate (Fig. 5C). The specimen comes from Sessacker near Oberscheld and is not as well preserved as would be expected from Sandberger & Sandberger's (1850–1856, pl. 4, fig. 3) beautiful illustration (Fig. 5D). It is strongly corroded with portions of the outer flanks and venter as well as the umbilical mar-

Table 1. Conch ontogeny (Figs 8, 9) of *Beloceras sagittarium* (Sandberger & Sandberger, 1851) from Büdesheim (up to 18 mm dm) and the Rhenish and Thuringian Mountains (larger stages).

dm	conch shape	whorl cross section shape	aperture
1.5 mm	thinly discoidal; subevolute (ww/dm ~ 0.38; uw/dm ~ 0.39)	weakly depressed; weakly embracing (ww/wh ~ 1.05; IZR ~ 0.12)	high (WER ~ 2.20)
4 mm	extremely discoidal; subevolute (ww/dm ~ 0.25; uw/dm ~ 0.40)	weakly compressed; weakly embracing (ww/wh ~ 0.80; IZR ~ 0.14)	high (WER ~ 2.15)
8 mm	extremely discoidal; subevolute (ww/dm ~ 0.25; uw/dm ~ 0.35)	weakly compressed; moderately embracing (ww/wh ~ 0.60; IZR ~ 0.20)	high (WER ~ 2.25)
18 mm	extremely discoidal; subinvolute (ww/dm ~ 0.25; uw/dm ~ 0.17)	strongly compressed; strongly embracing (ww/wh ~ 0.45; IZR ~ 0.32)	extremely high (WER ~ 2.55)
50 mm	extremely discoidal; involute (ww/dm ~ 0.18; uw/dm ~ 0.10)	strongly compressed; strongly embracing (ww/wh ~ 0.35; IZR ~ 0.35)	extremely high (WER ~ 2.55)
100 mm	extremely discoidal; involute (ww/dm ~ 0.18; uw/dm ~ 0.10)	strongly compressed; strongly embracing (ww/wh ~ 0.30; IZR ~ 0.35)	very high (WER ~ 2.40)

gin missing; it does not provide a complete picture of the suture line. The shell surface is also poorly preserved, but some shell remains show that there are five strong spiral lines on the outer flank. It is difficult to obtain conch measurements from this corroded specimen, but it can be estimated that the umbilicus was about one tenth of the conch diameter.

The best-preserved available specimen is MB.C.19180 (Denckmann 1902 Coll.; Fig. 6A) from Beul ('Beuel b. Balve' according to the label). It has a conch diameter of 117 mm and is nearly complete, being extremely discoidal and involute (ww/dm = 0.17; uw/dm = 0.10) with a very high aperture (WER = 2.40). A faint rim accompanies the umbilical seam and the umbilical wall is shallow and slightly concave. The conch is widest in the midflank area, from where the flanks converge slowly towards the umbilicus and the subacute venter. Most of the specimen is covered by the shell, which appears to be completely smooth. Faint growth lines can only be seen on the outer flanks.

Specimen MB.C.19182 (Denckmann 1888 Coll.) from 'Schmidt's Steinbruch am Kalkofen b. Braunau' is a fragment of the largest available specimen. The phragmocone is nearly completely preserved at 100 mm in diameter, and another half a volution of the phragmocone is visible in parts but the body chamber is missing. The total size of the specimen has been estimated to be approximately 250 mm in diameter. Shell remains are not preserved, but the specimen displays parts of the suture line characteristic for an advanced species of *Beloceras*.

Specimen MB.C.4504 (Denckmann Coll.) from the Charlottenzug Mine near Bredelar is a fragment of a phragmocone approximately 80 mm in diameter and allows for the study of parts of the suture line. At a whorl height of about 36 mm, the suture line shows seven secondary external lobes, all lanceolate with the tendency to become narrower towards the venter. The saddles between the first external and lateral lobe as well as between the first and fourth external lobes are tectiform, the saddles between the fourth and the seventh external lobe are rounded.

A specimen with a conch diameter of 50 mm (MB.C.4502; Hubach Collection) labelled 'Staatliche Grube, Oberscheld' is the specimen with the best preserved shell ornament in the Berlin collection (Fig. 6B, C). It is preserved in haematitic iron ore and possesses extremely fine growth lines, which extend almost linearly across the flanks. They form a low projection on the outer flank, where they become stronger, and turn back to form a very deep and narrow ventral sinus. On the tabulate venter they are lamellar, being arranged in distances of 0.2 mm. The umbilical wall is very shallow with a faint rim near the umbilical seam.

The sectioned specimen MB.C.19175 (Fig. 9) shows, at a conch diameter of 67 mm the characteristic shape of the umbilicus. The umbilical wall is very shallow and possesses a weak umbilical rim at the umbilical seam.

Description of material from the Thuringian Mountains. – Specimen MB.C.19194 (Bartzsch & Weyer 1985 Coll.) from the Vogelsberg near Göschitz is the best preserved specimen from that locality (Fig. 7). It is slightly deformed and has a conch diameter of 106 mm. Most of this specimen represents the phragmocone, and only a very short portion of the body chamber is preserved. The conch has the appearance of a flat disc (ww/dm = 0.15) and is involute (uw/dm = 0.10) with an extremely high aperture (WER = 2.63). The umbilical margin is broadly rounded and separates the umbilical wall from the flanks, which converge to the narrowly rounded, almost subacute venter. Shell remains are present in the specimen, but their preservation is poor because of the strong pressure solution of its surface.

The suture line of this specimen (Fig. 8C) was drawn where the whorl height is 34 mm, corresponding to a conch diameter of about 66 mm. Six secondary prongs of the external lobe are present here; all are lanceolate and show a tendency to become narrower towards the venter. The lateral lobe is lanceolate with nearly parallel flanks, and the six visible umbilical lobes are V-shaped. The

Table 2. Conch dimensions (in mm) and proportions for reference specimens of *Beloceras sagittarium* (Sandberger & Sandberger, 1851) from Büdesheim.

	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.22003.1	17.7	4.6	9.7	3.0	6.6	0.26	0.47	0.17	2.53	0.32
MB.C.22004.2	11.0	2.9	4.9	3.4	3.8	0.26	0.59	0.31	2.31	0.23
MB.C.22004.4	7.6	1.8	2.9	2.9	2.5	0.23	0.61	0.38	2.24	0.13
MB.C.22003.3	6.92	1.75	2.74	2.46	2.22	0.25	0.64	0.36	2.17	0.19
	4.70	1.27	1.72	1.83	1.48	0.27	0.74	0.39	2.13	0.14
	3.22	0.91	1.15	1.30	1.00	0.28	0.79	0.40	2.11	0.13
	2.22	0.67	0.77	0.89	0.70	0.30	0.86	0.40	2.13	0.09
	1.52	0.58	0.56	0.59	0.50	0.38	1.04	0.39	2.21	0.11
	1.02	0.56	0.38	0.28	0.32	0.54	1.48	0.27	2.14	0.14

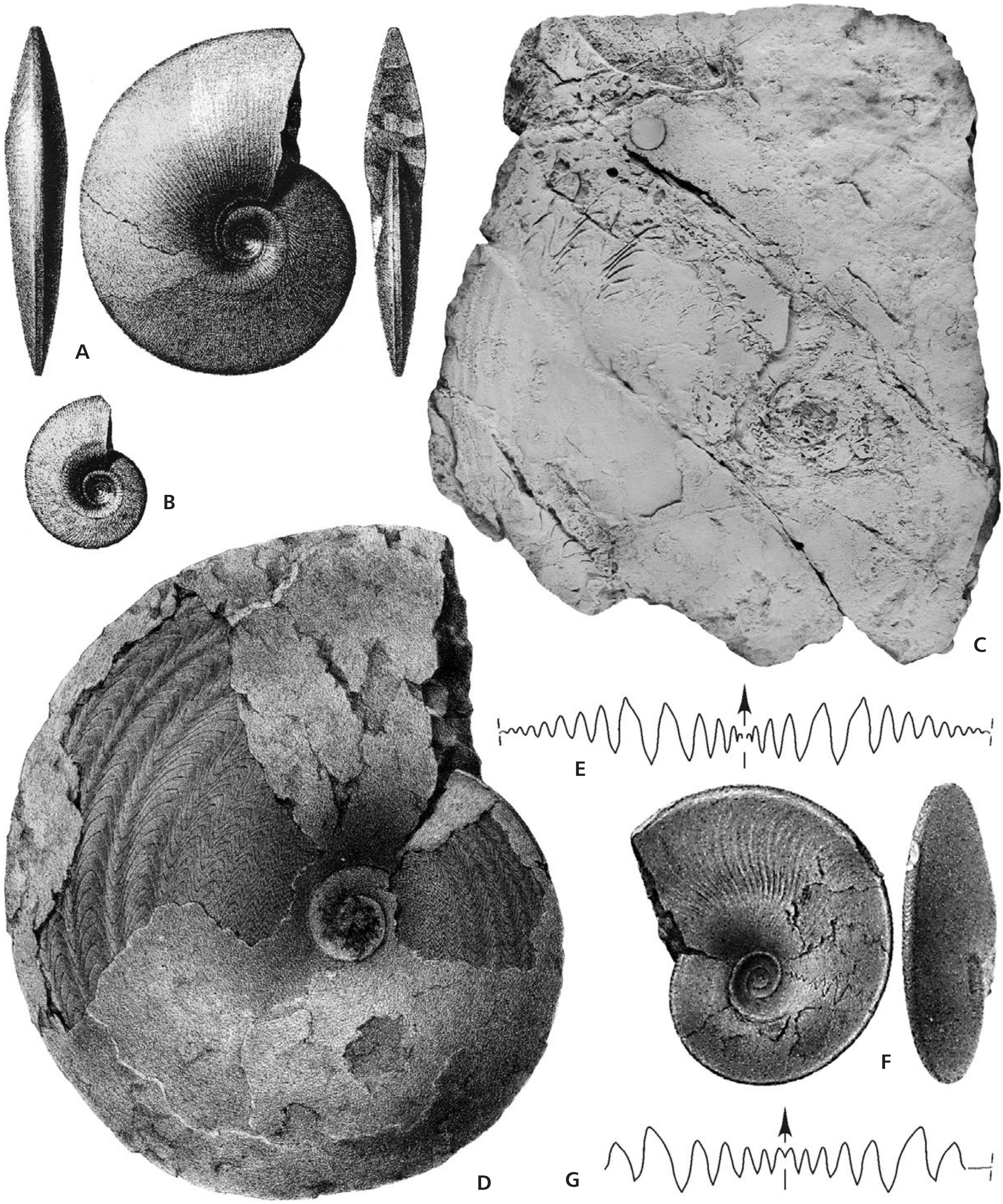


Figure 5. Reproductions of historical specimens of *Beloceras*. • A, B – *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842); '*Goniatites tenuistriatus*' figured by d'Archiac & de Verneuil (1842, pl. 26, fig. 7, 8). • C – *Beloceras sagittarium* (Sandberger & Sandberger, 1851), lectotype MB.C.4501 (Dannenberg Coll.) from Sessacker near Oberscheld; × 1.0. • D – *Beloceras sagittarium* (Sandberger & Sandberger, 1851); '*Goniatites sagittarius*' figured by Sandberger & Sandberger (1850–1856, pl. 4, fig. 3). • E, F – *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842); '*Goniatites sagittarius*' figured by Sandberger & Sandberger (1850–1856, pl. 4, fig. 3c, e). • G – '*Ammonites multilobatus*' figured by Beyrich (1837, pl. 1, fig. 9).

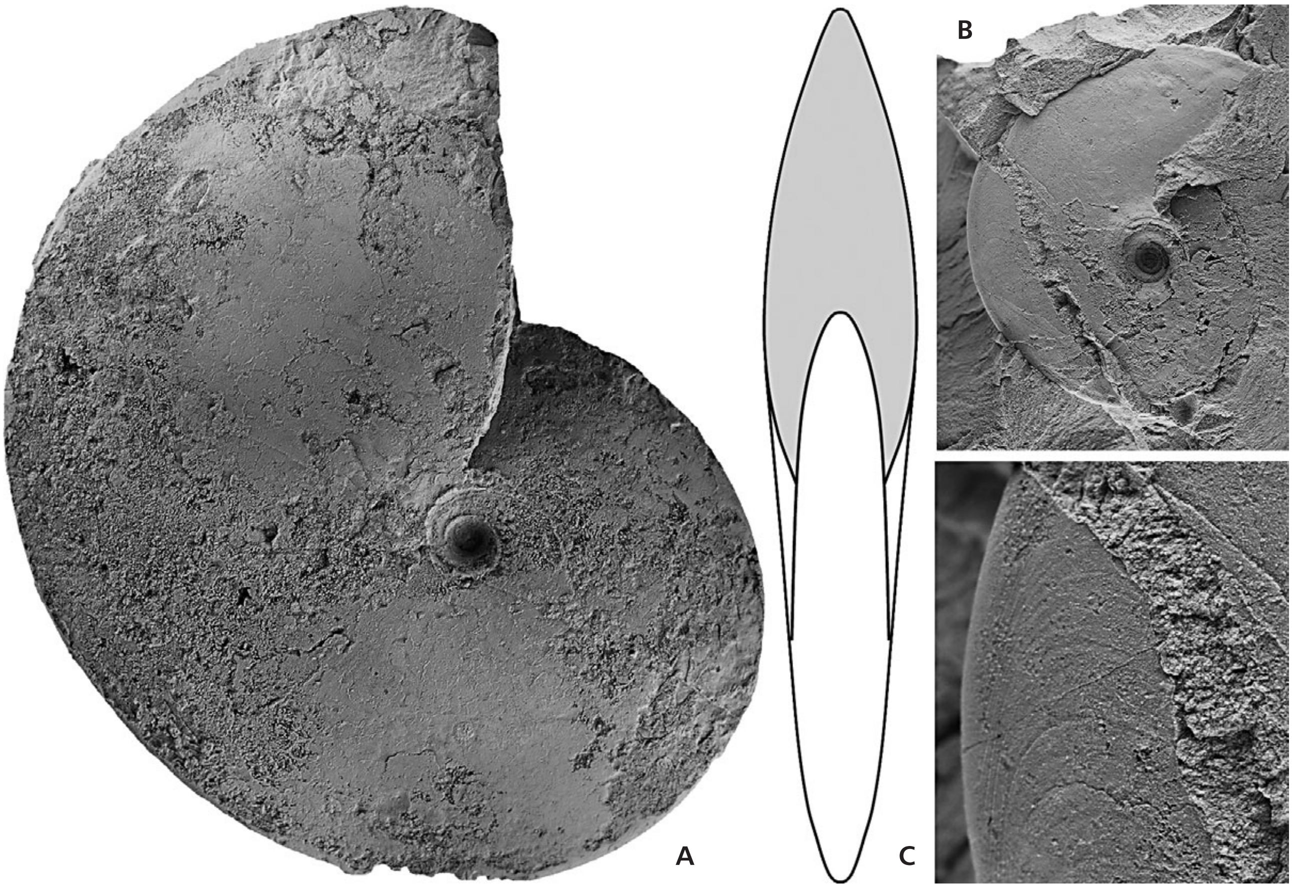


Figure 6. *Beloceras sagittarium* (Sandberger & Sandberger, 1851) from the Rhenish Mountains. • A – specimen MB.C.19180 (Denckmann 1902 Coll.) from Beul; × 1.0. • B – specimen MB.C.4502 (Hubach Coll.) from the Staatliche Grube, Oberscheld; × 1.0. • C – the same specimen, enlargement × 4.0.

Table 3. Conch dimensions (in mm) and proportions for reference specimens of *Beloceras sagittarium* (Sandberger & Sandberger, 1851) from the Rhenish Mountains.

	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.19180	116.6	20.1	64.3	11.6	41.3	0.17	0.31	0.10	2.40	0.36
MB.C.19182	102.2	21.8	58.4	10.5	–	0.21	0.37	0.10	–	–
MB.C.19176	98.3	20.0	54.6	10.5	–	0.20	0.37	0.11	–	–
MB.C.19171	84.1	13.6	47.7	9.1	31.3	0.16	0.29	0.11	2.54	0.34
MB.C.19173	66.4	11.1	38.3	6.2	24.8	0.17	0.29	0.09	2.54	0.35
MB.C.19174	35.0	8.8	19.5	3.5	–	0.25	0.45	0.10	–	–
MB.C.19175	72.3	11.5	41.2	6.1	27.7	0.16	0.28	0.08	2.63	0.33
	44.6	8.5	25.1	4.3	16.8	0.19	0.34	0.10	2.57	0.33
	27.8	5.8	15.2	3.5	10.2	0.21	0.38	0.13	2.50	0.33
	17.6	4.4	9.0	3.1	6.6	0.25	0.49	0.18	2.58	0.26
	10.9	2.79	5.47	2.55	4.19	0.26	0.51	0.23	2.63	0.23
	6.74	1.87	2.91	2.00	2.37	0.28	0.64	0.30	2.38	0.18
	4.36	1.42	1.82	1.50	1.61	0.33	0.78	0.34	2.52	0.12
	2.75	0.94	1.04	1.00	0.92	0.34	0.91	0.36	2.26	0.11
	1.83	0.82	0.71	0.67	0.64	0.45	1.15	0.37	2.35	0.11
	1.19	0.62	0.44	0.44	0.35	0.52	1.40	0.36	2.01	0.21

three saddles between the lateral lobe and the E_6 lobe are tectiform.

The cross section of specimen MB.C.19199 (Fig. 8A) with a conch diameter of 129 mm shows the transformation into the adult stage, in which the whorl cross section becomes wider (ww/dm = 0.20; Table 4) and the umbilical wall steeper in comparison with the inner whorls. The whorl cross section has here a flattened triangular shape with strongly converging flanks and a very narrow, subacute venter.

The largest of the Thuringian specimens is MB.C.19183 (Schultz 1967 Coll.); it is a fully septate individual with a 135 mm conch diameter and showing the adult suture line. Unfortunately, the specimen has suffered during previous preparation attempts (it was too deeply polished), so that the conch shape has altered. The suture line (Fig. 8E), however, could be drawn at the maximum diameter and possesses seven lanceolate secondary prongs of the external lobe and an 8th, incipient one. Ten umbilical lobes are present on the inner flank.

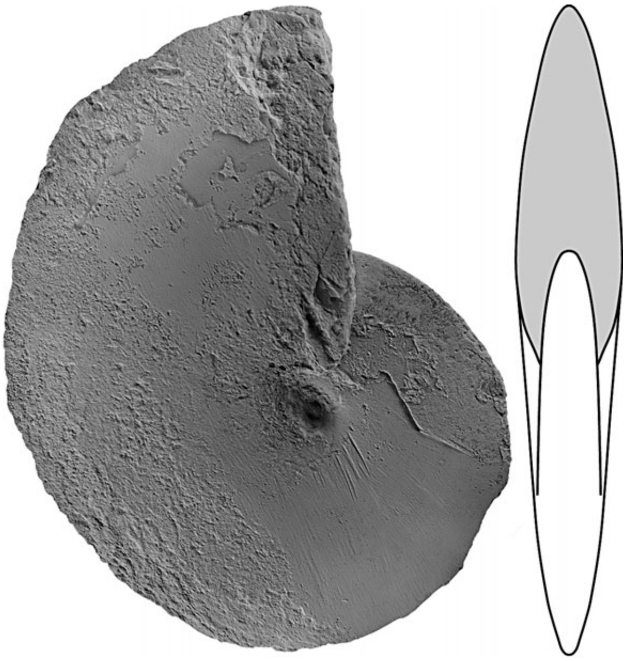


Figure 7. *Beloceras sagittarium* (Sandberger & Sandberger, 1851) from the Thuringian Mountains, specimen MB.C.19194 (Bartzsch & Weyer 1985 Coll.) from the Vogelsberg near Göschitz; × 0.8.

Description of material from Büdesheim. – The ontogenetic development of the material shows several trends. The initial stage (1 mm in dm) is thickly discoidal (ww/dm = 0.54), but the conch becomes rapidly more slender, being extremely discoidal already at 2 mm in dm (ww/dm = 0.30). All larger stages up to 18 mm in dm range between 0.23 and 0.28. The umbilicus is rather wide between 2 and 5 mm in dm (uw/dm = 0.40) but thereafter rapidly becomes narrower (uw/dm = 0.17 at 18 mm in dm). The whorl expansion rate is, with WER = 2.10–2.20, rather stable up to 7 mm in dm and then increases to a value of 2.50 at 18 mm in dm.

One small specimen (MB.C.22003.3; 7 mm in dm) was sectioned (Fig. 10A). It has three and a half whorls, which show a rapid ontogenetic transformation in their cross section. While the first whorl (up to 1 mm in dm) is kidney-shaped in the section, the second whorl is (up to 2.2 mm in dm) circular or slightly oval and compressed. The flanks become flattened in the third whorl, and at the largest visible diameter, the venter is slightly applanate. Specimen MB.C.22003.1 is the largest one within the

Table 4. Conch dimensions (in mm) and proportions for reference specimens of *Beloceras sagittarium* (Sandberger & Sandberger, 1851) from the Thuringian Mountains.

	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.19199	129.0	25.8	70.8	14.7	47.8	0.20	0.36	0.11	2.52	0.33
MB.C.19196	106.2	15.8	61.8	9.8	39.2	0.15	0.26	0.09	2.51	0.37
MB.C.19194	105.7	15.7	55.3	10.1	41.3	0.15	0.28	0.10	2.63	0.33
MB.C.19186	78.2	10.9	44.4	7.8	–	0.14	0.25	0.10	–	–
MB.C.19184	59.3	9.6	30.0	5.5	–	0.16	0.32	0.09	–	–
MB.C.19185	35.9	7.6	17.8	3.9	–	0.21	0.43	0.11	–	–
MB.C.19192	90.8	16.5	51.2	8.7	33.2	0.18	0.32	0.10	2.48	0.35
	57.7	10.5	31.0	7.5	19.8	0.18	0.34	0.13	2.32	0.36
	37.9	7.0	19.2	5.8	12.9	0.18	0.36	0.15	2.31	0.32
	25.0	5.0	13.0	4.0	9.1	0.20	0.38	0.16	2.46	0.30
	15.9	3.5	8.0	3.5	6.0	0.22	0.43	0.22	2.59	0.24
	9.88	2.32	4.44	2.93	3.61	0.23	0.52	0.30	2.48	0.19
	6.27	1.71	2.50	2.28	2.05	0.27	0.68	0.36	2.21	0.18
	4.21	1.09	1.48	–	1.27	0.26	0.74	–	2.05	0.14

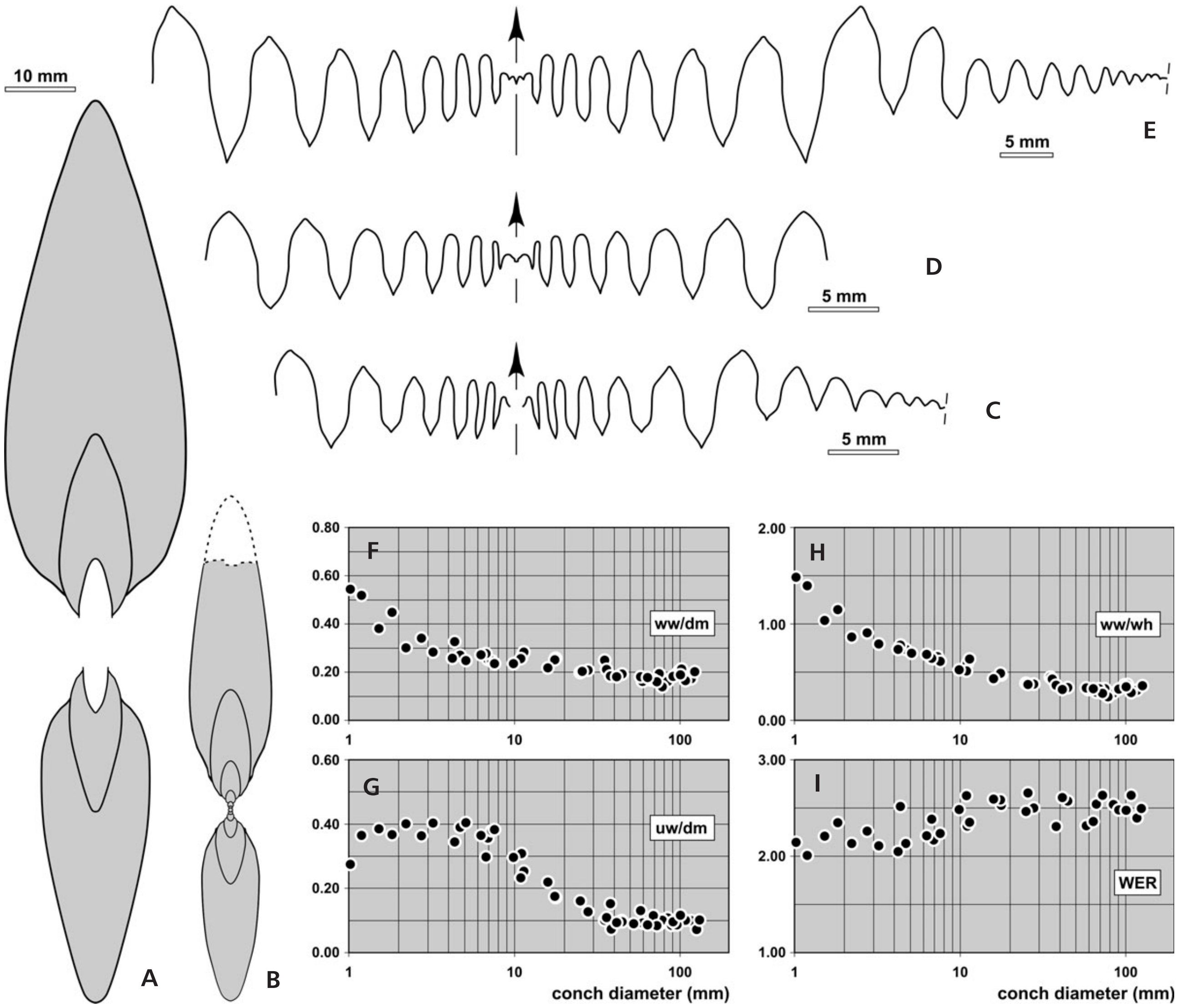


Figure 8. *Beloceras sagittarium* (Sandberger & Sandberger, 1851) from the Rhenish Mountains and Thuringian Mountains. • A – cross section of specimen MB.C.19199 (Bartzsch & Weyer 1985 Coll.) from the Vogelsberg near Göschitz; × 1.0. • B – cross section of specimen MB.C.19175 from Bredelar; × 1.0. • C – suture line of specimen MB.C.19194 (Bartzsch & Weyer 1985 Coll.) from the Vogelsberg near Göschitz, at 11.6 mm ww, 34.0 mm wh; × 2.0. • D – suture line of specimen MB.C.4504 (Denckmann Coll.) from Charlottenzug near Bredelar, at 10.1 mm ww, 36.2 mm wh; × 2.0. • E – suture line of specimen MB.C.19183 (Schultz 1967 Coll.) from the Braunsberg near Tegau, at 128.5 mm dm, 26.5 mm ww, 67.5 mm wh; × 1.5. • F–I – 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 all available specimens.

material; it is a well-preserved fragment of a specimen that had a phragmocone diameter of at least 25 mm.

The ontogeny of the suture line (Fig. 10B–H) is characterised by a rather simple stage at 1.3 mm whorl height (specimen MB.C.22004.4; appr. 2 mm in dm), where the external lobe is still trifid with a median saddle reaching almost half of the E lobe depth. On the flank follows a wide triangular lateral saddle with a narrowly rounded top, a V-shaped lateral lobe, and a smaller umbilical lobe on the umbilical seam (Fig. 10B). A further subdivided E lobe can be seen at 2.5 mm whorl height (specimen MB.C.22003.2; Fig. 10C); the U lobe has already migrated towards the flank.

During later ontogeny, the number of flank lobes increases from four at 7.5 mm conch diameter (specimen MB.C.22004.4; Fig. 10D) to ten at 11.3 mm whorl height (specimen MB.C.22003.1; Fig. 10H), which correlates with a conch diameter of 20 mm. In this stage, which represents the largest specimen in our collection, the ventral lobe and all the secondary external lobes are deep and lanceolate with almost parallel flanks. Particularly the lobes E_2, E_3, and E_4 are very narrow, being more than twice as deep as wide. The two saddles between the L lobe and the E_2 lobe are tectiform at their top.

The largest specimen MB.C.22002 (Ebbighausen Coll.;

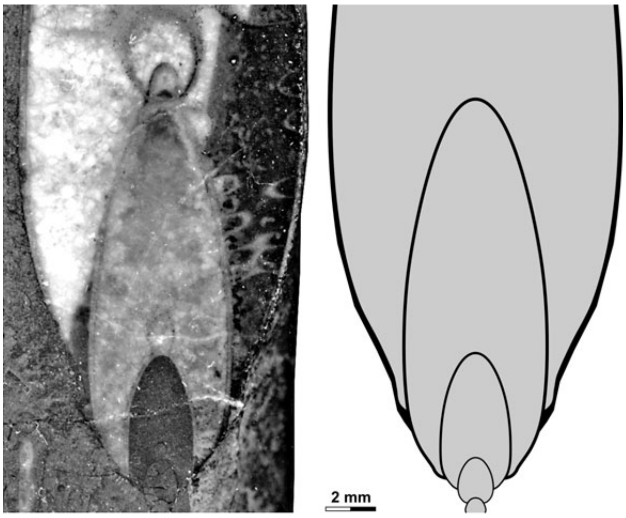


Figure 9. The umbilical region in *Beloceras sagittarium* (Sandberger & Sandberger, 1851), shown in the sectioned specimen MB.C.19175, polished surface and digitized cross section; × 4.0.

Fig. 10I) is preserved as a dolomitic steinkern fragment. It belongs to a specimen in which the phragmocone had a diameter of at least 100 mm. In this stage, seven secondary prongs of the external lobe can be counted, the first six of them being lanceolate and the 7th very small and V-shaped. Four saddles between the lateral lobe and the E_8 lobe are tectiform at their top.

Remarks. – Material belonging to this species has often been described under the species names *multilobatum* or *sagittarium*. Schindewolf (1940, p. 492) noticed the preoccupation of the species name '*Ammonites multilobatus* Beyrich, 1837' by '*Ammonites multilobatus* Bronn, 1832'; he suggested that '*Goniatites sagittarius* Sandberger & Sandberger, 1851' is a junior synonym of '*Goniatites tenuistriatus* d'Archiac & de Verneuil, 1842'. Schindewolf did not cast any doubt that the specimens figured by d'Archiac & de Verneuil (1842, pl. 26, fig. 7, 8) represent the same species as '*Goniatites sagittarius* Sandberger & Sandberger, 1851'. Several subsequent authors accepted this concept (*e.g.* Korn & Klug 2002), but in this article, we separate the two species on the basis of differences in conch shape and suture line.

Comparisons. – *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842) is a similar species but possesses a wider umbilicus. While the uw/dm ratio in *B. sagittarium* has a stable value at 0.10 in growth stages larger than 30 mm in diameter, it is about 0.15 or higher in *B. tenuistriatum*.

B. sagittarium in Bogoslovsky (1969) = '*Mesobeloceras bogoslovskyi* Yatskov, 1990' usually has a wider umbilicus (uw/dm = 0.16), but there also exist narrowly umbilicate specimens. This has to be solved on the basis of the original material. At 28.7 mm whorl height (corresponding to a conch diameter of about 55 mm), five of the saddles on the flank have a tectiform top unlike *B. sagittarium*, in which only two or three of these saddles are tectiform.

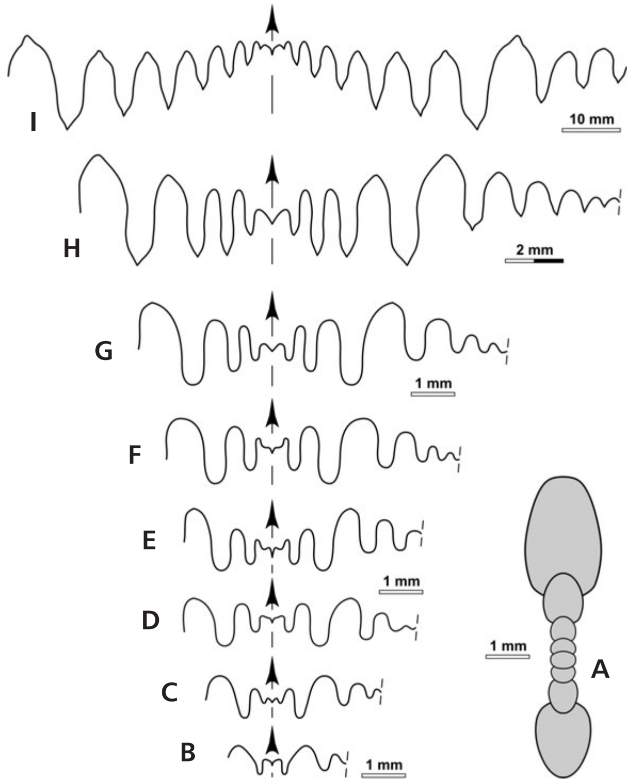


Figure 10. *Beloceras sagittarium* (Sandberger & Sandberger, 1851) from Büdesheim. • A – cross section of specimen MB.C.22003.3; × 5.7. • B – suture line of specimen MB.C.22004.4, at 0.9 mm ww, 1.3 mm wh; × 5.7. • C – suture line of specimen MB.C.22003.2, at 1.7 mm ww, 2.5 mm wh; × 5.7. • D – suture line of specimen MB.C.22004.4, at 7.6 mm dm, 1.6 mm ww, 2.7 mm wh; × 5.7. • E – suture line of specimen MB.C.22004.1, at 8.0 mm dm, 1.7 mm ww, 3.2 mm wh; × 5.7. • F – suture line of specimen MB.C.22003.2, at 9.4 mm dm, 2.4 mm ww, 4.4 mm wh; × 5.7. • G – suture line of specimen MB.C.22003.4, at 10.5 mm dm, 2.5 mm ww, 4.5 mm wh; × 5.7. • H – suture line of specimen MB.C.22003.1, at 4.6 mm ww, 11.3 mm wh; × 3.8. • I – suture line of specimen MB.C.22002 (Ebbighausen Coll.), at 25 mm ww, *ca* 70 mm wh; × 0.75.

B. stenumbilicatum Bogoslovsky, 1958 has a very similar conch shape, but differs in the shallower, less lanceolate secondary prongs of the external lobe.

B. sagittarium in Glenister (1958) = '*Mesobeloceras glenisteri* Yatskov, 1990' has a wider umbilicus (uw/dm = 0.19 at 125 mm dm, uw/dm = 0.15 at 85 mm dm, uw/dm = 0.15 at 35 mm dm) than *B. sagittarium*. The largest specimen figured by Glenister (1958, pl. 13, fig. 4) shows that the umbilicus is being widened rapidly in the adult stage, visible in the callus preserved on the penultimate volution.

B. sagittarium in Schulz (1967) = '*Ceratobeloceras schulzi* House & Kirchgasser, 1985' has a very similar conch shape with a very narrow umbilicus (uw/dm = less than 0.10 at 70 mm conch diameter). The peculiar anomaly of the suture line, *i.e.* the secondary serration of the L lobe and U_2 lobe led House & Kirchgasser (1985) to introduce the new genus *Ceratobeloceras*. However, as Schulz (1967) already demonstrated, the serration of the lobes is usually asymmetric on both sides of the conch and many specimens of his collection do not display any secondary serration. It is therefore questionable if a valid character is represented here, and if the material in fact belongs to a separate species or genus. Other reasons for the serration have to be discussed, *e.g.* pathology. One has to keep in mind that the L lobe and the U_2 lobe are lanceolate, possessing three tie points according to Seilacher (1975). The trifid serration of the lobes is possibly caused by the inactivity of the middle of these three tie points. Yatskov (1990) treated *Ceratobeloceras* as a subgenus of *Beloceras* and accepted the separation of the species. He introduced the new species name '*Beloceras* (*Beloceras*) *gallicum* Yatskov, 1990' for the specimens with non-serrated suture lines and '*Beloceras* (*Ceratobeloceras*) *schulzi* House & Kirchgasser, 1985' for those with serration.

Beloceras tenuistriatum (d'Archiac & de Verneuil, 1842)

Figures 5A, B, E, F, 11, 12

* 1842 *Goniatites tenuistriatus* d'Archiac & de Verneuil, p. 343, pl. 26, fig. 7, 8.
1851 *Goniatites sagittarius* Sandberger & Sandberger, pl. 4, fig. 3c–e.
1940 *Beloceras tenuistriatum*. – Schindewolf, p. 492, pl. 1, fig. 17.
non 1959 *Beloceras tenuistriatum* var. ?. – Petter, p. 184, pl. 10, fig. 1, text-fig. 44A. [= *Beloceras petterae* Yatskov, 1990]
non 1999 *Beloceras tenuistriatum*. – Belka *et al.*, p. 10 [= *Beloceras petterae* Yatskov, 1990]
non 2002 *Beloceras tenuistriatum*. – Korn & Klug, text-fig. 112. [= *Beloceras glenisteri* (Yatskov, 1990)]
non 2002 *Beloceras tenuistriatum*. – Korn & Klug, text-fig. 114, 115B, E. [= *Beloceras bogoslovskyi* (Yatskov, 1990)]

Type material. – The type material of the species from Oberscheld has probably never been studied after the original description. It is presently not known where it is stored.

Material. – Specimens from the eastern margin of the Rhenish Mountains are available for study: 21 specimens (15–71 mm in conch diameter) come from the Martenberg near Adorf, one specimen 75 mm in dm is labelled 'Bredelar' and is probably from the Charlottenzug Mine, and eleven specimens with conches measuring up to 100 mm in diameter come from the vicinity of Oberscheld.

Diagnosis. – Species of *Beloceras* with subinvolute conch (uw/dm = 0.15 in stages larger than 50 mm dm). Suture line with six or seven secondary prongs of the external lobe, a V-shaped lateral lobe, and six umbilical lobes on the flanks at 50 mm conch diameter; 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}. All prongs of the external lobe are lanceolate, the E_5 and E_6 lobes are very narrow and deep; three or four of the larger saddles (between the L lobe and the E_4 lobe) are weakly tectiform. The adult suture is with an increasing number of very shallow U lobes.

Description. – The well-preserved specimen MB.C.4506 (71 mm in dm; Müller Coll.; Fig. 11B) from the Martenberg near Adorf is extremely discoidal with a narrow umbilicus (ww/dm = 0.16; uw/dm = 0.15) and an extremely high aperture (WER = 2.61). It shows a narrowly rounded venter and the very shallow umbilical margin, which separates the flat flank from the strongly oblique umbilical wall. The shell surface is almost smooth.

Specimen MB.C.22006 (Reinke 1882 Coll.; Fig. 11A) with a conch diameter of 75 mm from 'Bredelar' (probably from the Charlottenzug Mine according to the lithology) is, in its conch proportions, similar to the preceding specimen (ww/dm = 0.18; uw/dm = 0.16; WER = 2.46). The umbilical area is well-preserved; it shows a pronounced umbilical seam, a faint rim on the inner umbilical wall, followed by a shallow spiral groove, and a very shallow umbilical wall with a broadly rounded umbilical margin. There are well-preserved shell remains on the specimen, which show delicate growth lines with a shallow dorsal sinus and a low ventrolateral projection. The growth lines are much coarser on the outer flank and form a very deep and narrow ventral sinus.

Specimen MB.C.22007 (Denckmann 1893 Coll.; Fig. 11C) from the Martenberg is a well-preserved specimen measuring 50 mm in diameter. It is also extremely discoidal and subinvolute (ww/dm = 0.20; uw/dm = 0.15) with a comparatively low aperture (WER = 2.15). An umbilical rim and an accompanying spiral groove are developing on the last volution, where the umbilical wall becomes much shallower than in the inner whorls. The steinkern of the body chamber shows the Ritzstreifung, which is composed of delicate radial lines, which extend in a protracted direction across the flank.

Comparisons. – *B. sagittarium* is similar but possesses a narrower umbilicus in growth stages larger than 50 mm (uw/dm = 0.15 in *B. tenuistriatum* and 0.10 in *B. sagittarium*). While in *B. sagittarium* the umbilicus is continuously closing, it begins to open in *B. tenuistriatum* at a

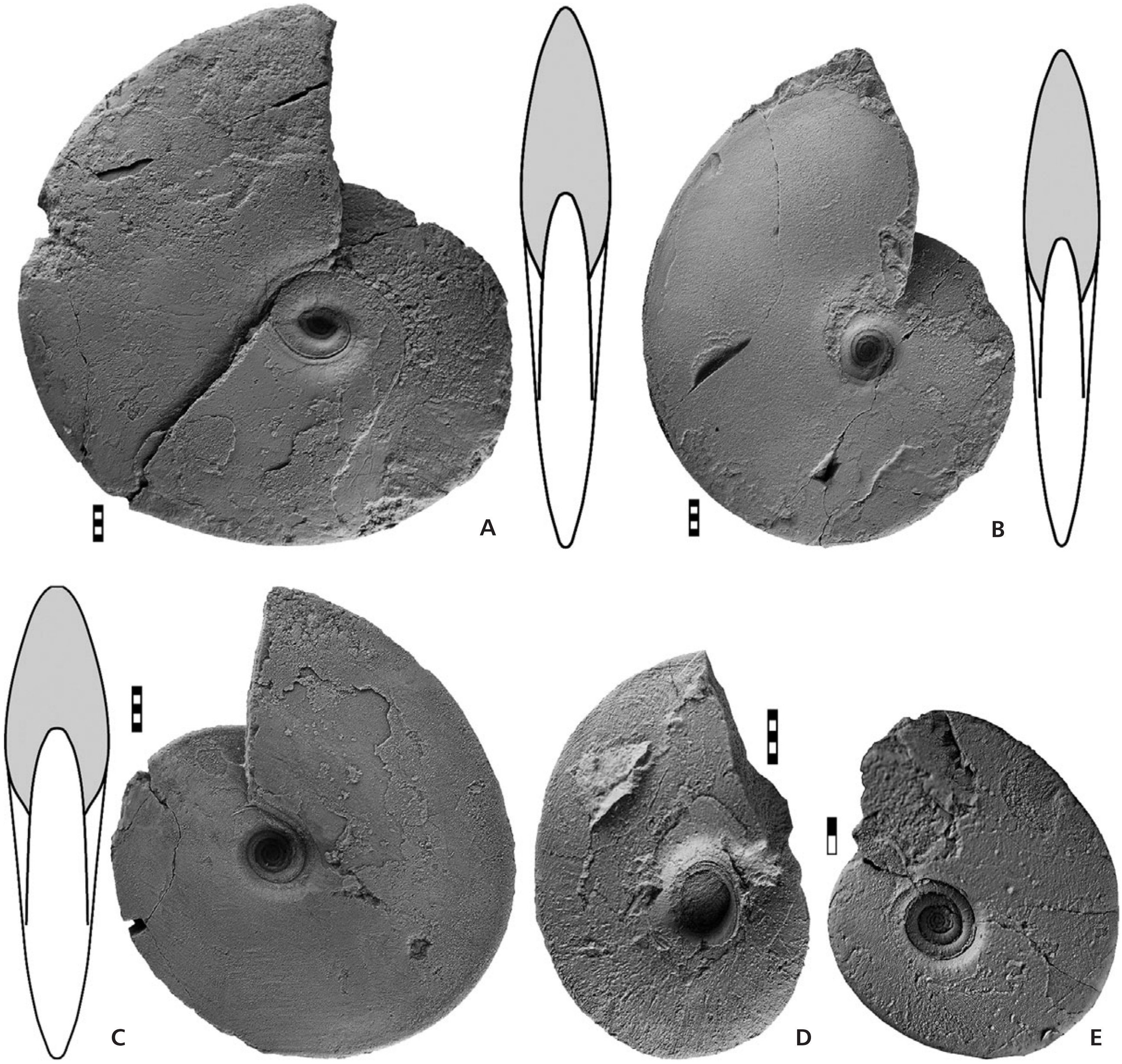


Figure 11. *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842) from the Rhenish Mountains. • A – specimen MB.C.22006 (Reinke 1882 Coll.) from Bredelar; × 1.0. • B – specimen MB.C.4506 (Müller Coll.) from the Martenberg near Adorf; × 1.0. • C – specimen MB.C.22007 (Denckmann 1893 Coll.) from the Martenberg near Bredelar; × 1.25. • D – specimen MB.C.22011 (Denckmann 1902 Coll.) from the Martenberg near Bredelar; × 1.5. • E – specimen MB.C.4057.4 (Müller Coll.) from the Martenberg near Bredelar; × 2.5.

conch diameter of about 50 mm. This is already visible in the figure of d'Archiac & de Verneuil (1842, pl. 26, fig. 7), which is refigured here (Fig. 5A). The umbilical rim is more pronounced in *B. tenuistriatum*.

B. webbelense has similar conch dimensions and ratios. The two species differ in the suture line, which is more complex in *B. tenuistriatum* (six secondary external lobes; Fig. 12B, C) than in *B. webbelense* (four secondary external lobes). Additionally, *B. webbelense* possesses a more conspicuous umbilical rim.

B. glenisteri, from the Canning Basin of Australia, is very similar. The suture figure in Glenister (1958, text-fig. 15d) is from a specimen measuring 50 mm in diameter, thus similar in size to specimen MB.C.22013.1. Both show six secondary prongs of the external lobe, and the difference between them is only in the shape of the lobes and saddle, with more lanceolate lobes and tectiform saddles in *B. glenisteri*. An additional difference between the two species lies in the conch ontogeny as *B. glenisteri* is more widely umbilicate in the adult stage.

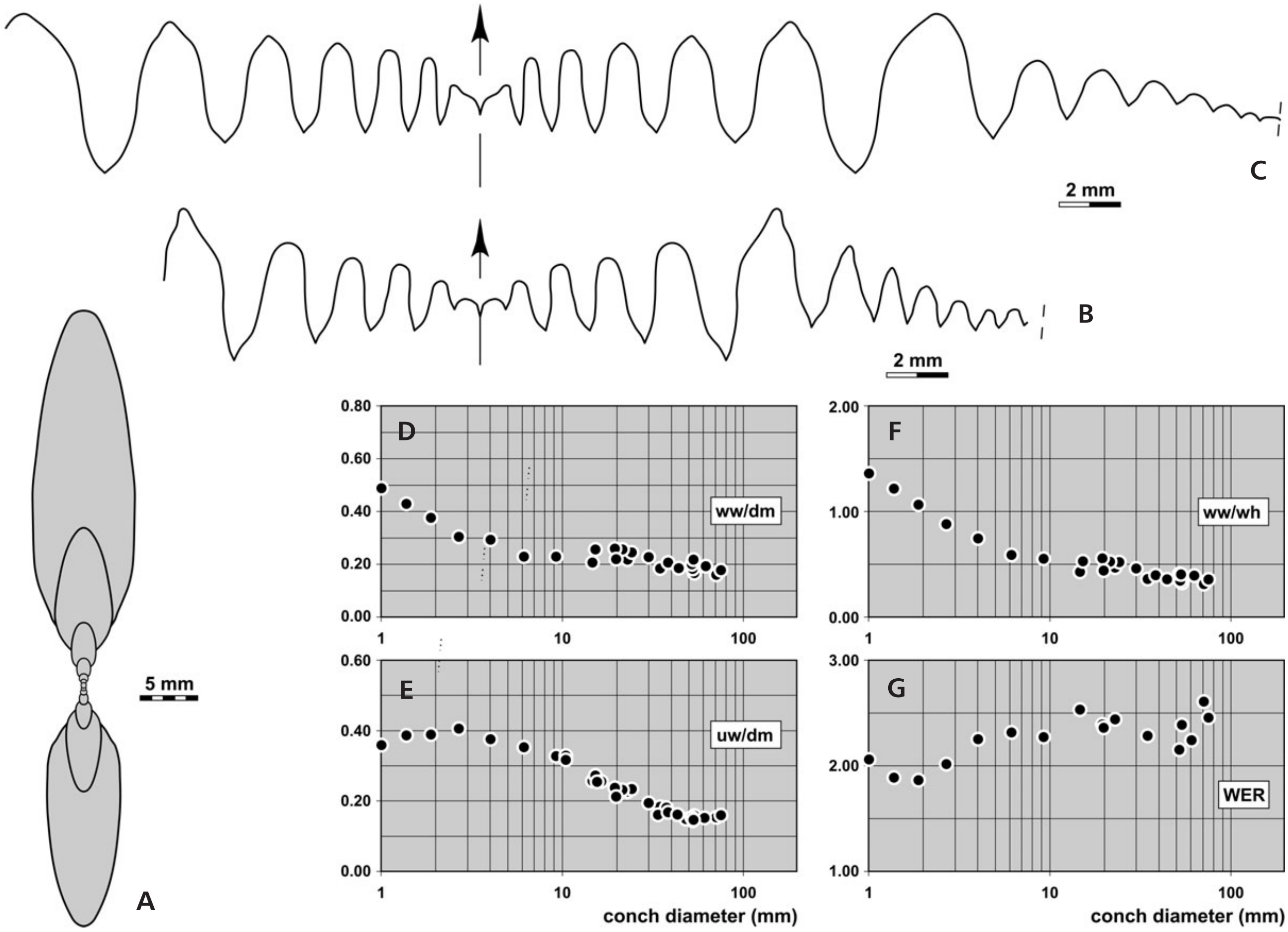


Figure 12. *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842) from the Rhenish Mountains. • A – cross section of specimen MB.C.22010 (Paeckelmann 1928 Coll.) from the Martenberg near Adorf; × 1.5. • B – suture line of specimen MB.C.22007 (Denckmann 1893 Coll.) from the Martenberg near Adorf, at 37.0 mm dm, 9.0 mm ww, 19.0 mm wh; × 4.0. • C – suture line of specimen MB.C.22013.1 from the Martenberg near Adorf, at 27.0 mm wh; × 4.0. • D–G – 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 all available specimens.

Beloceras webbelense **sp. nov.**
Figures 13, 14

1882 *Goniatites multilobatus*. – Holzapfel, p. 237, pl. 45, figs 2–6.
1913 *Beloceras multilobatum*. – Wedekind, p. 48, text-fig. 5a2.
1918 *Beloceras multilobatum*. – Wedekind, p. 129, text-fig. 38a2, pl. 21, fig. 13.

Derivation of name. – After the Webbel Mine near Adorf.

Holotype. – Specimen MB.C.22025 (Paeckelmann 1920 Coll.); illustrated here in Fig. 13A.

Type locality and horizon. – Martenberg near Adorf; 'Webeler Kalk' (red Frasnian cephalopod limestones).

Material. – Sixteen specimens from the vicinity of Adorf are available for study.

Diagnosis. – Species of *Beloceras* with subinvolute conch (uw/dm = 0.17 in stages larger than 50 mm in dm). Two distinct spiral rims on the umbilical wall. Suture line with four secondary prongs of the external lobe, a V-shaped lateral lobe, and four umbilical lobes on the flanks at 45 mm conch diameter; formula of the ventral suture line in this growth stage (E_2 E_3 E_4 E_5 E_1 E_5 E_4 E_3 E_2) L U_2 U_4 U_6 U_8). Prongs of the external lobe are narrowly V-shaped to lanceolate; the saddle between the L lobe and the E_2 lobe is weakly tectiform.

Description. – Holotype MB.C.22025 (Paeckelmann 1920 Coll.) is an incomplete but well-preserved specimen, measuring 89 mm in diameter, from the 'Webeler Kalk' of the Martenberg near Adorf (Fig. 13A). It is preserved with

Table 5. Conch ontogeny (Fig. 11, 12) of *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842).

dm	conch shape	whorl cross section shape	aperture
1.5 mm	thinly discoidal; subevolute (ww/dm ~ 0.45; uw/dm ~ 0.40)	weakly depressed; moderately embracing (ww/wh ~ 1.25; IZR ~ 0.22)	moderate (WER ~ 1.95)
4 mm	extremely discoidal; subevolute (ww/dm ~ 0.28; uw/dm ~ 0.38)	weakly compressed; moderately embracing (ww/wh ~ 0.75; IZR ~ 0.15)	high (WER ~ 2.25)
8 mm	extremely discoidal; subevolute (ww/dm ~ 0.23; uw/dm ~ 0.35)	weakly compressed; moderately embracing (ww/wh ~ 0.55; IZR ~ 0.18)	very high (WER ~ 2.30)
18 mm	extremely discoidal; subinvolute (ww/dm ~ 0.25; uw/dm ~ 0.22)	strongly compressed; strongly embracing (ww/wh ~ 0.45; IZR ~ 0.30)	very high (WER ~ 2.40)
50 mm	extremely discoidal; subinvolute (ww/dm ~ 0.20; uw/dm ~ 0.15)	strongly compressed; strongly embracing (ww/wh ~ 0.40; IZR ~ 0.32)	very high (WER ~ 2.30)
75 mm	extremely discoidal; subinvolute (ww/dm ~ 0.18; uw/dm ~ 0.16)	strongly compressed; moderately embracing (ww/wh ~ 0.35; IZR ~ 0.27)	very to extremely high (WER ~ 2.4–2.65)

Table 6. Conch dimensions (in mm) and proportions for reference specimens of *Beloceras tenuistriatum* (d'Archiac & de Verneuil, 1842).

	dm	ww	Wh	Uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.22006	75.1	13.3	37.5	12.0	27.2	0.18	0.35	0.16	2.46	0.27
MB.C.4506	70.8	11.3	36.3	10.9	27.0	0.16	0.31	0.15	2.61	0.26
MB.C.22007	51.8	10.3	25.4	7.9	16.5	0.20	0.41	0.15	2.15	0.35
MB.C.22011	37.6	9.7	19.0	6.8	–	0.26	0.51	0.18	–	–
MB.C.4507.4	19.5	5.1	9.1	4.6	6.9	0.26	0.56	0.24	2.39	0.24
MB.C.22010	53.6	8.9	27.5	8.5	18.9	0.17	0.32	0.16	2.39	0.31
	34.7	6.4	17.7	6.4	11.7	0.18	0.36	0.18	2.28	0.34
	23.0	5.0	10.7	5.2	8.3	0.22	0.47	0.23	2.44	0.23
	14.7	3.0	7.1	3.8	5.5	0.21	0.43	0.26	2.53	0.23
	9.24	2.12	3.84	3.02	3.11	0.23	0.55	0.33	2.27	0.19
	6.13	1.40	2.38	2.17	2.10	0.23	0.59	0.35	2.32	0.12
	4.03	1.18	1.59	1.51	1.34	0.29	0.75	0.38	2.25	0.15
	2.68	0.82	0.93	1.09	0.79	0.30	0.88	0.41	2.02	0.15
	1.89	0.71	0.67	0.73	0.51	0.38	1.06	0.39	1.87	0.24
	1.38	0.59	0.49	0.53	0.38	0.43	1.22	0.39	1.89	0.23
	1.01	0.49	0.36	0.36	0.31	0.49	1.36	0.36	2.06	0.16

parts of the body chamber, and the phragmocone is filled with sparry calcite; suture lines are therefore not preserved. The conch is extremely discoidal (ww/dm = 0.16) and subinvolute (uw/dm = 0.17) with a very high aperture (WER = 2.43). The conch is thickest at some distance from the umbilicus, and the umbilical wall is very shallow with the last whorl connecting smoothly with the preceding volution. A rim marks the umbilical seam, and the umbilical wall possesses a shallow groove. The flanks converge slowly towards the narrowly rounded venter. The shell surface is almost smooth but possesses extremely fine growth lines, which form a low ventrolateral projection. On the outer flank, the growth lines are more pronounced and turn back to form a very narrow and very deep ventral sinus. They are strengthened on the venter and look like chevron-shaped delicate riblets.

The smaller paratype MB.C.22029 (Paeckelmann 1920 Coll.; Fig. 13B) from the Webbel Mine near Adorf has similar conch proportions at a diameter of 72 mm (ww/dm = 0.17; uw/dm = 0.17; WER = 2.32). It also shows a rim near the umbilical seam and a shallow groove on the umbilical wall. The shell surface is not as well preserved as in the holotype, but also displays the strengthening of the growth lines on the outer flank and the venter. The wrinkle layer is well preserved in the dorsal whorl where parts of the body chamber are removed.

The juvenile paratype MB.C.22030 (Denckmann Coll.; Fig. 13B) has a conch diameter of 27 mm and is extremely discoidal and subinvolute (ww/dm = 0.19; uw/dm = 0.20) with a high aperture (WER = 2.16). The conch is widest near the umbilicus, and the umbilical wall does not possess a rim and groove as with the larger specimens. The shell surface is smooth on the inner and middle flank, but the

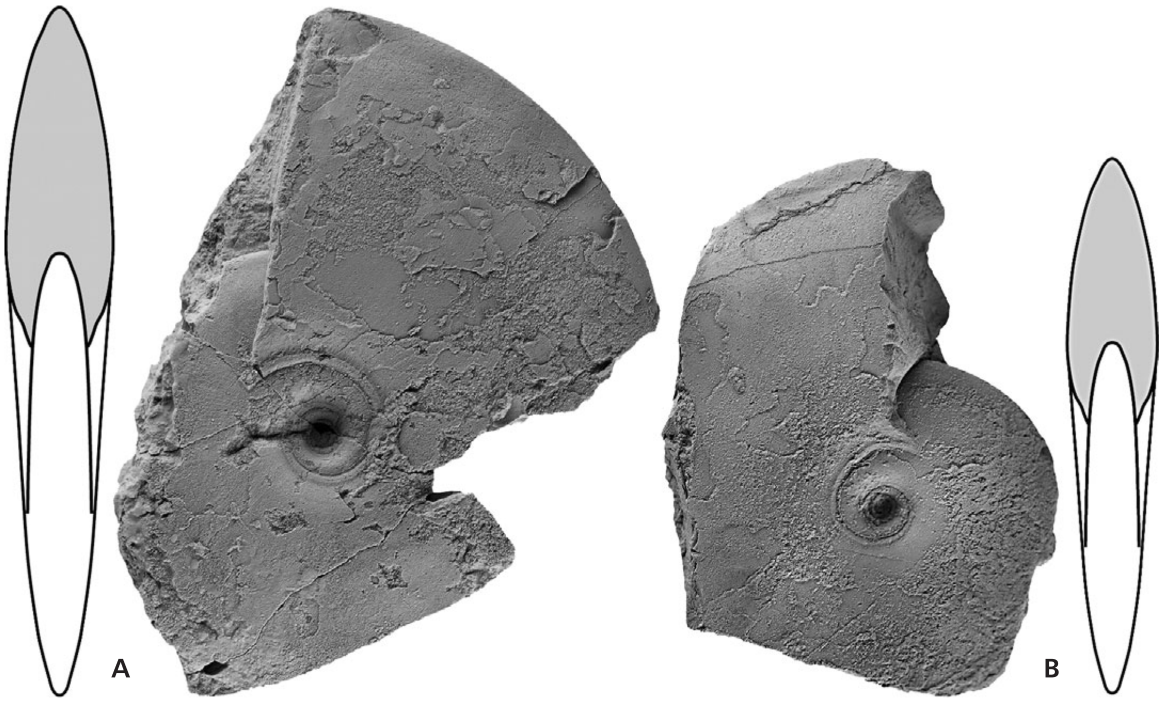


Figure 13. *Beloceras webbelense* sp. nov. from the Rhenish Mountains; all × 1.0. A – holotype MB.C.22025 (Paeckelmann 1920 Coll.) from the Martenberg near Adorf. • B – paratype MB.C.22029 (Paeckelmann 1920 Coll.) from the Webbel Mine near Adorf.

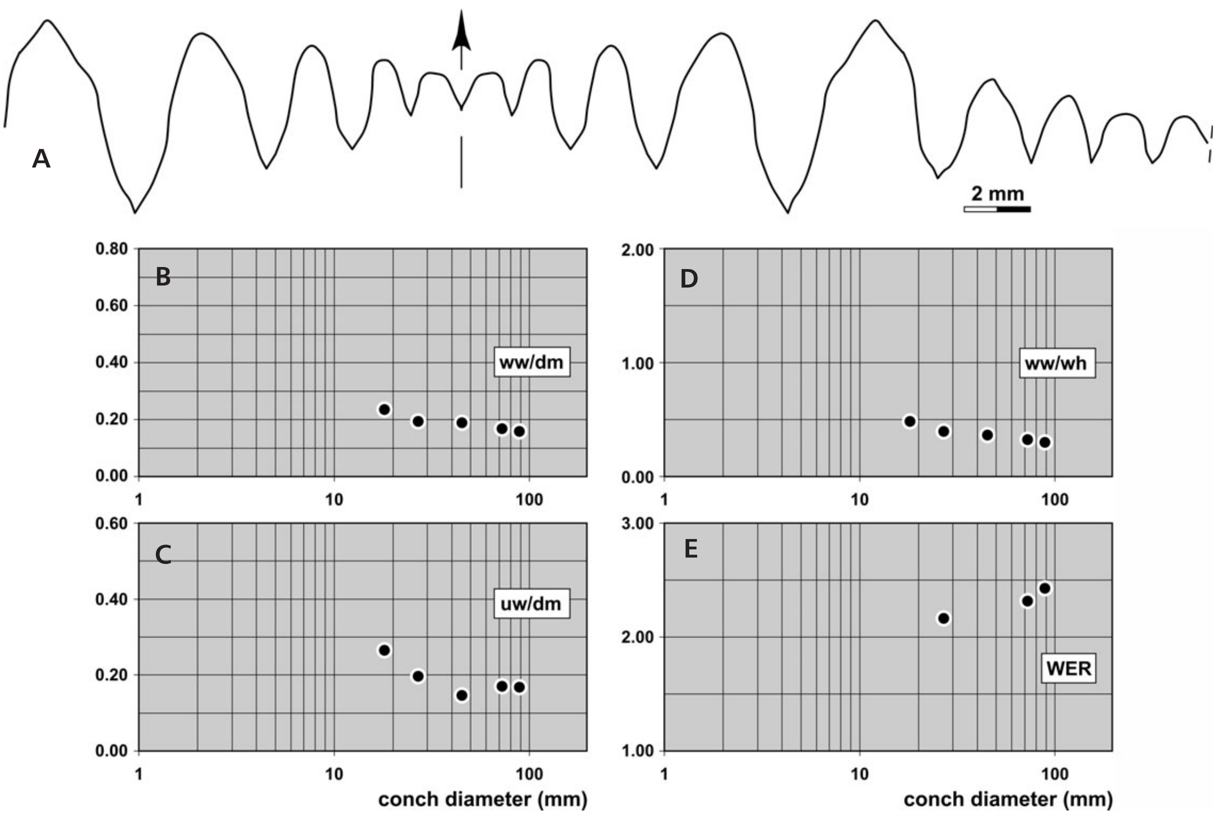


Figure 14. *Beloceras webbelense* sp. nov. from the Rhenish Mountains. • A – suture line of paratype MB.C.22026 (Paeckelmann 1920 Coll.) from the Martenberg near Adorf, at 8.4 mm ww, 23.6 mm wh; × 4.0. • B–E – ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh), and whorl expansion rate (WER) of all available specimens.

Table 7. Conch ontogeny (Fig. 13, 14) of *Beloceras webbelense* sp. nov.

dm	conch shape	whorl cross section shape	aperture
27 mm	extremely discoidal; subinvolute (ww/dm ~ 0.19; uw/dm ~ 0.20)	strongly compressed; strongly embracing (ww/wh ~ 0.40; IZR ~ 0.35)	high (WER ~ 2.15)
90 mm	extremely discoidal; subinvolute (ww/dm ~ 0.16; uw/dm ~ 0.16)	strongly compressed; strongly embracing (ww/wh ~ 0.30; IZR ~ 0.32)	very high (WER ~ 2.45)

Table 8. Conch dimensions (in mm) and proportions for reference specimens of *Beloceras webbelense* sp. nov.

	dm	ww	wh	uw	ah	ww/dm	Ww/wh	uw/dm	WER	IZR
MB.C.22025	88.8	14.0	46.8	14.9	31.8	0.16	0.30	0.17	2.43	0.32
MB.C.22029	72.3	12.2	37.8	12.3	24.8	0.17	0.32	0.17	2.32	0.34
MB.C.22030	26.9	5.2	13.2	5.3	8.6	0.19	0.40	0.20	2.16	0.35

growth lines are significantly strengthened on the outer flank, where they turn back for a very deep and narrow ventral sinus on the narrow, nearly flat venter.

Paratype MB.C.22026 (Paeckelmann 1920 Coll.; Fig. 14A) shows the suture line at a whorl height of about 24 mm (corresponding to a conch diameter of about 45 mm). At this stage, it has four secondary prongs of the external lobe; they are all narrowly V-shaped with a tendency towards a lanceolate shape towards the venter. The saddle between the E_1 lobe and the L lobe is tectiform with flanks slightly incurved in the upper part. The lateral lobe is lanceolate with a mammiform base. Three umbilical lobes are present on the flank; they are V-shaped and almost symmetrical.

Comparisons. – *B. webbelense* resembles *B. tenuistriatum* in conch shape but differs in the less advanced suture line and the much more pronounced spiral umbilical rims. At a conch diameter of about 45 mm, *B. webbelense* possesses four secondary prongs on the external lobe in contrast to *B. tenuistriatum*, which has already six of such additional lobes. The umbilical rim is more pronounced in *B. webbelense*.

B. petterae from the Anti-Atlas is similar with respect to conch shape and number of sutural elements, but in this species, the secondary prongs of the external lobe and the saddles between them form a rather regular zigzag pattern, while the secondary prongs in *B. webbelense* are more lanceolate with narrowly rounded saddles between them.

***Beloceras petterae* Yatskov, 1990**
Figures 15, 16

1959 *Beloceras tenuistriatum* var. ?. – Petter, p. 184, pl. 10, fig. 1, text-fig. 44A.
* 1990 *Beloceras* (*Beloceras*) *petterae* Yatskov, p. 48.
1999 *Beloceras tenuistriatum* – Belka *et al.*, p. 10.

Holotype. – The specimen figured by Petter (1959, pl. 10, fig. 1).

Type locality and horizon. – Ride de l'Adrar (Tafilalt, Anti-Atlas); Frasnian.

Material. – Thirty-seven specimens up to 114 mm conch diameter from the area around Erfoud in the eastern Anti-Atlas of Morocco.

Diagnosis. – Species of *Beloceras* with subinvolute conch (uw/dm = 0.18–0.22 in stages larger than 50 mm dm). Suture line with four secondary prongs of the external lobe, a V-shaped lateral lobe, and four umbilical lobes on the flanks at 80 mm conch diameter; formula of the ventral suture line in this growth stage (E_2 E_3 E_4 E_5 E_1 E_5 E_4 E_3 E_2) L U_2 U_4 U_6 U_8 U_{10} U_{12}). The prongs of the external lobe are narrowly V-shaped; the saddle between the L lobe and the E_2 lobe is tectiform.

Description. – Specimen MB.C.22034 (Bockwinkel Coll.; Fig. 15C) is a fully septate, partly corroded specimen with a conch diameter of 114 mm; it is extremely discoidal (ww/dm = 0.15) and subinvolute (uw/dm = 0.19) with a high aperture (WER = 2.24). The relatively wide umbilicus is caused by the fact that the shell, which partly overlaps the umbilicus, is missing on parts of the specimen.

Specimen MB.C.22032 (Bockwinkel Coll.; Fig. 15A) is a fully septate, well-preserved individual from Ouidane Chebbi. It possesses the characteristic conch proportions of the species; at 80 mm in diameter it is extremely discoidal (ww/dm = 0.16) and subinvolute (uw/dm = 0.17) with an extremely high aperture (WER = 2.73). The conch is widest at the rounded umbilical margin, which separates the shallow and slightly concave umbilical wall from the slowly converging flanks. The venter is subacute. Parts of the steinkern are covered with shell remains, which appear to be smooth. It can be seen that the shell forms an umbilical thickening that contributes to a closure of the umbilicus.

The two smaller specimens MB.C.22040.1 and MB.C.22040.2 (Wendt Coll.) from Lahmida closely

Table 9. Conch ontogeny (Fig. 15, 16) of *Beloceras petterae* Yatskov, 1990.

dm	conch shape	whorl cross section shape	aperture
2 mm	extremely discoidal; evolute (ww/dm ~ 0.32; uw/dm = 0.40–0.45)	weakly compressed; moderately embracing (ww/wh = 0.90–1.05; IZR = 0.15–0.18)	moderate (WER = 1.75–2.00)
8 mm	extremely discoidal; subevolute (ww/dm ~ 0.25; uw/dm = 0.35–0.45)	weakly compressed; moderately embracing (ww/wh ~ 0.75; IZR ~ 0.15)	moderate to high (WER = 1.90–2.20)
18 mm	extremely discoidal; subinvolute to subevolute (ww/dm ~ 0.25; uw/dm = 0.25–0.32)	weakly compressed; moderately embracing (ww/wh ~ 0.55; IZR ~ 0.25)	high (WER ~ 2.20)
50 mm	extremely discoidal; subinvolute (ww/dm = 0.17–0.20; uw/dm = 0.18–0.22)	extremely compressed; strongly embracing (ww/wh = 0.30–0.35; IZR ~ 0.30)	high to extremely high (WER = 2.15–2.60)
80 mm	extremely discoidal; subinvolute (ww/dm ~ 0.16; uw/dm ~ 0.18)	extremely compressed; strongly embracing (ww/wh = 0.30–0.35; IZR ~ 0.30)	very high to extremely high (WER = 2.30–2.75)

Table 10. Conch dimensions (in mm) and proportions for reference specimens of *Beloceras petterae* Yatskov, 1990.

	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.22034	113.7	16.6	55.7	21.2	37.7	0.15	0.30	0.19	2.24	0.32
MB.C.22039	92.7	15.0	45.1	18.5	30.1	0.16	0.33	0.20	2.19	0.33
MB.C.22032	80.7	13.3	40.2	14.1	31.9	0.16	0.33	0.17	2.73	0.21
MB.C.22040.1	55.5	9.2	27.0	10.1	19.1	0.17	0.34	0.18	2.33	0.29
MB.C.22040.2	50.0	9.1	22.7	10.9	16.0	0.18	0.40	0.22	2.17	0.29
MB.C.22038	92.5	14.3	41.6	18.9	28.9	0.15	0.34	0.20	2.12	0.30
	63.6	10.3	32.0	12.0	23.7	0.16	0.32	0.19	2.55	0.26
	39.9	7.7	19.6	7.8	14.2	0.19	0.39	0.20	2.41	0.28
	25.7	5.8	12.5	6.1	9.1	0.23	0.47	0.24	2.40	0.27
	16.6	4.0	7.1	5.5	5.5	0.24	0.56	0.33	2.22	0.23
	11.1	2.5	4.0	4.6	3.4	0.22	0.62	0.41	2.04	0.16
	7.79	1.92	2.56	3.45	2.18	0.25	0.75	0.44	1.93	0.15
	5.61	1.49	1.79	2.57	1.52	0.27	0.83	0.46	1.89	0.15
	4.09	1.15	1.26	1.95	1.09	0.28	0.92	0.48	1.86	0.13
	3.00	0.86	0.89	1.44	0.74	0.29	0.98	0.48	1.76	0.17
	2.26	0.70	0.68	–	0.56	0.31	1.04	–	1.76	0.18
MB.C.22046	51.8	10.4	23.7	10.9	16.6	0.20	0.44	0.21	2.16	0.30
	35.2	7.5	17.2	7.3	12.7	0.21	0.44	0.21	2.46	0.26
	22.5	4.9	10.7	5.0	7.6	0.22	0.46	0.22	2.29	0.29
	14.9	3.5	6.8	4.0	5.1	0.24	0.52	0.27	2.31	0.25
	9.77	2.38	4.04	3.26	3.31	0.24	0.59	0.33	2.28	0.18
	6.46	1.68	2.47	2.49	2.03	0.26	0.68	0.38	2.13	0.18
	4.43	1.16	1.51	1.89	1.28	0.26	0.77	0.43	1.98	0.15
	3.15	0.87	1.04	1.38	0.89	0.28	0.84	0.44	1.95	0.14
	2.26	0.67	0.74	0.93	0.64	0.30	0.91	0.41	1.95	0.13

resemble each other (Fig. 15D, E). With conch diameters measuring 55 and 50 mm respectively, they are lenticular (ww/dm = 0.17, 0.18) and subinvolute (uw/dm = 0.18, 0.22). The narrower umbilicus in specimen MB.C.22040.1 is due to the preserved shell that causes a stronger overlap of the whorl upon the preceding one. Both of them possess shell remains, which are chiefly smooth except for delicate growth lines. Additionally, specimen MB.C.22040.1 displays a well-preserved wrinkle layer.

The suture line of specimen MB.C.22032 possesses, at 80 mm dm, five secondary prongs of the external lobe (Fig. 16D). These lobes differ significantly in shape and width; while the E_1 lobe is V-shaped and rather wide, the E_3 and E_4 lobes show a tendency to become lanceolate and very narrow. The incipient E_5 lobe is shallow and rounded. Specimen MB.C.22033.1 (appr. 100 mm in dm) shows a similar suture line, but at this size, five secondary prongs of the external lobe are present (Fig. 16A).

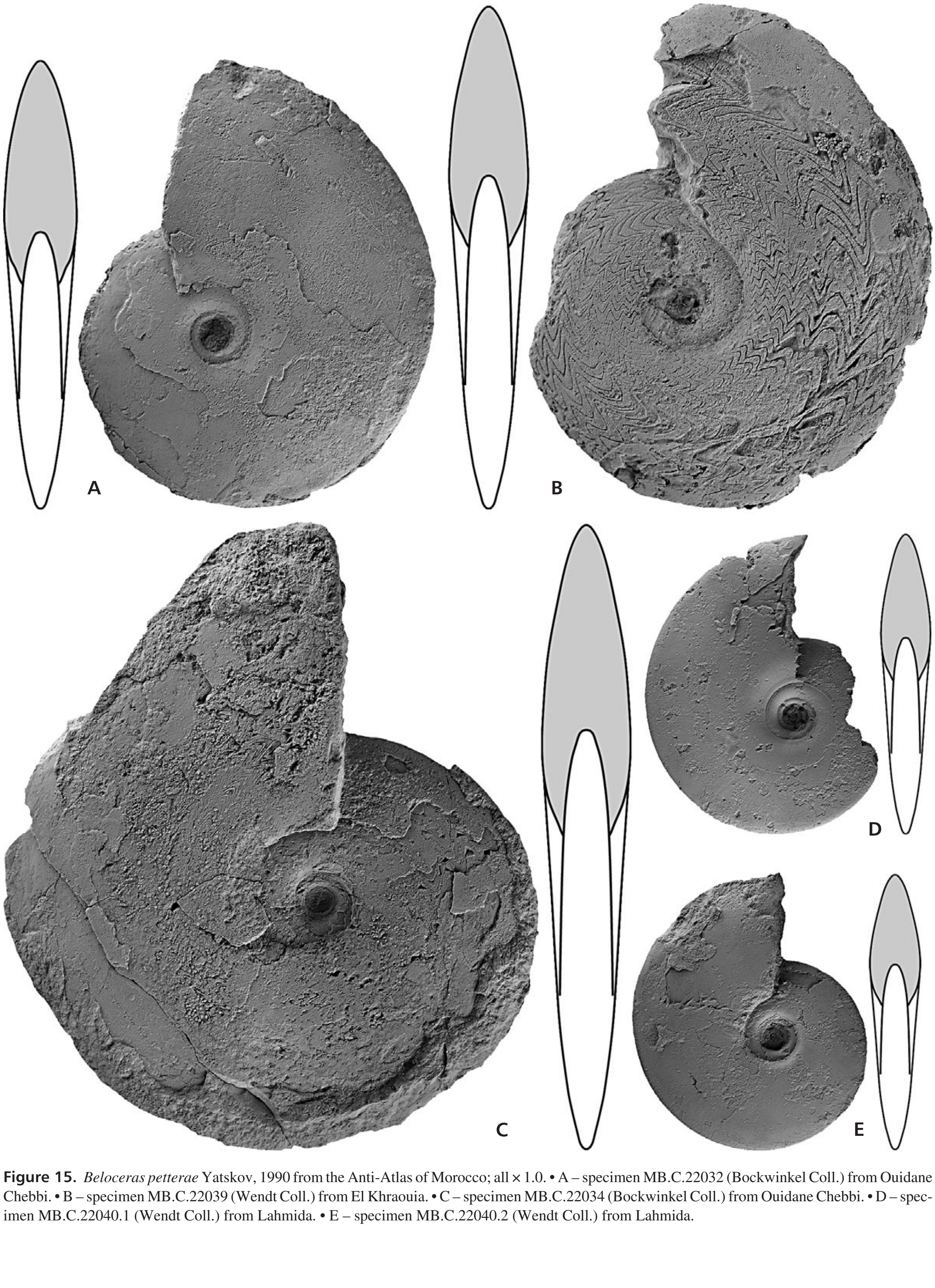


Figure 15. *Beloceras petterae* Yatskov, 1990 from the Anti-Atlas of Morocco; all × 1.0. • A – specimen MB.C.22032 (Bockwinkel Coll.) from Ouidane Chebbi. • B – specimen MB.C.22039 (Wendt Coll.) from El Khraouia. • C – specimen MB.C.22034 (Bockwinkel Coll.) from Ouidane Chebbi. • D – specimen MB.C.22040.1 (Wendt Coll.) from Lahmida. • E – specimen MB.C.22040.2 (Wendt Coll.) from Lahmida.

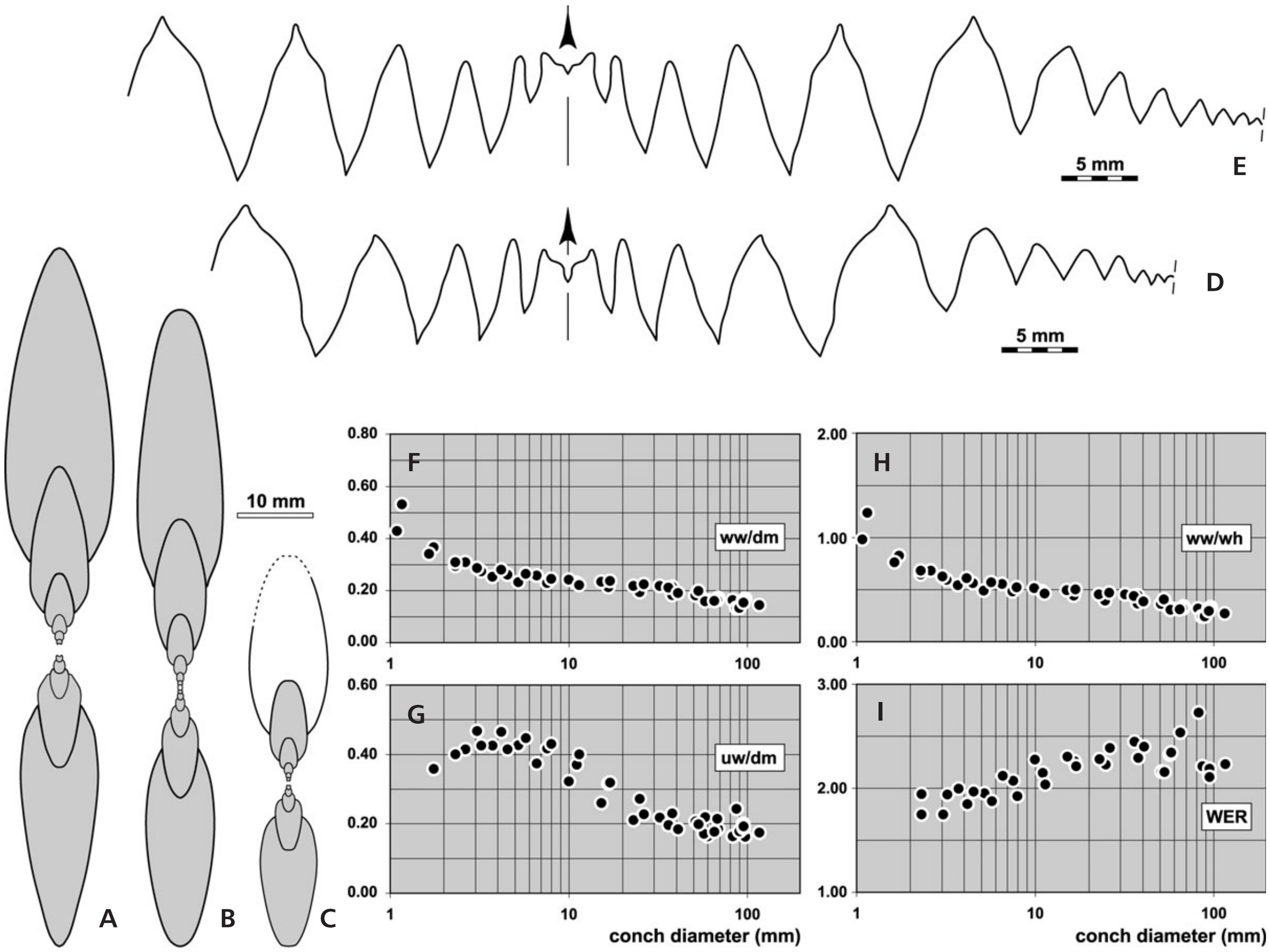


Figure 16. *Beloceras petterae* Yatskov, 1990 from the Anti-Atlas of Morocco. • A – cross section of specimen MB.C.22033.1 (Bockwinkel Coll.) from El Atrous; × 1.0. • B – cross section of specimen MB.C.22035 (Bockwinkel Coll.) from Ouidane Chebbi; × 1.0. • C – cross section of specimen MB.C.22046 (Ebbighausen Coll.) from El Haroun; × 1.0. • D – suture line of specimen MB.C.22032 (Bockwinkel Coll.) from Ouidane Chebbi, at 80.7 mm dm, 12.8 mm ww, 39.6 mm wh; × 2.0. • E – suture line of specimen MB.C.22033.1 (Bockwinkel Coll.) from Hassi Nebech, at 13.2 mm ww, ca 50 mm wh; × 2.0. • F–I – 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 all available specimens.

Comparisons. – *Beloceras petterae* differs from the *Beloceras* species from Central Europe (*B. webbelense*, *B. tenuistriatum*, and *B. sagittarium*), the Altay (*B. bogoslovskyi* and *B. stenumbilicatum*) as well as the Canning Basin (*B. glenisteri*) in the rather regular zigzag pattern of the secondary prongs of the external lobes and the saddles between them and thus can be easily recognised.

***Beloceras jorfense* sp. nov.**
Figures 17, 18

Derivation of name. – Named after the Jorf village near Erfoud.

Holotype. – Specimen MB.C.22047 (Wendt Coll.); illustrated here in Fig. 17.

Type locality and horizon. – Tantana near Jorf (eastern Anti-Atlas); greenish-grey Frasnian limestones.

Material. – The holotype and paratype MB.C.22048.

Diagnosis. – Species of *Beloceras* with subinvolute conch (uw/dm = 0.16 in stages larger than 50 mm in dm). Suture line with five secondary prongs of the external lobe, a V-shaped lateral lobe, and four umbilical lobes on the flanks at 60 mm conch diameter; formula of the ventral suture line in this growth stage (E_2 E_3 E_4 E_5 E_6 E_1 E_6 E_5 E_4 E_3 E_2) L U_2 U_4 U_6 U_8 U_{10}). Prongs of the external lobe are narrowly V-shaped to lanceolate; L lobe lanceolate; the saddles between the L lobe and the E_3 lobe are weakly tectiform.

Description. – Holotype MB.C.22047 (Wendt Coll.; Fig. 17) is a moderately well preserved, nearly fully septate

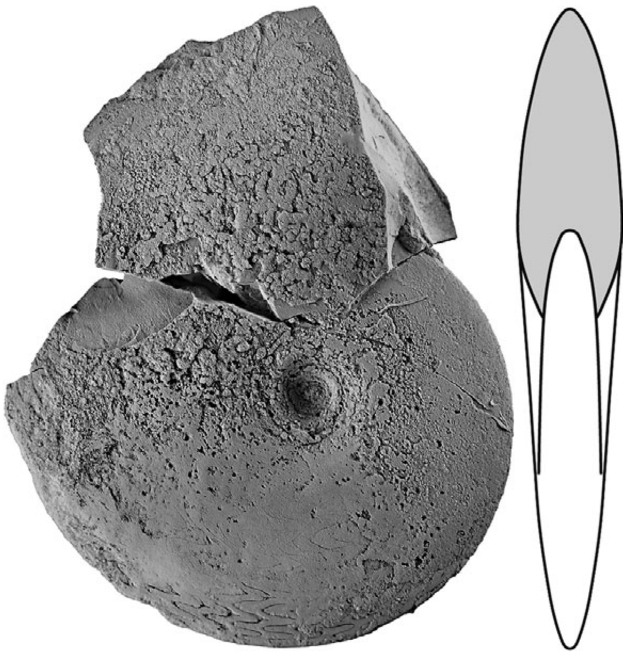


Figure 17. *Beloceras jorfense* sp. nov. from the Anti-Atlas of Morocco, holotype MB.C.22047 (Wendt Coll.) from Tantana; × 1.0.

specimen with 85 mm conch diameter. It is extremely discoidal and subinvolute (ww/dm = 0.16; uw/dm = 0.16) with a very high aperture (WER = 2.42). It has a slightly concave umbilical wall and a very narrow venter. The suture line, drawn at 61 mm conch diameter, shows five secondary prongs of the external lobe (Fig. 18B). These lobes differ markedly in their shape; the E_2 prong is lanceolate with diverging flanks, the E_3 prong is narrowly V-shaped with slightly sinuous flanks, the E_4 prong is lanceolate and asymmetric, the E_5 prong is lanceolate and slightly pouched, and the E_6 prong is narrowly V-shaped and acute. The saddles between the E lobe prongs also differ in their shape; while the E_2/E_3 saddle is tectiform, the E_3/E_4 saddle is triangular and narrowly rounded and the two following saddles are tongue-shaped and have a well-rounded top. The L lobe is lanceolate with almost parallel flanks, and the U lobes are small and V-shaped.

The smaller paratype MB.C.22048 is a fragment with a conch diameter measuring 50 mm. It is strongly corroded from one side, but the other side displays the suture line (Fig. 18A). At a whorl height of 19 mm (corresponding to about 40 mm in dm), there are four fully developed secondary prongs of the external lobe. As in the holotype, their shapes differ from each other. The saddles between the L lobe and the E_3 lobe are tectiform with a narrow lappet on the top.

Comparisons. – The new species differs from the other North African species *B. petterae* in the more advanced suture line with lanceolate lobes. *B. tenuistriatum* is similar but possesses more sutural elements (seven secondary prongs of the external lobe, six or more umbilical lobes on the flank).

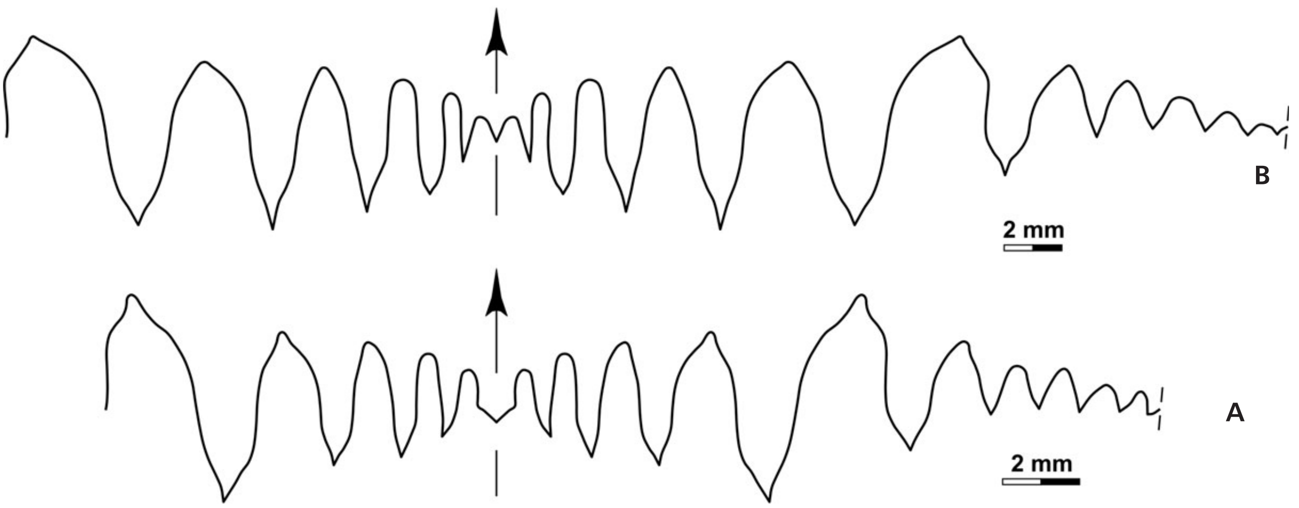


Figure 18. *Beloceras jorfense* sp. nov. from the Anti-Atlas of Morocco. • A – suture line of paratype MB.C.22048 (Wendt Coll.) from Tantana, at ca. 19 mm wh; × 4.0. • B – suture line of holotype MB.C.22047 (Wendt Coll.) from Tantana, at 61.1 mm dm, 10.7 mm ww, 30.0 mm wh; × 3.0.

Table 11. Conch dimensions (in mm) and proportions for the holotype of *Beloceras jorfense* sp. nov.

	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.22047	84.9	13.8	40.4	13.4	30.3	0.16	0.34	0.16	2.42	0.25

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Appendix

Investigated material of *Beloceras* (catalogue number in the Museum für Naturkunde, Berlin; locality details according to labels connected with the specimens; collector and year; size and preservation of the specimens; lithology of the rock material).

Beloceras sagittarium (Sandberger & Sandberger, 1851)

MB.C.4501	Sessacker bei Oberscheld	Dannenberg	115 mm	red-violet limestone
MB.C.4502	Oberscheld, Staatliche Grube	Hubach	51 mm	violet hematite ore
MB.C.4504	Charlottenzug bei Bredelar	Denckmann	70 mm, fragment	red iron limestone
MB.C.19171	Halde der Grube Charlottenzug bei Bredelar	Denckmann 1893	86 mm	red iron limestone
MB.C.19172	Halde der Grube Charlottenzug bei Bredelar	Denckmann 1893	62 mm	red iron limestone
MB.C.19173	Grube Charlottenzug bei Bredelar	Müller 1883	69 mm	red iron limestone
MB.C.19174	Grube Charlottenzug bei Bredelar	Müller 1882	37 mm	red iron limestone
MB.C.19175	Bredelar		67 mm	red-violet limestone
MB.C.19176	Sessacker b. Oberscheld	Lotz 1901	100 mm	red-violet limestone
MB.C.19177	Sessacker bei Oberscheld	Lotz 1901	77 mm	red-violet limestone
MB.C.19178	Arpe, östlich P. 547,6	Mempel	42 mm	light grey dolomitic limestone
MB.C.19179	Beuel bei Borg	Denckmann 1900	47 mm	grey limestone
MB.C.19180	Beuel bei Balve, Adorfer Kalk	Denckmann 1902	117 mm	light brown limestone
MB.C.19181	Schmidt's Kalkofen bei Braunau	Denckmann 1888	99 mm	light brown limestone
MB.C.19182	Schmidt's Steinbruch am Kalkofen bei Braunau	Denckmann 1888	105 mm	light grey limestone
MB.C.19183	Braunsberg bei Tegau, toI delta	E. Schultz 1967	135 mm	dark grey limestone
MB.C.19184	Braunsberg bei Tegau, toI delta	E. Schultz 1967	59 mm	dark grey limestone
MB.C.19185	Braunsberg bei Tegau, toI delta	E. Schultz 1967	34 mm	dark grey limestone
MB.C.19186	Braunsberg bei Tegau, toI delta	E. Schultz 1967	78 mm	dark grey limestone
MB.C.19187	Braunsberg bei Tegau, toI delta	E. Schultz 1967	40 mm	dark grey limestone
MB.C.19188	Braunsberg bei Tegau, toI delta	E. Schultz 1967	46 mm	dark grey limestone
MB.C.19189	Braunsberg bei Tegau, toI delta	E. Schultz 1967	86 mm	dark grey limestone
MB.C.19190	Braunsberg bei Tegau, toI delta	E. Schultz 1967	122 mm	dark grey limestone
MB.C.19191	Braunsberg bei Tegau, toI delta	E. Schultz 1967	49 mm	dark grey limestone
MB.C.19192	Braunsberg bei Tegau, toI delta	E. Schultz 1967	90 mm	dark grey limestone
MB.C.19193.1–9	Braunsberg bei Tegau, toI delta	E. Schultz 1967	nine fragments	dark grey limestone
MB.C.19194	Vogelsberg bei Göschitz	Bartzsch & Weyer 1985	106 mm	red-violet limestone
MB.C.19195	Vogelsberg bei Göschitz	Bartzsch & Weyer 1985	91 mm	red-violet limestone
MB.C.19196	Vogelsberg bei Göschitz	Bartzsch & Weyer 1985	106 mm	red-violet limestone
MB.C.19197	Vogelsberg bei Göschitz, sample VO3	Bartzsch & Weyer 1985	105 mm, incomplete	red-violet limestone
MB.C.19198	Vogelsberg bei Göschitz, sample VO3	Bartzsch & Weyer 1985	90 mm	red-violet limestone
MB.C.19199	Vogelsberg bei Göschitz, 31–41 cm über UKWK	Bartzsch & Weyer 1985	129 mm, incomplete	red-violet limestone
MB.C.19200	Vogelsberg bei Göschitz, sample B	Bartzsch & Weyer 1985	115 mm, incomplete	red-violet limestone
MB.C.21998	Vogelsberg bei Göschitz, bed 19	Bartzsch & Weyer 1985	fragment	red-violet limestone
MB.C.21999.1–2	Vogelsberg bei Göschitz, bed 21, 22	Bartzsch & Weyer 1985	two fragments	red-violet limestone
MB.C.22000.1–2	Schleiz, Geipel quarry, bet 4B	Bartzsch & Weyer 1995	two fragments, poorly preserved	grey limestone
MB.C.22001.1–4	Schleiz, Geipel quarry, bet 4A	Bartzsch & Weyer 1995	four fragments, poorly preserved	grey limestone
MB.C.22002	Büdesheim, Baugrube Lagerhalle 700 m ESE Kirche	Ebbighausen 2001	large fragment	nearly white dolomitic limestone
MB.C.22003.1	Büdesheim, Bahnhofstraße, Schicht B	Bockwinkel 1996	25 mm	pyritized

MB.C.22003.2	Büdesheim, Bahnhofstraße, Schicht B	Bockwinkel 1996	10 mm	pyritized
MB.C.22003.3	Büdesheim, Bahnhofstraße, Schicht B	Bockwinkel 1996	7 mm	pyritized
MB.C.22003.4	Büdesheim, Bahnhofstraße, Schicht B	Bockwinkel 1996	14 mm	pyritized
MB.C.22004.1	Büdesheim, Bahnhofstraße, Schicht C	Ebbighausen 1996	9 mm	pyritized
MB.C.22004.2	Büdesheim, Bahnhofstraße, Schicht D	Ebbighausen 1996	11 mm	pyritized
MB.C.22004.3	Büdesheim, Bahnhofstraße, Schicht B1	Ebbighausen 1996	11 mm	pyritized
MB.C.22004.4	Büdesheim, Bahnhofstraße, Schicht D	Ebbighausen 1996	8 mm	pyritized
MB.C.22004.5	Büdesheim, Bahnhofstraße, Schicht B1	Ebbighausen 1996	7 mm	pyritized
MB.C.22005	Büdesheim	Zich	25 mm	pyritized

Beloceras tenuistriatum (d'Archiac & de Verneuil, 1842)

MB.C.4505	Martenberg bei Bredelar	Müller	48 mm	red iron limestone
MB.C.4506	Martenberg bei Bredelar	Müller	71 mm	red limestone
MB.C.4507.1	Martenberg	Müller	16 mm	red-violet limestone
MB.C.4507.2	Martenberg	Müller	18 mm	red-violet limestone
MB.C.4507.3	Martenberg	Müller	31 mm	red-violet limestone
MB.C.4507.4	Martenberg	Müller	20 mm	red-violet limestone
MB.C.4507.5	Martenberg	Müller	17 mm	red-violet limestone
MB.C.4507.6	Martenberg	Müller	21 mm	red-violet limestone
MB.C.7701	zw. Adorf und Giershagen	von Koenen	64 mm	red limestone
MB.C.22007	Grube Martenberg bei Adorf	Denckmann 1893	51 mm	red limestone
MB.C.22006	Bredelar	Reinke 1882	75 mm	red iron limestone
MB.C.22008	Martenberg	Denckmann 1893	70 mm	reddish grey limestone
MB.C.22010	Martenberg-Klippe	Paeckelmann 1928	54 mm	red limestone
MB.C.22011	Martenberger Tagebau	Denckmann	73 mm	red limestone
MB.C.22012.1	Martenberg bei Adorf	Hugo Kemna	42 mm	red-violet limestone
MB.C.22012.2	Martenberg bei Adorf	Hugo Kemna	30 mm	red-violet limestone
MB.C.22012.3	Martenberg bei Adorf	Hugo Kemna	24 mm	red-violet limestone
MB.C.22012.1–4	Martenberg bei Adorf		four fragments	red limestone
MB.C.22014	Oberscheld, Königszug Mine	Lotz 1901–1902	80 mm	red-violet ironstone
MB.C.22015	Oberscheld	Euel 1901	52 mm	red-violet ironstone
MB.C.22016	Oberscheld	Dannenberg	fragment	red-violet ironstone
MB.C.22017	Grube Stillingseisenzug, bei dem Lager auf 60 m	Euel 1902	fragment	red-violet ironstone
MB.C.22018	Grube Stillingseisenzug, bei dem Lager auf 60 m	Euel 1902	fragment	red-violet ironstone
MB.C.22019	Tagebau Diana bei Oberscheld	Lotz 1901	71 mm	brown limestone
MB.C.22020	Tagebau Diana bei Oberscheld	Lotz 1901	40 mm	brown limestone
MB.C.22021	Tagebau Diana bei Oberscheld	Lotz 1901	49 mm	brown limestone
MB.C.22022	Tagebau Diana bei Oberscheld	Lotz 1901	fragment	brown limestone
MB.C.22023	Tagebau Diana bei Oberscheld	Lotz 1901	fragment	brown limestone
MB.C.22024	Tagebau Diana bei Oberscheld	Lotz 1901	fragment	brown limestone

Beloceras webbelense sp. nov.

MB.C.22025	Martenberg (Klippe) b. Adorf, Webeler Kalk	Paeckelmann 1920	91 mm	red limestone
MB.C.22026	Martenberg (Klippe) b. Adorf, Webeler Kalk	Paeckelmann 1920	52 mm	red ironstone
MB.C.22027.1–7	Gr. Webbel bei Giershagen		seven fragments	red limestone
MB.C.22028.1–4	Webbel bei Adorf	Denckmann	four fragments	red limestone
MB.C.22029	Versuchsschacht 200 m ö. Tagebau Webbel, Webbeler Kalk	Paeckelmann 1920	36 mm	red limestone
MB.C.22030	Webbel bei Adorf	Denckmann	27 mm	red limestone
MB.C.22009	Martenberg-Klippe	Paeckelmann 1928	76 mm	red limestone

Beloceras petterae Yatskov, 1990

MB.C.22032	Ouidane Chebbi	Bockwinkel	81 mm	light-grey limestone
MB.C.22033.1–7	Hassi Nebech N 30º56.028, W 3º48.170	Bockwinkel 03.03.2010	seven fragments	light-grey limestone
MB.C.22034	Ouidane Chebbi	Bockwinkel	114 mm	light-grey limestone
MB.C.22035	Ouidane Chebbi	Bockwinkel	85 mm	light-grey limestone
MB.C.22036	Ouidane Chebbi	Bockwinkel	83 mm	light-grey limestone
MB.C.22037.1–12	Rich Haroun Kasbah N 31º18.981 N, W 4º11.380	Bockwinkel	twelve fragments	light-grey limestone
MB.C.22039	El Khraouia	Wendt	93 mm	red-stained grey limestone
MB.C.22040.1	Rheris, Barrage et Canal Lahmida	Wendt	56 mm	light-grey limestone
MB.C.22040.2	Rheris, Barrage et Canal Lahmida	Wendt	52 mm	light-grey limestone
MB.C.22038	El Atrous, blaue Lage	Bockwinkel	94 mm	dark-grey limestone
MB.C.22041.1–2	Rich Haroun	Weyer	two incomplete specimens	light-grey limestone
MB.C.22042	Ouidane Chebbi	Korn 1993	107 mm, incomplete	light-grey limestone
MB.C.22043	Bou N'Chebbi	Ebbighausen 2000	fragment	light-grey limestone
MB.C.22044.1–2	Mkarig	Ebbighausen 2001	two fragments	light-grey limestone
MB.C.22045.1–4	Hassi Nebech N 30º56.240, W 3º47.058	Ebbighausen	four incomplete specimens	light-grey limestone
MB.C.22046	Rich Haroun	Ebbighausen 2010	50 mm	light-grey limestone

Beloceras jorfense sp. nov.

MB.C.22047	Tantana	Wendt	85 mm	light-grey limestone
MB.C.22048	Tantana	Wendt	61 mm	light-grey limestone

Beloceras sp. indet.

MB.C.22049	Sessacker bei Oberscheld	Dannenberg	fragment	red-violet limestone
MB.C.22052	südwestlich Ober-Valbert	Henke 1913	fragment	light-grey limestone
MB.C.22053	Weg von Langenholthausen nach Garbeck	Denckmann 1900	fragment	dark-grey limestone
MB.C.22054	Kalkbruch b. Dorlar	Henke 1909	fragment	light-grey limestone
MB.C.22055	Deutmecke	Henke 1911	fragment	light-grey limestone
MB.C.22056	Eisborn, Weg nach Mailinde	Denckmann 1902	94 mm	light-grey limestone
MB.C.22057	Beuel, Recke (Horster) Stbr.	Denckmann 1902	fragment	red limestone
MB.C.22058.1–3	Martenberg bei Adorf		three fragments	red limestone
MB.C.22059	Grube Martenberg bei Adorf	Denckmann	fragment	red limestone
MB.C.22050	Sessacker bei Oberscheld	Dannenberg	fragment	red limestone
MB.C.22051	Sessacker bei Oberscheld	Dannenberg	fragment	red limestone
MB.C.22060	Hauern, Schmidt's Kalkofen	Denckmann 1892	110 mm	light-grey limestone
MB.C.22061	M'Doura west side	Wendt	strongly weathered	light-grey limestone
MB.C.22062	Rich el Haroun	Wendt	strongly weathered	light-grey limestone