

## Research article

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# The early gephuroceratid ammonoids from the Roteisenstein Formation of Dillenburg (Cephalopoda, Ammonoidea)

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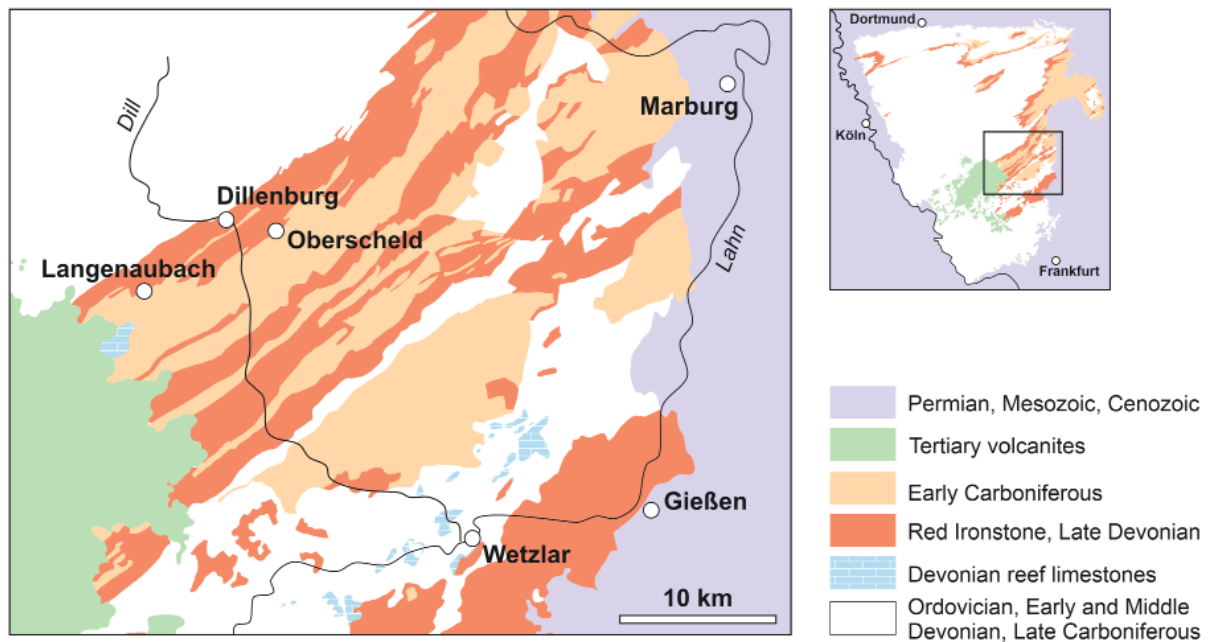
**Abstract.** The ammonoids of the suborder Gephuroceratina from the Roteisenstein (Red Ironstone) Formation of the area around Dillenburg (eastern Rhenish Mountains) are revised, mainly based on historical collections stored in the Museum für Naturkunde, Berlin. The new species *Ponticeras materni* sp. nov. is described and the species *Pseudoproboloceras pernai* (Wedekind, 1918), *Pseudoproboloceras applanatum* (Wedekind, 1918), *Ponticeras aequabile* (Beyrich, 1837), *Darkaoceras galeatum* (Matern, 1931), *Taouzites acutus* (Matern, 1931), *Koenenites lamellosus* (Sandberger & Sandberger, 1851), *Acanthoclymenia forcipifera* (Sandberger & Sandberger, 1851) and *Acanthoclymenia planorbis* (Sandberger & Sandberger, 1851) are revised. The stratigraphic distribution of the genera is discussed; they are assigned to three assemblages: (1) *Pseudoproboloceras pernai* Zone (latest Givetian; genera *Pseudoproboloceras*, *Ponticeras*, *Darkaoceras* and *Taouzites*), (2) *Koenenites lamellosus* Zone (early Frasnian, containing *Koenenites lamellosus* and *Acanthoclymenia forcipifera*) and (3) *Mesoboloceras kayseri* Zone (middle Frasnian, containing *Acanthoclymenia planorbis*).

**Keywords.** Ammonoidea, Middle Devonian, Late Devonian, Rhenish Mountains, taxonomy.

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## Introduction

Ammonoids from the Roteisenstein (Red Ironstone) Formation near Dillenburg on the eastern edge of the Rhenish Mountains (Fig. 1) are among the objects widely found in fossil collections. They already became quite well known in the 19<sup>th</sup> century and were already published by the pioneers in palaeontology (von Buch 1832; Beyrich 1837; d'Archiac & de Verneuil 1842; Sandberger & Sandberger 1850–1856). Even after that, there was quite a lot of interest in these fossils; they were especially investigated in the studies of Frech (1888), Wedekind (1918) and Matern (1931).



**Fig. 1.** The geographic position of the fossil localities in the Rhenish Mountains.

Three important clades of ammonoids are represented in the Red Ironstone of Dillenburg, represented by the suborders Pharciceratina Korn, 1998, Tornoceratina Wedekind, 1914 and Gephuroceratina Ruzhencev, 1957. The latter can be subdivided into two groups, mainly according to stratigraphic criteria. Only the older forms (genera *Pseudoproboloceras* Bensaïd, 1974, *Ponticeras* Matern, 1929, *Darkaoceras* Bockwinkel, Becker & Ebbighausen, 2009, *Taouzites* Korn, 2001, *Koenenites* Wedekind, 1913 and *Acanthoclymenia* Hyatt, 1900) are dealt with here. These are mainly genera with a rather small number of species. On the other hand, the stratigraphically younger forms belong to rather species-rich genera (*Manticoceras* Hyatt, 1884, *Beloceras* Hyatt, 1884), which will be dealt with in a further study.

In two recently published monographs (Korn & Bockwinkel 2021, 2022), the material of the suborder Pharciceratina and Tornoceratina from Dillenburg was studied in detail. Here follows the third part with the description of the early representatives of the Gephuroceratina from the Roteisenstein Formation of the Dillenburg region. As in the other parts, this description is largely based on material in the Museum für Naturkunde, Berlin.

### Ammonoid stratigraphy

The stratigraphic occurrence of the species of the suborder Pharciceratina has already been discussed by Korn & Bockwinkel (2022). There, it was concluded that these forms originate from three intervals, in ascending order: (1) *Maenioceras terebratum* Zone, (2) *Pseudoproboloceras pernai* Zone and (3) *Sandbergeroceras costatum* Zone.

The gephuoceratids described here also come from three, but partly different, stratigraphic intervals, in ascending order (Fig. 2):

- (1) *Pseudoproboloceras pernai* Zone (late Givetian), in which species of the genera *Pseudoproboloceras*, *Ponticeras*, *Darkaoceras* and *Taouzites* co-occur with various pharciceratids (genera *Pharciceras* Hyatt, 1884, *Evopharciceras* Korn & Bockwinkel, 2021, *Extropharciceras* Bockwinkel, Becker & Ebbighausen, 2009, *Stenopharciceras* Montesinos & Henn, 1986, *Synpharciceras* Schindewolf, 1940,

*Pluripharciceras* Bockwinkel, Becker & Ebbighausen, 2013). For instance, the gephuroid ceratids are known from localities (e.g., Prinzkessel Mine and “Tiefe Grube” near Oberscheld) and lithology, which yielded specimens of the genera *Pharciceras*, *Lunupharciceras* Korn in Korn & Klug, 2002 and *Synpharciceras*.

- (2) *Koenenites lamellosus* Zone (early Frasnian), containing *Koenenites lamellosus* (Sandberger & Sandberger, 1851) and *Acanthoclymenia forcipifera* (Sandberger & Sandberger, 1851). All of the specimens of *Koenenites lamellosus* in the MfN collection, except for one, are from a very dense haematite ore, four of which from the Koch collection (probably from the second half of the 19<sup>th</sup> century) of the Anna Mine near Oberscheld. From the same lithology at the same locality, Koch also collected numerous specimens of *Acanthoclymenia forcipifera* as well as specimens of *Pharciceras*, *Lunupharciceras* and *Synpharciceras*, but the latter are from a haematitic limestone.
- (3) *Mesobeloceras kayseri* Zone (middle Frasnian), containing *Acanthoclymenia planorbis* (Sandberger & Sandberger, 1851). Two of the specimens of *Acanthoclymenia planorbis* in the MfN collection are on one slab that also contains a specimen of *Mesobeloceras kayseri* (Holzapfel, 1882), which indicates a middle Frasnian age.

		“standard zones”	Rhenish Mountains	
L. DEVONIAN	FRASNIAN	<i>Crickites holzapfeli</i>	<i>Crickites holzapfeli</i> , <i>Cr. rickardi</i>	
		<i>Archoceras varicosum</i>	<i>Archoceras varicosum</i>	
		<i>Neomanticoceras paradoxum</i>	<i>N. paradoxum</i> , <i>Mat. sandbergeri</i>	
		<i>Playfordites tripartitus</i>	<i>Playf. tripartitus</i> , <i>C. nodulosum</i>	
		<i>Beloceras tenuistriatum</i>	<i>Beloceras tenuistriatum</i>	
		<i>Mesobeloceras kayseri</i>	<i>Mesobeloceras kayseri</i>	★ <i>Acanthoclymenia planorbis</i>
		<i>Prochorites alveolatus</i>		
		<i>Probeloceras lutheri</i>		
		<i>Sandbergeroceras syngonum</i>	<i>Sandbergeroceras costatum</i>	
		<i>Timanites keyserlingi</i>	<i>Koenenites lamellosus</i>	★ <i>Koenenites lamellosa</i>
		<i>Koenenites styliophilus</i>		★ <i>Acanthoclymenia forcipifera</i>
		<i>Petteroceras feisti</i>	<i>Ponticeras</i> spp.	
M. DEVONIAN	GIVETIAN	<i>Petteroceras errans</i>	<i>Ponticeras kayseri</i>	
		<i>Pseudoproboloceras pernai</i>	<i>Pseudoproboloceras pernai</i>	★ <i>Pseudoproboloceras</i>
		<i>Synpharciceras clavilobum</i>	<i>Synpharciceras clavilobum</i>	★ <i>Ponticeras</i>
		<i>Stenopharciceras lataseptatum</i>	<i>Stenopharciceras lunulicosta</i>	★ <i>Darkaoceras</i>
		<i>Pharciceras amplexum</i>	<i>Pharciceras tridens</i>	★ <i>Taouzites</i>
		<i>Afromaenioceras sulcatostriatum</i>	<i>Afromaenioc. cf. sulcatostriatum</i>	
		<i>Maenioceras terebratum</i>	<i>Maenioceras terebratum</i>	
		<i>Maenioceras molarium</i>		
		<i>Maenioceras undulatum</i>	<i>Maenioceras undulatum</i>	

**Fig. 2.** Givetian and Frasnian ammonoid stratigraphy (after Becker & House 2000), probable extent of the Red Ironstone of Dillenburg and probable position of the ammonoid assemblages described here.

## Material and methods

There was a total of 84 specimens available for our study, most from the area of Dillenburg at the eastern margin of the Rhenish Mountains (Fig. 1). The specimens are preserved in iron-rich micritic or sparitic limestone or in haematitic ironstone, some of them in a nearly pure haematite ore. Most specimens are tectonically deformed laterally, but often the shell ornamentation is well preserved. Inner whorls and septa are often destroyed and replaced by coarse calcite, so that the important features of conch ontogeny and suture line are sometimes destroyed.

We studied the following species (with the number of specimens from the Red Ironstone):

*Pseudoproboloceras pernai* (Wedekind, 1918) – 10 specimens

*Pseudoproboloceras applanatum* (Wedekind, 1918) – 2 specimens

*Ponticeras aequabile* (Beyrich, 1837) – 18 specimens

*Ponticeras materni* sp. nov. – 6 specimens

*Darkaoceras galeatum* (Matern, 1931) – 15 specimens

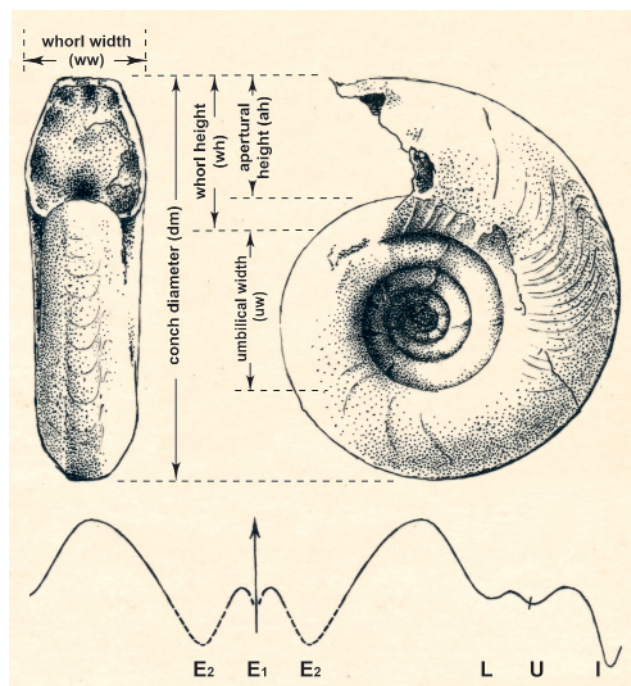
*Taouzites acutus* (Matern, 1931) – 3 specimens

*Koenenites lamellosus* (Sandberger & Sandberger, 1851) – 12 specimens

*Acanthoclymenia forcipifera* (Sandberger & Sandberger, 1851) – 14 specimens

*Acanthoclymenia planorbis* (Sandberger & Sandberger, 1851) – 4 specimens

The description of the material largely follows the scheme for Palaeozoic ammonoids outlined by Korn (2010) and Klug *et al.* (2015) (Fig. 3). However, due to the limited ontogenetic data, some descriptions must remain incomplete. The embedding of most specimens in very hard ironstone did not always allow for a complete preparation. Furthermore, many of the specimens are tectonically deformed, so that photographing dorsal and ventral views was not possible in some cases. In the following, we therefore present reconstructed dorsal projections to give a better picture of the geometry of the conchs.



**Fig. 3.** The morphological terms used in the description of the ammonoid conchs and suture lines. Illustration from an ink drawing of *Acanthoclymenia neapolitana* (Clarke, 1892) by Jerzy Dzik (Warsaw).



### Abbreviations

ah	=	apertural height
dm	=	conch diameter
IZR	=	imprint zone rate
MB.C.	=	collection of fossil cephalopods in the Museum für Naturkunde, Berlin
SMF.Mbg.	=	former collection of the Marburg University, now Senckenberg Museum, Frankfurt
uw	=	umbilical width
WER	=	whorl expansion rate
wh	=	whorl height
ww	=	whorl width

### Results

Order Agoniatitida Ruzhencev, 1957  
Suborder Gephuroceratina Ruzhencev, 1957  
Superfamily Gephuroceratoidea Frech, 1897

Family **Ponticeratidae** Korn in Korn & Klug, 2002

### Diagnosis

Gephuroceratoidea with sutural formula ( $E_2 E_1 E_2$ ) L:I or ( $E_2 E_1 E_2$ ) L:U I; lateral lobe simple, usually rounded.

### Included subfamilies

Ponticeratinae Korn in Korn & Klug, 2002; Gogoceratinae Korn in Korn & Klug, 2002.

Subfamily **Ponticeratinae** Korn in Korn & Klug, 2002

### Diagnosis

Ponticeratidae with moderately wide to wide umbilicus; growth lines with high ventrolateral projection.

### Included genera

*Pseudoproboloceras* Bensaïd, 1974; *Ponticeras* Matern, 1929; *Uchtites* Bogoslovsky, 1958; *Chutoceras* Becker & House, 2000 (synonym of *Uchtites*).

Genus ***Pseudoproboloceras*** Bensaïd, 1974

### Type species

*Pseudoproboloceras nebechense* Bensaïd, 1974 (original designation).

### Diagnosis

Genus of the subfamily Ponticeratinae with extremely discoidal, subevolute conch. Without ventrolateral grooves. Suture line with relatively narrow external lobe, very low median saddle, very small  $E_2$  lobe, shallow and rounded lateral lobe. Suture line formula ( $E_2 E_1 E_2$ ) L:I.

### Included species

*Pseudoproboloceras nebechense* Bensaïd, 1974, Anti-Atlas; *Gephyroceras Pernai* var. *applanata* Wedekind, 1918, Rhenish Mountains; *Gephyroceras Barroisi* Wedekind, 1918, Rhenish Mountains

(synonym of *P. pernai*); *Gephyroceras Pernai* Wedekind, 1918, Rhenish Mountains; *Manticoceras pontiformis* Termier & Termier, 1950, Anti-Atlas; *Pseudoproboloceras praecox* Bockwinkel, Becker & Ebbighausen, 2013, Anti-Atlas; *Ponticeras sahlgrundense* Matern, 1931, Rhenish Mountains (synonym of *P. pernai*).

### Remarks

*Pseudoproboloceras* can be considered the stratigraphically earliest and morphologically simplest genus of the gephyroceratids. The most important morphological feature is the very low median saddle, which is indicative of a newly acquired trait. In the early forms of *Ponticeras*, which have the same suture line formula as *Pseudoproboloceras*, the median saddle is already much more prominent and the external lobe is much wider than in *Pseudoproboloceras*.

### *Pseudoproboloceras pernai* (Wedekind, 1918)

Figs 4A, C, 5–6

*Gephyroceras Pernai* Wedekind, 1918: 122, 166, pl. 21 figs 1–2, text-fig. 28e.

*Gephyroceras Barroisi* Wedekind, 1918: 122, 167, pl. 21 fig. 7, text-fig. 28a.

*Ponticeras sahlgrundense* Matern, 1931: 80, pl. 2 fig. 12.

*Ponticeras pernai pernai* – Matern 1931: 79. — House in House & Ziegler 1977: 79, pl. 1 figs 18–22.

*Pseudoproboloceras pernai* – Korn & Klug 2002: 98.

non *Proboloceras pernai* – Petter 1959: 153, pl. 11 figs 5–6, text-fig. 40c.

non *Ponticeras pernai* – House *et al.* 1985: pl. 1 figs 1–2.

non *Pseudoproboloceras pernai* – Bockwinkel *et al.* 2013a: 10, text-figs 5–6; 2015: 129, text-figs 4b, f–h, 5a–b; 2017: 315, text-figs 4–5.

### Diagnosis

Species of *Pseudoproboloceras* reaching about 70 mm conch diameter with thinly discoidal, subevolute conch between 30 and 50 mm dm (ww/dm decreasing from ~ 0.30 to ~ 0.25; uw/dm increasing from ~ 0.30 to ~ 0.38); coiling rate moderate (WER ~ 1.95). Whorl profile weakly compressed (ww/wh = 0.65–0.80); umbilical wall oblique, umbilical margin broadly rounded, venter rounded. Growth lines very fine. Suture line with V-shaped external lobe with strongly diverging flanks, median saddle low, E<sub>2</sub> lobe small, rounded or pointed, ventrolateral saddle almost symmetrically rounded, lateral lobe broadly rounded.

### Material examined

#### Lectotype

GERMANY • Rhenish Mountains, Oberscheld (Grube Prinzkessel); late Givetian (Red Ironstone); Welsch 1912 Coll.; SMF.Mbg.2322. Illustrated by Wedekind (1918: pl. 21 figs 1–2) and House & Ziegler (1977: pl. 1 figs 21–22); re-illustrated here in Fig. 4A.

#### Additional material

GERMANY • 1 specimen; Rhenish Mountains, Oberscheld; late Givetian (Red Ironstone); Erbreich Coll.; MB.C.7696 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Gründchesseite); late Givetian (Red Ironstone); Lotz 1901–1902 Coll.; MB.C.30415 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Prinzkessel); late Givetian (Red Ironstone); Fremdling 1922 Coll.; MB.C.4287 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Volpertseiche); late Givetian (Red Ironstone); Bender 1901 Coll.; MB.C.30416 • 3 specimens; Rhenish Mountains, Oberscheld (“Tiefe Grube”); late Givetian (Red

Ironstone); Etzold 1910 Coll.; MB.C.22164, MB.C.30417.1, MB.C.30417.2 • 1 specimen; Rhenish Mountains, Oberscheld; late Givetian (Red Ironstone); MB.C.30418 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Prinzkessel); late Givetian (Red Ironstone); Welsch 1913 Coll.; SMF.MB.C.2326.

### Description

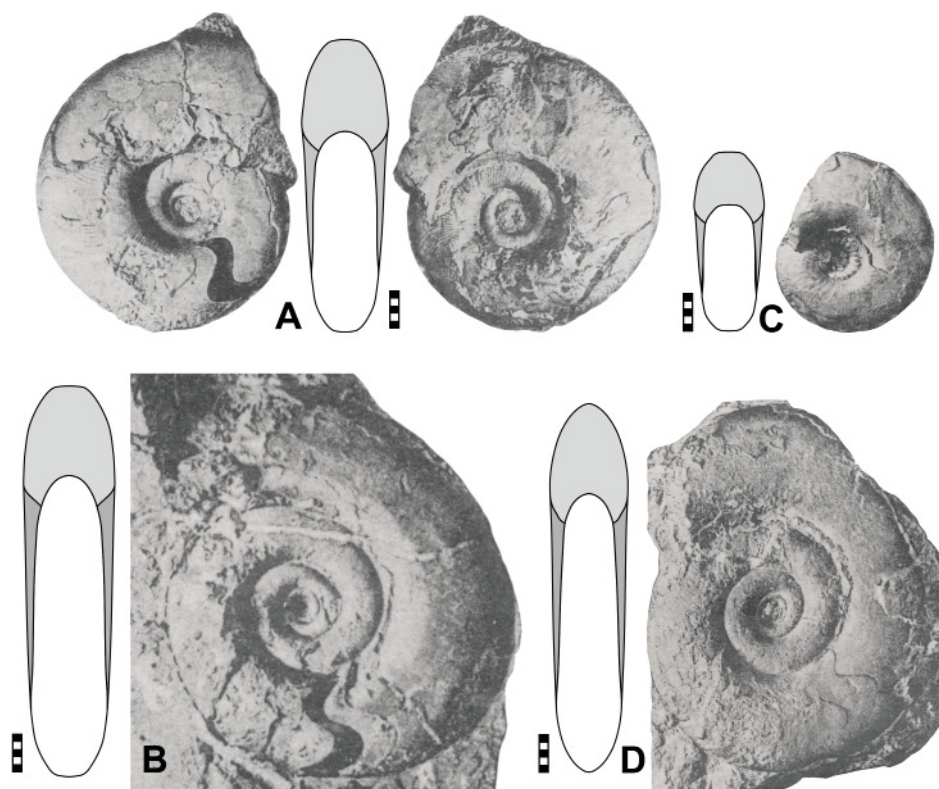
Seven specimens are selected for description and illustration:

Lectotype SMF.Mbg.2322: rather well-preserved specimen with 38 mm diameter, shell surface and suture line preserved (Fig. 4A).

Specimen Mbg.2326, the holotype of “*Gephyroceras Barroisi*”: is a specimen with 51 mm diameter (Fig. 4C).

MB.C.22164: fragmentary, somewhat corroded specimen with 53 mm conch diameter in haematitic, micritic limestone; one third of the last volution belongs to the body chamber (Fig. 5B).

MB.C.4287: rather complete, somewhat corroded specimen with 46 mm conch diameter in haematitic, sparitic limestone; one quarter of the last volution belongs to the body chamber (Fig. 5C).



**Fig. 4.** Specimens of *Pseudoproboloceras* Bensaïd, 1974 and *Ponticeras* Matern, 1929; reproductions from Wedekind (1918). **A.** *Pseudoproboloceras pernai* (Wedekind, 1918), lectotype SMF.Mbg.2322 (Welsch 1912 Coll.) from Oberscheld (Prinzkessel Mine). **B.** *Pseudoproboloceras applanatum* (Wedekind, 1918), holotype SMF.Mbg.2323 (Welsch Coll.) from Oberscheld (Prinzkessel Mine). **C.** *Pseudoproboloceras pernai* (Wedekind, 1918), holotype SMF.Mbg.2326 (Welsch 1913 Coll.) of “*Gephyroceras Barroisi*” from Oberscheld (Prinzkessel Mine). **D.** *Ponticeras aequabile* (Beyrich, 1837), holotype SMF.Mbg.2324 (Meuhsen 1855 Coll.) of “*Gephyroceras Kayseri*” from Oberscheld (Königszug Mine). Scale bar units = 1 mm.

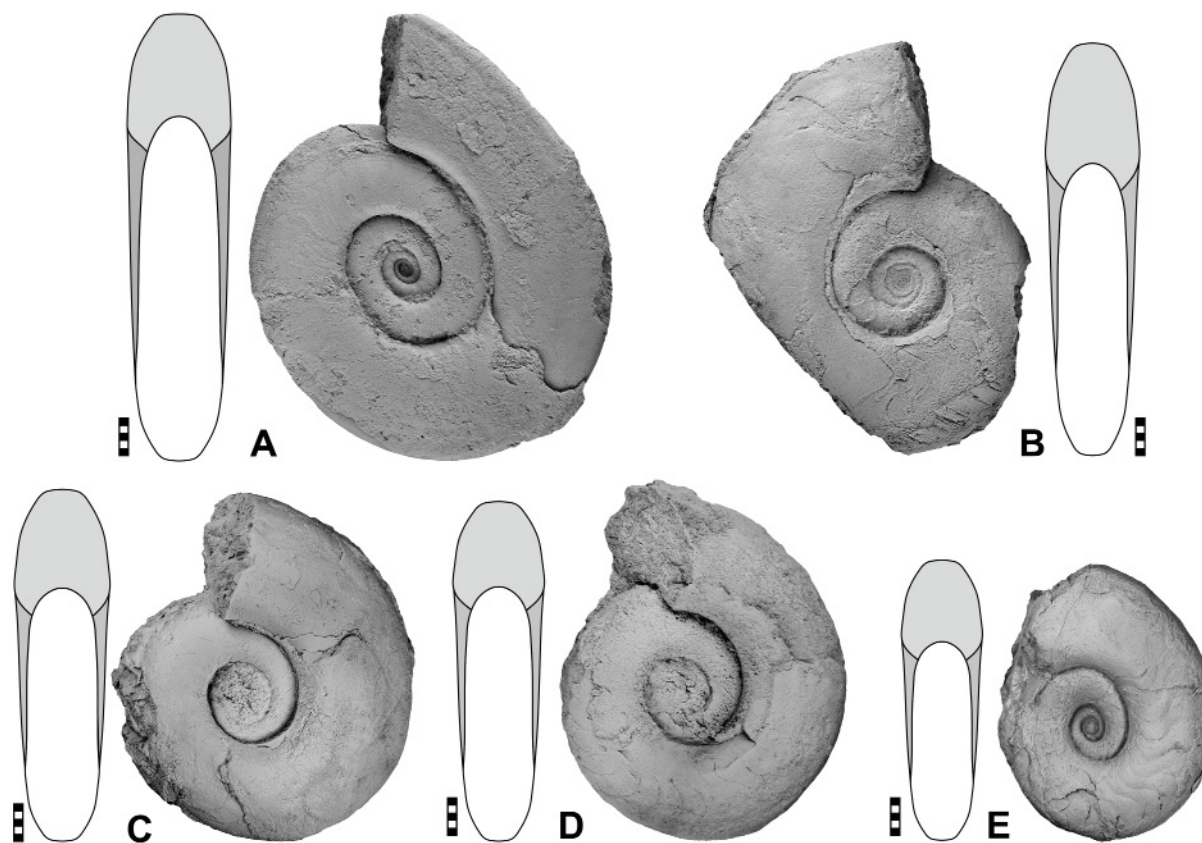
MB.C.7696: rather complete, somewhat corroded specimen with 45 mm conch diameter in haematitic limestone; one half of the last volution belongs to the body chamber (Fig. 5D).

MB.C.30417.1: exfoliated specimen with 37 mm conch diameter in haematitic limestone; only a small part belongs to the body chamber (Fig. 5E).

MB.C.30418: deformed but otherwise rather well-preserved specimen with 59 mm conch diameter in haematitic sparitic limestone; conch widely covered with shell. Part of the external suture line visible (Fig. 5A).

Lectotype SMF.Mbg.2322 is a specimen with 38 mm diameter (Fig. 4A). It is thinly discoidal; the venter is weakly flattened. It is separated, on the last quarter whorl, from the converging flanks by a pronounced ventrolateral shoulder. The specimen has rather coarse growth lines, particularly in inner whorls; they become lamellar on last volution with a high ventrolateral projection.

Specimen SMF.Mbg.2326, the holotype of *Pseudoproboloceras barroisi*, is a specimen 51 mm in diameter (Fig. 4C). Its umbilical wall is oblique, the flanks converge and the ventrolateral shoulder is prominent. On the last half volution, the specimen shows the transformation from the preadult stage into the adult stage by a rather rapid opening of the umbilicus. The shell ornamentation is poorly preserved.



**Fig. 5.** *Pseudoproboloceras pernai* (Wedekind, 1918). **A.** Specimen MB.C.30418, probably from Oberscheld. **B.** Specimen MB.C.22164 (Etzold 1910 Coll.) from Oberscheld ("Tiefe Grube"). **C.** Specimen MB.C.4287 (Fremdling 1922 Coll.) from Oberscheld (Prinzkessel Mine). **D.** Specimen MB.C.7696 (Erbreich Coll.) from Oberscheld. **E.** Specimen MB.C.30417.1 (Etzold 1910 Coll.) from Oberscheld ("Tiefe Grube"). Scale bar units = 1 mm.



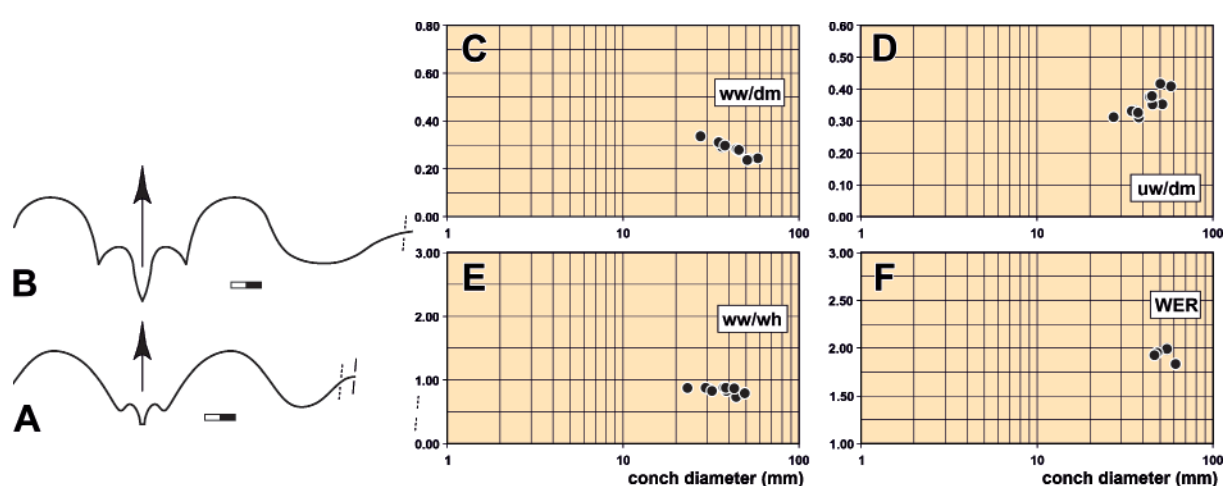
**Table 1.** Conch dimensions (partly reconstructed) and ratios of selected specimens of *Pseudoproboloceras pernai* (Wedekind, 1918).

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30418	58.7	14.2	20.4	24.1	15.0	0.24	0.70	0.41	1.80	0.26
MB.C.22164	52.4	12.5	19.5	18.6	15.0	0.24	0.64	0.35	1.96	0.23
SMF.Mbg.2326	51.1	12.0	15.5	21.4	–	0.23	0.77	0.42	–	–
MB.C.4287	46.2	12.6	17.2	16.3	12.9	0.27	0.73	0.35	1.92	0.25
MB.C.7696	44.5	12.5	15.9	16.4	12.2	0.28	0.79	0.38	1.90	0.23
SMF.Mbg.2322	38.2	11.3	15.4	12.5	–	0.30	0.73	0.33	–	–
MB.C.30417.1	36.8	10.7	14.0	12.3	–	0.29	0.76	0.33	–	–

The additional material allows the study of the proportions, ornamentation and suture lines of the shell in a growth interval between 27 and 59 mm diameter (Fig. 5). In the interval between 30 and 50 mm diameter, the conch becomes slenderer (ww/dm decreasing from  $\sim 0.35$  to  $\sim 0.25$ ) and more widely umbilicate (uw/dm increasing from  $\sim 0.30$  to  $\sim 0.28$ ). The coiling rate is moderately high (WER  $\sim 1.95$ ) at 50 mm dm. The compressed whorl profile (ww/wh decreasing from  $\sim 0.80$  to  $\sim 0.65$ ) has an oblique umbilical wall, rounded umbilical margin, weakly converging flanks and rounded venter. Shell remains are poorly preserved in the material; the ornament is obviously very weak.

Specimen MB.C.30418 shows the transformation from the pre-adult to adult morphology (Fig. 5A). Up to a conch diameter of 45 mm the proportions are similar to the other specimens, but thereafter there is a rapid change in the rate of overlap of the earlier whorls and a reduction in the rate of coiling. Although the specimen is somewhat distorted by tectonics, it shows the differences from the pre-adult stage. At 59 mm conch diameter, the whorl profile is compressed with a rounded umbilical margin, weakly convergent flanks, subangular ventrolateral shoulders and a weakly flattened venter.

Parts of the suture line are visible in several specimens. In specimen MB.C.30417.1 it shows the outline characteristic of the genus with a V-shaped external lobe with strongly diverging flanks, a very low lateral saddle, a deep  $E_1$  lobe and narrowly rounded  $E_2$  lobe. The ventrolateral saddle is almost symmetrical and broadly rounded, the lateral lobe is broadly rounded (Fig. 6A).



**Fig. 6.** *Pseudoproboloceras pernai* (Wedekind, 1918). A. Suture line of specimen MB.C.30417.1 (Etzold 1910 Coll.) from Oberscheld (“Tiefe Grube”), at dm = 27.0 mm, ww = 9.0 mm, wh = 11.0 mm. B. Suture line of specimen MB.C.30418, probably from Oberscheld, at dm = 48.3 mm, ww = 11.9 mm, wh = 15.6 mm. C–F. Ontogenetic trajectories of the cardinal conch parameters. Scale bar units = 1 mm.

**Remarks**

*Pseudoproboloceras barroisi* is here synonymised with *P. pernai*, although its holotype is not well preserved and thus does not allow an accurate description. Up to about 40 mm conch diameter, it closely resembles the typical morphology of *P. pernai*; on the last half volution it shows the transformation to the adult morphology with its opened umbilicus.

*Pseudoproboloceras pernai* differs from *P. applanatum* (Wedekind, 1918) in the shape of the venter; this is rounded in *P. pernai*, whereas in *P. applanatum* it is slightly flattened and bordered by a narrow, rounded ventrolateral shoulder on the flanks.

The specimens from Hassi Nebech attributed to *P. pernai* by Petter (1959), House *et al.* (1985) and Bockwinkel *et al.* (2013a) differ by their much higher coiling rate (WER = 2.30–2.45 between 27 and 32 mm dm) from the material from the type region (WER ~ 1.90 at 45 mm dm). They have to be attributed to the species *Pseudoproboloceras nebechense* Bensaïd, 1974, as originally stated by Bensaïd (1974).

***Pseudoproboloceras applanatum* (Wedekind, 1918)**

Figs 4B, 7

*Gephyroceras Pernai* var. *applanata* Wedekind, 1918: 122, 167, pl. 21 fig. 3, text-fig. 28b.

*Ponticeras pernai applanata* – Matern 1931: 80. — House in House & Ziegler 1977: 79, pl. 1 figs 16–17, 26–27.

*Pseudoproboloceras applanatum* – Korn & Klug 2002: 98.

**Diagnosis**

Species of *Pseudoproboloceras* reaching about 50 mm conch diameter with thinly discoidal, subinvolute conch at 30 mm dm (ww/dm ~ 0.35; uw/dm ~ 0.28); coiling rate moderate (WER ~ 1.95). Whorl profile weakly compressed (ww/wh ~ 0.85); umbilical wall oblique, umbilical margin broadly rounded, venter weakly flattened, ventrolateral shoulder narrowly rounded. Growth lines very fine, strongly biconvex with linguiform ventrolateral projection. Suture line with V-shaped external lobe with diverging flanks; median saddle low, E<sub>2</sub> lobe small, rounded, ventrolateral saddle almost symmetrically rounded, lateral lobe asymmetrically rounded.

**Material examined****Holotype**

GERMANY • Rhenish Mountains, Oberscheld (Grube Prinzkessel); late Givetian (Red Ironstone); Welsch 1912 Coll.; SMF.Mbg.2323. Illustrated by Wedekind (1918: pl. 21 fig.3) and House & Ziegler (1977: pl. 1 figs 26–27); re-illustrated here in Fig. 4B.

**Additional material**

GERMANY • 1 specimen; Rhenish Mountains, Oberscheld (Grube Volpertseiche); late Givetian (Red Ironstone); Koch Coll.; MB.C.22157.

**Description**

Two specimens are selected for description and illustration:

Holotype SMF.Mbg.2323: rather well-preserved specimen with 24 mm diameter in haematitic limestone (Fig. 4B).

**Table 2.** Conch dimensions and ratios of selected specimens of *Pseudoproboloceras applanatum* (Wedekind, 1918).

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.22157	35.0	11.9	14.8	9.5	—	0.34	0.80	0.27	—	—
SMF.Mbg.2323	23.8	9.3	11.2	6.3	—	0.39	0.83	0.26	—	—

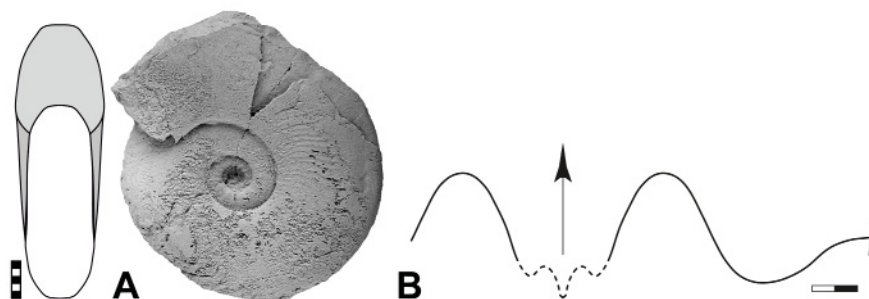
MB.C.22157: incomplete specimen with about 44 mm diameter in haematitic limestone; more than half of the last volution belong to the body chamber (Fig. 7A).

Holotype SMF.Mbg.2323 with 24 mm diameter is discoidal and subinvolute (Fig. 4B). Its umbilical wall is rounded; the flanks slightly flattened and converge to the rather broad venter. A pronounced, weakly angular ventrolateral shoulder is present on the entire last volution. The growth lines are lamellar; there are faint riblets around the umbilicus. The suture line has a large, subdivided external lobe with very small  $E_1$  prongs, a low median saddle and a very deep  $E_m$  lobe.

Specimen MB.C.22157, 35 mm in diameter, has a thinly discoidal and subinvolute conch with a compressed whorl profile (Fig. 7A). It is widest near the mid-flank and has an oblique umbilical wall and broadly rounded umbilical margin; the flanks are convex and weakly convergent, the outer flanks are weakly concave and separated from the weakly flattened venter by a narrowly rounded ventrolateral shoulder. The shell remains show rhythmically strengthened growth lines with broadly rounded dorsolateral projection, a wide lateral sinus and a narrow and high, lingulate ventrolateral projection. The suture line is barely visible in the ventral portion because of poor preservation; it possesses a V-shaped external lobe, a narrowly rounded ventrolateral saddle and a broadly rounded lateral lobe (Fig. 7B).

### Remarks

*Pseudoproboloceras applanatum* differs in the slightly stouter conch shape ( $ww/dm \sim 0.35$ ) from *P. pernai* ( $ww/dm = 0.20\text{--}0.30$ ) and the narrower umbilicus ( $uw/dm \sim 0.28$  in contrast to  $\sim 0.33$ ). The main distinguishing character to separate *P. applanatum* from *P. pernai* is the shape of the venter; while this is rounded in *P. pernai*, in *P. applanatum* it is slightly flattened and bordered by a narrowly rounded ventrolateral shoulder from the flanks.



**Fig. 7.** *Pseudoproboloceras applanatum* (Wedekind, 1918). Specimen MB.C.22157 (Koch Coll.) from Oberscheld (Volpertseiche Mine). **A.** Lateral view and dorsal projection. **B.** Suture line, at  $ww = 11.8$  mm. Scale bar units = 1 mm.

Genus *Ponticeras* Matern, 1929

**Type species**

*Ammonites aequabilis* Beyrich, 1837 (original designation).

**Diagnosis**

Genus of the subfamily Ponticeratinae with extremely discoidal, subevolute to evolute conch. Often with ventrolateral grooves. Suture line with very wide external lobe, moderately high median saddle, small  $E_2$  lobe, shallow and rounded lateral lobe. Suture line formula  $(E_2 E_1 E_2) L:I$  or  $(E_2 E_1 E_2) L:U I$ .

**Included species**

*Ammonites aequabilis* Beyrich, 1837, Rhenish Mountains; *Ponticeras altaicum* Bogoslovsky, 1958, Altay; *Gephyroceras auritum* Holzapfel, 1899, Timan; *Goniatites bisulcatus* Keyserling, 1844, Timan; *Ponticeras discoidale* Glenister, 1958, Western Australia; *Gephyroceras Domanicense* Holzapfel, 1899, Timan; *Gephyroceras Kayseri* Wedekind, 1918, Rhenish Mountains; *Gephyroceras Keyserlingi* Holzapfel, 1899, Timan; *Gephyroceras Lebedeffi* Holzapfel, 1899, Timan; *Ponticeras orientale* Bogoslovsky, 1958, Altay; *Goniatites complanatus perlatus* Hall, 1874, New York; *Gephyroceras regale* Holzapfel, 1899, Timan; *Gephyroceras Tschernyschewi* Holzapfel, 1899, Timan; *Gephyroceras uralicum* Holzapfel, 1899, Timan; *Ponticeras materni* sp. nov., Rhenish Mountains, and questionably:

*Ponticeras acutilobatum* Bogoslovsky, 1958, Altay; *Probeloceras costulatum* Petter, 1959, Ougarta; *Manticoceras (Prochorites) prumiense platystoma* Clausen, 1969, Eifel Mountains; *Goniatites Prumiensis* Steininger, 1853, Eifel Mountains; *Ponticeras regulare* Chao, 1956, Guangxi; *Goniatites Wildungensis* Waldschmidt, 1885, Rhenish Mountains.

**Remarks**

*Ponticeras* is, next to *Pseudoprobeloceras*, the stratigraphically oldest genus of the Gephuroceratoidea. The two genera mainly differ in the shape of the external lobe; in *Pseudoprobeloceras* it is quite narrow with a low median saddle and in *Ponticeras* it is very broad with a quite high median saddle. The genera of the closely related family Gephuroceratidae differ from *Ponticeras* in the acute lateral lobe, which is rounded in *Ponticeras*.

***Ponticeras aequabile* (Beyrich, 1837)**

Figs 4D, 8–10

*Ammonites aequabilis* Beyrich, 1837: 34, pl. 2 fig. 1.

*Gephyroceras Kayseri* Wedekind, 1918: 123, 167, pl. 21 fig. 13, text-fig. 28d.

*Goniatites aequabilis* – Roemer 1843: 34, pl. 9 fig. 14. — Sandberger & Sandberger 1850–1856: 94, pl. 8 fig. 11.

*Gephyroceras aequabile* – Wedekind 1918: 123, 167, pl. 21 figs 5–6, text-fig. 28c.

*Ponticeras aequabile* – Matern 1931: 85. — Schindewolf 1969: 47, text-fig. 7a. — House in House & Ziegler 1977: 77, pl. 1 fig. 25. — Korn & Klug 2002: 98.

*Ponticeras barroisi* – House in House & Ziegler 1977: 78, pl. 1 figs 1–2.

*Ponticeras kayseri* – House in House & Ziegler 1977: 78, pl. 1 figs 3–4, 11–12.

? *Probeloceras aequabile* – Clausen 1969: 150, pl. 24 fig. 7, text-fig. 18h, h1–h3.

non *Gephyroceras aequabile* var. nov. – Wedekind 1913: 70, pl. 6 fig. 14, text-fig. 14b.



### Diagnosis

Species of *Ponticeras* reaching about 120 mm conch diameter with extremely discoidal, subevolute conch between 40 and 60 mm dm ( $ww/dm = 0.20\text{--}0.25$ ;  $uw/dm = 0.40\text{--}0.45$ ); coiling rate low ( $WER = 1.70\text{--}1.75$ ). Whorl profile weakly compressed ( $ww/wh = 0.65\text{--}0.75$ ); umbilical wall oblique and flattened, venter narrowly rounded. Growth lines very fine, strongly biconvex. Flanks often with a spiral ridge on the outer side of the umbilicus parallel to the umbilical seam. Suture line with V-shaped external lobe; median saddle moderately high,  $E_2$  lobe small, pointed, ventrolateral saddle and lateral lobe asymmetrically rounded.

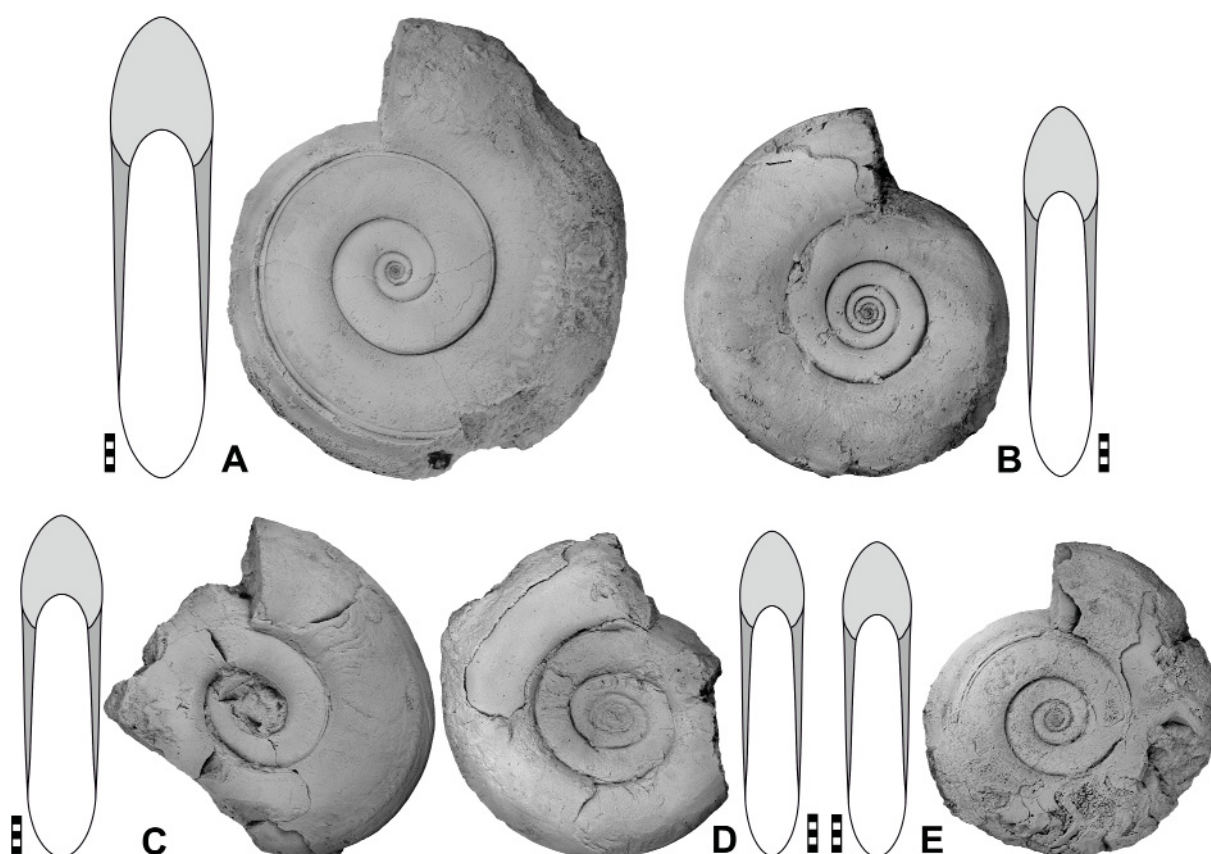
### Material examined

#### Lectotype

GERMANY • Rhenish Mountains, Oberscheld (Sessacker); late Givetian (Red Ironstone); Beyrich 1835 Coll.; MB.C.4289.1. Illustrated here in Fig. 8D.

#### Paralectotypes

GERMANY • 1 specimen; Rhenish Mountains, Oberscheld (Sessacker); late Givetian (Red Ironstone); Beyrich 1835 Coll.; MB.C.30425 • 1 specimen; Rhenish Mountains, Oberscheld; late Givetian (Red Ironstone); Beyrich 1835 Coll.; MB.C.5600.



**Fig. 8.** *Ponticeras aequabile* (Beyrich, 1837). **A.** Specimen MB.C.4291 (Koch Coll.) from Oberscheld. **B.** Specimen MB.C.4290 (Kauth Coll.) from Oberscheld. **C.** Specimen MB.C.5576 (Erbreich Coll.) from Oberscheld. **D.** Lectotype MB.C.4289.1 (Beyrich 1835 Coll.) from Oberscheld (Sessacker). **E.** Specimen MB.C.4289.2 (Erbreich Coll.) from Oberscheld. Scale bar units = 1 mm.

**Additional material**

GERMANY • 1 specimen; Rhenish Mountains, Dillenburg; late Givetian (Red Ironstone); Erbreich Coll.; MB.C.4293 • 1 specimen; Rhenish Mountains, Dillenburg; late Givetian (Red Ironstone); MB.C.30419 • 1 specimen; Rhenish Mountains, Nanzenbach (Grube Königszug); late Givetian (Red Ironstone); Dannenberg Coll.; MB.C.30420 • 2 specimens; Rhenish Mountains, Oberscheld; late Givetian (Red Ironstone); Erbreich Coll.; MB.C.4289.2, MB.C.5576 • 3 specimens; Rhenish Mountains, Oberscheld; late Givetian (Red Ironstone); Kauth Coll.; MB.C.4290, MB.C.30421.1, MB.C.30421.2 • 1 specimen; Rhenish Mountains, Oberscheld; late Givetian (Red Ironstone); Liebe Coll.; MB.C.30422 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Königszug); late Givetian (Red Ironstone); Jung 1902 Coll.; MB.C.30423 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Volpertseiche); late Givetian (Red Ironstone); Kauth Coll.; MB.C.30424 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Volpertseiche); late Givetian (Red Ironstone); Koch Coll.; MB.C.4291 • 1 specimen; Rhenish Mountains, Oberscheld (Sessacker); late Givetian (Red Ironstone); Dannenberg Coll.; MB.C.30426 • 1 specimen; Rhenish Mountains, Oberscheld (Staatliche Grube); late Givetian (Red Ironstone); Hubach 1920 Coll.; MB.C.4300 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Königszug); late Givetian (Red Ironstone); Meuhse 1855 Coll.; SMF.Mbg.2324 • 1 specimen; Rhenish Mountains, Langenaubach; late Givetian (Red Ironstone); GZG 389-82.

**Description**

Nine specimens are selected for description and illustration:

Holotype MB.C.4289.1: rather poorly preserved, worn specimen with 43 mm conch diameter in haematitic ironstone. Shell ornament barely visible (Fig. 8D).

MB.C.4291: fully septate, incomplete but rather well-preserved specimen with 61 mm conch diameter in haematitic limestone, phragmocone filled with white calcite (Fig. 8A).

MB.C.4290: rather well-preserved specimen with 50 mm conch diameter in haematitic ironstone; fully covered with shell (Fig. 8B).

MB.C.4289.2: moderately preserved specimen with 42 mm diameter in haematitic ironstone, phragmocone filled with white calcite (Fig. 8E).

MB.C.5576: incomplete specimen with 45 mm diameter in haematitic limestone; shell surface well-visible (Fig. 8C).

MB.C.30421.1: rather well-preserved, laterally deformed specimen with 36 mm conch diameter in reddish-ochre limestone; almost fully covered with shell.

MB.C.30419: sectioned specimen with 60 mm conch diameter in haematitic limestone (Fig. 9A).

Specimen SMF.Mbg.2324, the holotype of “*Gephyroceras Kayseri*”, is a specimen with 58 mm diameter (Fig. 4C).

Specimen GZG 389-82, the invalid neotype of *Ponticeras aequabile*, is an incomplete specimen with about 105 mm conch diameter in haematitic limestone (Fig. 10).

The material allows the study of conch geometry between 36 and 105 mm conch diameter. Only slight changes in proportions can be recognised in this growth interval (Fig. 9A). The conch is always extremely discoidal and subevolute to evolute ( $ww/dm = 0.20–0.25$ ;  $uw/dm = 0.39–0.47$ ) with a weak tendency towards a wider umbilicus at a larger diameter. The whorl profile of the sectioned specimen MB.C.30419

**Table 3.** Conch dimensions and ratios of selected specimens of *Ponticeras aequabile* (Beyrich, 1837).

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.4291	60.8	13.5	19.8	25.3	14.9	0.22	0.68	0.42	1.75	0.25
MB.C.4290	49.5	9.8	14.0	22.1	11.5	0.20	0.70	0.45	1.70	0.18
MB.C.5576	45.1	9.7	14.5	18.3	10.6	0.22	0.67	0.41	1.71	0.27
MB.C.4289.1	42.9	8.4	13.1	20.0	10.4	0.20	0.64	0.47	1.74	0.21
MB.C.4289.2	41.4	9.5	13.4	18.4	9.7	0.23	0.71	0.44	1.71	0.28
MB.C.30421.1	35.7	8.6	12.9	14.1	8.8	0.24	0.67	0.39	1.76	0.32

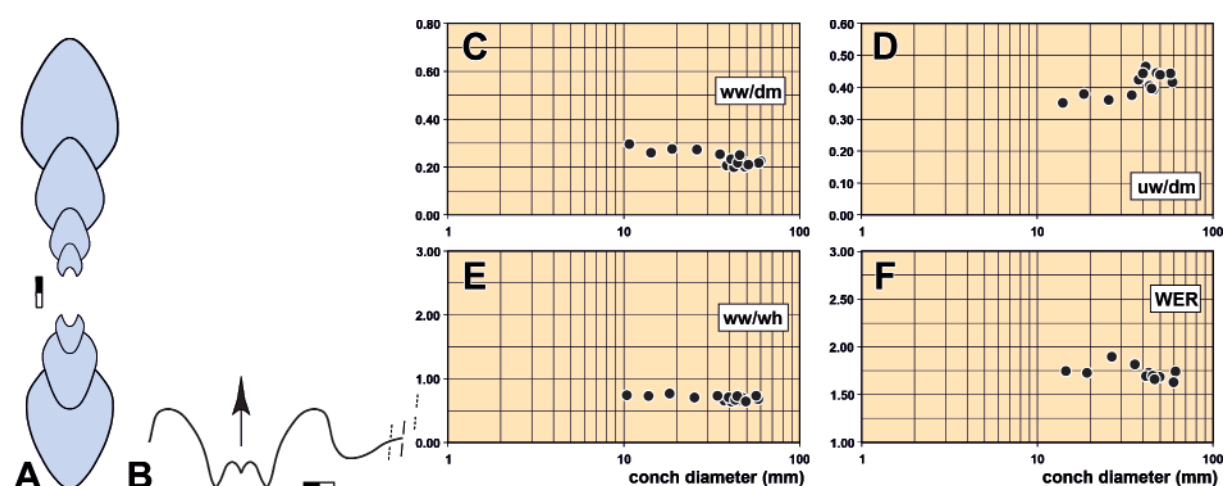
is always compressed ( $ww/wh = 0.64\text{--}0.70$ ) with a broadly rounded or slightly flattened and oblique umbilical wall, a rounded umbilical margin, strongly converging flanks and a narrowly rounded venter. Rarely, as in specimen MB.C.4290, there is a weak depression visible in the ventrolateral area (Fig. 8B).

The ornament is preserved in several specimens. In specimen MB.C.4290 the shell is decorated with irregular coarse growth lines with a strongly biconvex course; the dorsolateral projection is low, the ventrolateral projection is very high and narrow and the ventral sinus is narrow and very deep. Specimen MB.C.4291 shows three faint spiral lines in the middle flank area (Fig. 8A).

Several of the specimens, such as MB.C.4291, possess a spiral ridge, of approximately 0.5 mm width, on the midflank parallel to the umbilical seam of the next volution. In specimen MB.C.4290, such a ridge is only developed on the right side.

### Remarks

House in House & Ziegler (1977: 77: pl. 1 fig. 25) stated that the original specimen could not be traced and proposed a neotype from the Göttingen Collection (GZG 389-82), which was figured by Wedekind (1918: pl. 21 fig. 6). However, specimen MB.C.4289.1 (Beyrich 1835 Coll.) is stored in the MfN collection; it was figured by Beyrich (1837: pl. 2 fig. 1) and is re-illustrated here in Fig. 8D. As there were other specimens in the Beyrich collection, it is designated the lectotype here.



**Fig. 9.** *Ponticeras aequabile* (Beyrich, 1837). **A.** Cross section of specimen MB.C.30419 from the Dillenburg area. **B.** Suture line of lectotype MB.C.4289.1 (Beyrich 1835 Coll.) from Oberscheld (Sessacker), at  $dm = 31.5$  mm,  $wh = 10.0$  mm. **C–F.** Ontogenetic trajectories of the cardinal conch parameters. Scale bar units = 1 mm.

Wedekind (1913) regarded specimens with a weakly applanate venter as belonging to *P. aequabile* var. nov. In a later paper, Wedekind (1918) introduced the new species “*Gephyroceras Kayseri*” (Fig. 4D) that is characterised by a narrow, blunt venter but clearly shows the morphology of the lectotype of *P. aequabile*.

*Ponticeras aequabile* differs from *P. materni* sp. nov., which also occurs in the Oberscheld assemblages, in the narrowly rounded venter, which is flattened in the latter species.

*Ponticeras aequabile* is also distinguished from the other species of the genus by the closely rounded venter, which is either broadly rounded (*P. lebedeffi*, *P. uralicum*, *P. altaicum*, *P. uchtense*, *P. discoidale*), flattened (*P. auritum*) or separated from the flanks by ventrolateral longitudinal grooves (*P. tschernyschewi*, *P. domanicense*, *P. keyserlingi*, *P. regale*).



**Fig. 10.** *Ponticeras aequabile* (Beyrich, 1837); specimen GZG 389-82 from Langenaubach; the specimen erroneously proposed as neotype by House in House & Ziegler (1977). Scale bar units = 1 mm.

***Ponticeras materni* sp. nov.**

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Figs 11–12

*Gephyroceras aequabile* var. nov. – Wedekind 1913: 70, pl. 6 fig. 14, text-fig. 14b.

**Diagnosis**

Species of *Ponticeras* reaching about 80 mm conch diameter with thinly discoidal, subevolute conch at 5 mm dm (ww/dm ~ 0.45; uw/dm ~ 0.42), with extremely discoidal, subevolute conch at 15 mm dm



(ww/dm  $\sim$  0.32; uw/dm  $\sim$  0.33) and with extremely discoidal, subevolute conch at 50 mm dm (ww/dm  $\sim$  0.25; uw/dm  $\sim$  0.40); coiling rate usually low to moderately high (WER = 1.70–1.85). Whorl profile depressed in early ontogeny (ww/wh  $\sim$  1.40 at 5 mm dm) and compressed in late ontogeny (ww/wh  $\sim$  0.70 at 50 mm dm); umbilical wall oblique and broadly rounded, venter weakly flattened. Growth lines fine, rhythmically strengthened to weak plications, strongly biconvex. Sometimes with a spiral ridge on the outer side of the umbilicus parallel to the umbilical seam. Suture line with V-shaped external lobe with strongly diverging flanks; median saddle comparatively high, E<sub>2</sub> lobe deep, pointed, ventrolateral saddle and lateral lobe rounded.

### Etymology

Named after Hans Matern to honour his work on Devonian ammonoids.

### Material examined

#### Holotype

GERMANY • Rhenish Mountains, Oberscheld (Grube Volpertseiche); late Givetian (Red Ironstone); Koch Coll.; MB.C.22159. Illustrated in Fig. 11A.

#### Paratypes

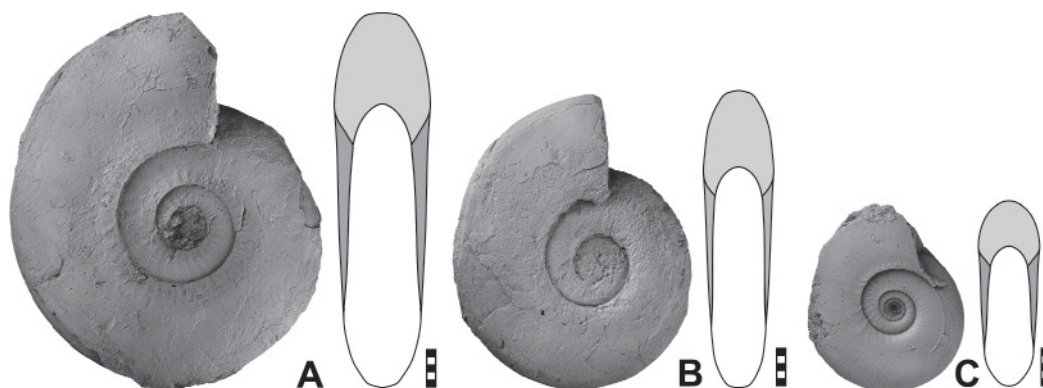
GERMANY • 1 specimen; Rhenish Mountains, Dillenburg; late Givetian (Red Ironstone); Kauth Coll.; MB.C.22178 • 1 specimen; Rhenish Mountains, Oberscheld (?); late Givetian (Red Ironstone); Dannenberg Coll.; MB.C.4297 • 1 specimen; Rhenish Mountains, Oberscheld (?); late Givetian (Red Ironstone); MB.C.22158 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Prinzkessel; late Givetian (Red Ironstone); Zimmermann 1936 Coll.; MB.C.22175 • 1 specimen; Rhenish Mountains, Oberscheld (Sessacker); late Givetian (Red Ironstone); Dannenberg Coll.; MB.C.30427.

### Description

Five specimens are selected for description and illustration:

MB.C.22159: incomplete but rather well-preserved specimen with 49 mm conch diameter in haematitic ironstone (Fig. 11A).

MB.C.22175: moderately preserved specimen with 38 mm conch diameter in haematitic ironstone; the last quarter of the last volution belongs to the body chamber (Fig. 11B).



**Fig. 11.** *Ponticeras materni* sp. nov. **A.** Holotype MB.C.22159 (Koch Coll.) from Oberscheld (Volpertseiche Mine). **B.** Paratype MB.C.22175 (Zimmermann 1936 Coll.) from Oberscheld (Prinzkessel Mine). **C.** Paratype MB.C.22178 (Kauth Coll.) from Dillenburg. Scale bar units = 1 mm.

MB.C.22178: well-preserved specimen with 25 mm conch diameter in haematitic limestone (Fig. 11C).

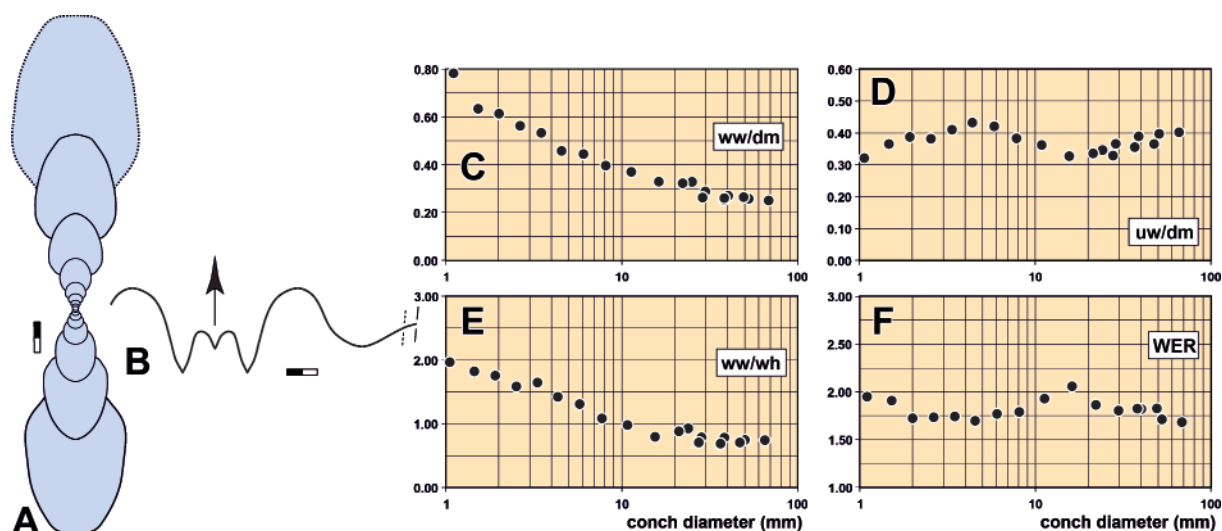
MB.C.22158: specimen with 68 mm conch diameter in micritic haematite-rich limestone; cut for a cross section (Fig. 12A).

MB.C.4297: incomplete specimen with approximately 80 mm conch diameter in micritic haematite-rich limestone.

Holotype MB.C.22159 is, at 49 mm conch diameter, extremely discoidal and subevolute (Fig. 11A); the whorl profile shows a flattened, oblique umbilical wall, a rounded umbilical margin, weakly convergent flanks with a faint longitudinal ventrolateral depression and a rounded venter that is separated from the flanks by a weakly angular shoulder. The shell ornament is not well-preserved, but it appears that growth lines are fine and only strengthened rhythmically on the umbilical wall. The penultimate whorl shows very weak, short plications on the umbilical margin. Only a small portion of the ventral suture line is visible in the specimen; it shows the shape of the external lobe typical for *Ponticeras*.

Paratype MB.C.22175 has an extremely discoidal and subevolute conch with moderate coiling rate at 38 mm diameter; the whorl profile is compressed with oblique, broadly rounded umbilical wall that continues into the broadly rounded umbilical margin (Fig. 11B). The flanks are subparallel and separated from the narrowly rounded venter by a weakly angular ventrolateral shoulder. The venter becomes subacute during the last volution. Few shell remains show biconvex growth lines that form a very high, narrow ventrolateral projection and a deep ventral sinus. The suture line has a V-shaped external lobe with a median saddle reaching almost half of the height of the lobe depth. The ventrolateral saddle is rounded; the lateral lobe reaches only 60% of the E lobe depth and is broadly rounded (Fig. 12B).

The smaller paratype MB.C.22178 with 25 mm conch diameter does not show the suture line, species assignment is thus not completely clear. However, it shows the shell ornament well-preserved with strongly concavo-convex growth lines, which form a high linguiform ventrolateral salient. As in the holotype, the growth lines are strengthened rhythmically on the umbilical wall and the umbilical margin has weak plications (Fig. 11C).



**Fig. 12.** *Ponticeras materni* sp. nov. A. Cross section of paratype MB.C.22158, probably from Oberscheld. B. Suture line of paratype MB.C.22175 (Zimmermann 1936 Coll.) from Oberscheld (Prinzkessel Mine), at dm = 29.0 mm, ww = 7.4 mm, wh = 11.1 mm. C–F. Ontogenetic trajectories of the cardinal conch parameters. Scale bar units = 1 mm.

**Table 4.** Conch dimensions and ratios of selected specimens of *Ponticeras materni* sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.22159	49.2	12.7	18.2	18.0	12.8	0.26	0.70	0.37	1.83	0.30
MB.C.22175	38.1	9.4	14.0	13.5	9.9	0.25	0.67	0.35	1.83	0.29
MB.C.22178	25.1	8.1	8.8	8.7	—	0.32	0.92	0.35	—	—
MB.C.22158	68.33	16.72	22.79	27.56	15.67	0.24	0.73	0.40	1.68	0.31
MB.C.22158	40.24	10.62	13.71	15.70	10.43	0.26	0.77	0.39	1.82	0.24
MB.C.22158	22.19	7.04	8.05	7.47	5.93	0.32	0.87	0.34	1.86	0.26
MB.C.22158	11.33	4.13	4.25	4.11	3.18	0.36	0.97	0.36	1.93	0.25
MB.C.22158	6.09	2.68	2.06	2.57	1.51	0.44	1.30	0.42	1.77	0.27
MB.C.22158	3.51	1.86	1.13	1.44	0.85	0.53	1.64	0.41	1.74	0.25
MB.C.22158	2.02	1.23	0.70	0.78	0.48	0.61	1.75	0.39	1.73	0.31
MB.C.22158	1.11	0.87	0.44	0.36	0.32	0.78	1.96	0.32	1.95	0.29

The specimens allow the study of a growth interval between 25 and nearly 60 mm diameter. The material is somewhat variable with respect to the shape of the whorl profile, which in specimens MB.C.22159 and MB.C.22158 (the sectioned one) has a slightly flattened, oblique umbilical wall and a more pronounced umbilical margin when compared with specimen MB.C.4297. The shape of the venter also shows some variation; it is more strongly flattened in specimen MB.C.22158 (Fig. 12A) than in specimen MB.C.22159 (Fig. 11A).

All of the specimens show the shell ornament, which consists of very fine but rhythmically strengthened growth lines. These have a biconvex course with a low dorsolateral projection, a wide and shallow lateral sinus, a high and narrow ventrolateral projection and a deep ventral sinus. In the immature stage between about 15 and 30 mm diameter, there are weak and short radial plications visible on the umbilical margin. In specimen MB.C.22158, a faint spiral ridge accompanies the umbilical seam.

Specimen MB.C.22158 was sectioned and allows the study of conch geometry from the initial stage up to 68 mm conch diameter (Fig. 12A). The ontogenetic trajectories of the cardinal conch parameters are strikingly different: (1) The ww/dm and the ww/wh ratios are nearly monophasic with nearly continuously decreasing values; between 1 and 68 mm conch diameter, the ww/dm ratio decreases from 0.80 to 0.24 and the ww/wh ratio from nearly 2.00 to 0.75. (2) The uw/dm trajectory is triphasic with early ontogenetic increase from 0.32 to 0.43 between 1 and 4.5 mm dm, followed by a decrease to 0.33 at 16 mm dm and an adult re-increase to 0.40 at 40 mm. The umbilical ratio then remains at this value. (3) The WER trajectory is also triphasic with an early juvenile decrease from 2.00 at 1 mm dm to 1.73 at 2 mm dm, followed by an accelerated increase to a maximum value of 2.06 at 16 mm dm and a terminal decrease to around 1.70 in the largest stage. The whorl profile is crescent-shaped in the early juvenile stage up to 2 mm diameter and then becomes increasingly compressed. At about 10 mm conch diameter, the ww/wh ratio becomes lower than 1.00. Already at 8 mm diameter, the umbilical wall becomes very flat and connects with the preceding whorl in a very small angle. At 22 mm diameter, the umbilical wall is weakly incurved, a character that is maintained until the terminal stage. The venter is narrowly rounded at 30 mm diameter, but in the last one and a half whorls, it becomes flattened and gets bordered from the flanks by a pronounced, subangular ventrolateral shoulder.

## Remarks

*Ponticeras materni* sp. nov. is similar to *P. aequabile* but differs in the flattened venter, which is narrowly rounded in the latter species. *Ponticeras materni* sp. nov. differs from the other species with a flattened venter (*P. auritum*) in the much wider umbilicus (uw/dm = 0.35–0.40 in *P. materni* sp. nov. but only ~ 0.20 in *P. auritum*).

Family **Taouzitidae** Korn, 2001

**Diagnosis**

Gephuroceratoidea with sutural formula  $(E_2 E_1 E_2) L U_2 : U_3 U_1 I$  to  $(E_2 E_1 E_2) L U_2 U_4 U_6 U_8 : U_7 U_5 U_3 U_1 I$ ; lateral saddle narrow, rounded; lateral lobe simple, rounded or acute.

**Included genera**

*Mzerrebites* Becker & House, 1994; *Darkaoceras* Bockwinkel, Becker & Ebbighausen, 2009; *Keuppites* Bockwinkel, Becker & Ebbighausen, 2009; *Taouzites* Korn, 2001.

**Remarks**

The lineage of the family Taouzitidae partly resembles the morphological evolution of two Frasnian lineages of gephyroceratids, the koenenitids and the beloceratoids (e.g., Korn 2001). However, the major difference between the taouzitids and the beloceratids is that in the taouzitids the external lobe retained its original shape, whereas in the beloceratids there was a proliferation of both the umbilical lobes and the external lobes. In the koenenitids, the external lobe remained tripartite and there was the development of only three umbilical lobes in the terminal genus *Timanites*.

Genus ***Darkaoceras*** Bockwinkel, Becker & Ebbighausen, 2009

**Type species**

*Timanites meridionalis* Petter, 1959 (original designation).

**Diagnosis**

Genus of the family Taouzitidae with extremely discoidal, subinvolute to involute conch; venter subacute or acute in the adult stage. With single ventrolateral grooves. Suture line with wide external lobe, high median saddle, V-shaped  $E_2$  lobe, V-shaped lateral lobe and shallow, rounded umbilical lobes. Suture line formula  $(E_2 E_1 E_2) L U_2 U_4 : U_3 U_1 I$ .

**Included species**

*Timanites meridionalis* Petter, 1959, Ougarta; *Timanites complanatum* Petter, 1959, Saoura Valley; *Koenenites galeatus* Matern, 1931, Rhenish Mountains; *Darkaoceras velox* Bockwinkel, Becker & Ebbighausen, 2013, Anti-Atlas.

**Remarks**

*Darkaoceras* (with subacute venter and four umbilical lobes) is morphologically intermediate between *Mzerrebites* (with narrowly rounded venter and three umbilical lobes) and *Taouzites* (with sharp venter and up to eight umbilical lobes).

***Darkaoceras galeatum*** (Matern, 1931)

Figs 13–14

*Koenenites galeatus* Matern, 1931: 75, pl. 2 fig. 11.

*Hoeninghausia galeatus* – Korn & Klug 2002: 118.

*Darkaoceras galeatum* – Bockwinkel *et al.* 2013: 261, text-figs 3–4.



### Diagnosis

Species of *Darkaoceras* reaching about 60 mm conch diameter with extremely discoidal, subinvolute conch between 30 and 50 mm dm ( $ww/dm = 0.25\text{--}0.30$ ;  $uw/dm = 0.15\text{--}0.25$ ). Whorl cross section strongly compressed ( $ww/wh = 0.45\text{--}0.60$ ); venter acute with pronounced keel. Growth lines fine, bundled around the umbilicus, strongly biconvex with moderately high dorsolateral projection and very high and narrow ventrolateral projection; ventrolateral shoulder with weak spiral groove. Suture line with high median saddle, V-shaped prongs of the E lobe, V-shaped L lobe, and shallow and rounded  $U_2$  lobe.

### Material examined

#### Holotype

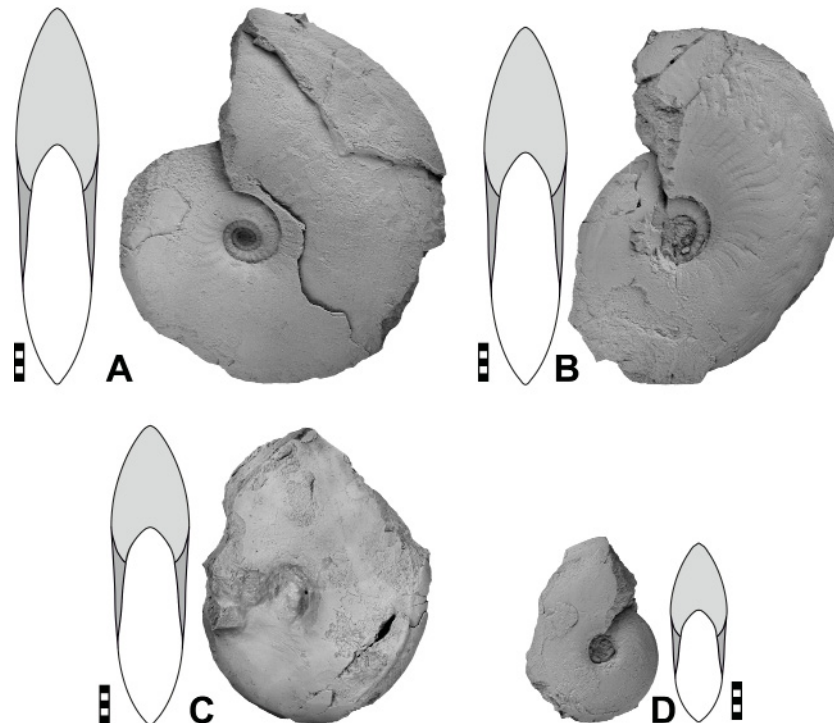
GERMANY • Rhenish Mountains, Oberscheld (Westfeld der Grube Königszug, Firste der 120–150 m-Sohle); late Givetian (Red Ironstone); Ahlburg Coll.; MB.C.3652. Illustrated by Matern (1931: pl. 2 fig. 10a, d), re-illustrated here in Fig. 13C.

#### Paratypes

GERMANY • 10 specimens; Rhenish Mountains, Oberscheld (Westfeld der Grube Königszug, Firste der 120–150 m-Sohle); late Givetian (Red Ironstone); Ahlburg Coll.; MB.C.3629, MB.C.3633, MB.C.3635, MB.C.3645, MB.C.3649, MB.C.3650, MB.C.3651, MB.C.3657, MB.C.3658, MB.C.3665.

#### Additional material

GERMANY • 1 specimen; Rhenish Mountains, Nanzenbach (Grube Königszug); late Givetian (Red Ironstone); Dannenberg Coll.; MB.C.30428 • 1 specimen; Rhenish Mountains, Oberscheld; late Givetian



**Fig. 13.** *Darkaoceras galeatum* (Matern, 1931). **A.** Specimen MB.C.3658 (Ahlburg Coll.) from Oberscheld (Königszug Mine). **B.** Specimen MB.C.3635 (Ahlburg Coll.) from Oberscheld (Königszug Mine). **C.** Holotype MB.C.3652 (Ahlburg Coll.) from Oberscheld (Königszug Mine). **D.** Specimen MB.C.30429 (Fremdling Coll.) from Oberscheld (Prinzkessel Mine). Scale bar units = 1 mm.

(Red Ironstone); Hubach Coll.; MB.C.3616 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Gründchessseite); late Givetian (Red Ironstone); Lotz 1901–1902 Coll.; MB.C.22153 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Prinzkessel); late Givetian (Red Ironstone); Fremdling Coll.; MB.C.30429.

### Description

Five specimens are selected for description and illustration:

MB.C.3658: well-preserved, slightly deformed specimen with 48 mm conch diameter in iron-rich micritic limestone; largely covered with shell (Fig. 13A).

MB.C.3635: laterally deformed specimen with 48 mm conch diameter in iron-rich micritic limestone; largely covered with shell (Fig. 13B).

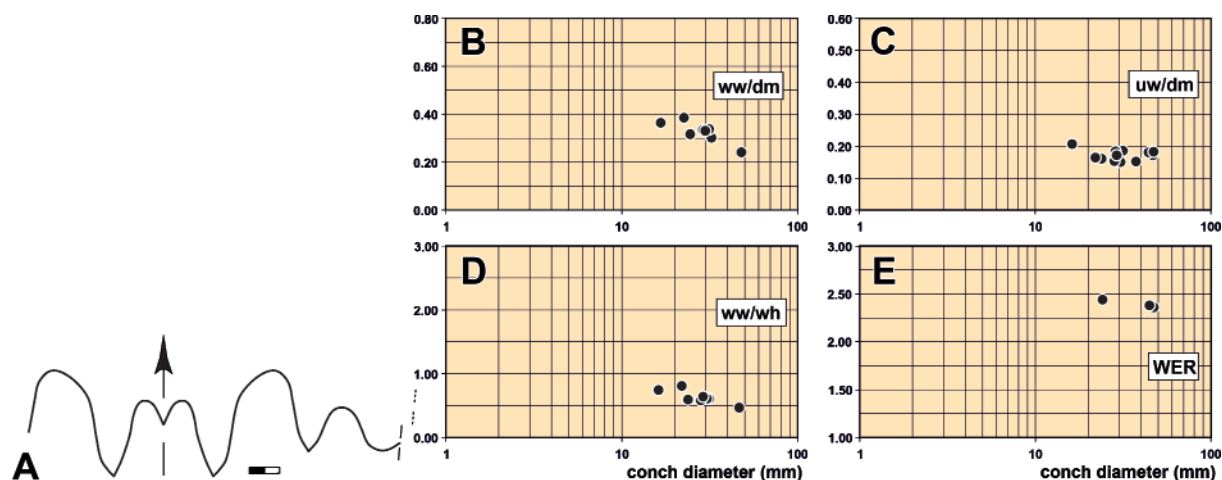
MB.C.3633: deformed specimen with about 50 mm conch diameter in iron-rich micritic limestone; cut for a cross section but inner whorls not preserved. Outer suture line visible (Fig. 14A).

Holotype MB.C.3652: rather poorly preserved, slightly deformed specimen with about 42 mm conch diameter in iron-rich micritic limestone; specimen suffered from rough preparation (Fig. 13C).

MB.C.30429: incomplete, slightly deformed specimen with 24 mm conch diameter in iron-rich sparitic limestone; partly covered with shell (Fig. 13D).

The two specimens MB.C.3658 and MB.C.3635, both with about 48 mm conch diameter, have an extremely discoidal and subinvolute conch with very high coiling rate and strongly compressed whorl profile (Fig. 13A–B). The umbilical wall is very shallow and the flanks converge towards the subacute venter. The ornament consists of fine growth lines with biconvex course; the ventrolateral projection is high and narrow. Faint short riblets are present around the umbilicus.

The suture line of specimen MB.C.3633 has a wide external lobe; this is subdivided by a median saddle that has a height of two thirds of the external lobe depth (Fig. 14A). The prongs of the external lobe are slightly asymmetric and V-shaped. On the flank follows a V-shaped lateral lobe and, on the umbilical margin, a broadly rounded umbilical lobe.



**Fig. 14.** *Darkaoceras galeatum* (Matern, 1931). A. Suture line of specimen MB.C.3633 (Ahlburg Coll.) from Oberscheld (Königszug Mine), at  $ww = 10.7$  mm,  $wh = 16.5$  mm. B–E. Ontogenetic trajectories of the cardinal conch parameters. Scale bar units = 1 mm.

**Table 5.** Conch dimensions and ratios of selected specimens of *Darkaoceras galeatum* (Matern, 1931).

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.3658	47.9	11.1	24.1	8.2	16.8	0.23	0.46	0.17	2.37	0.30
MB.C.3635	45.3	11.0	22.1	8.2	16.0	0.24	0.50	0.18	2.39	0.28
MB.C.3652	29.8	9.6	15.2	5.1	–	0.32	0.63	0.17	–	–
MB.C.3657	28.9	9.4	15.5	4.4	10.1	0.33	0.61	0.15	2.36	0.35
MB.C.30429	24.5	7.5	12.9	3.9	8.9	0.31	0.59	0.16	2.45	0.31

### Remarks

The specimens from Dillenburg are quite large; smaller specimens from 3 up to 38 mm conch diameter were described by Bockwinkel *et al.* (2013b) from Hagen-Herbeck, northern margin of the Rhenish Mountains.

A similar species to *D. galeatum* is *D. meridionale*, but this species differs in having slightly thicker inner whorls. *D. velox* Bockwinkel, Becker & Ebbighausen, 2013 also differs by the broader inner whorls.

Genus *Taouzites* Korn, 2001

### Type species

*Pharciceras taouzensis* Termier & Termier, 1950 (original designation).

### Diagnosis

Genus of the family Taouzitidae with extremely discoidal, involute conch; venter acute in the adult stage. With single ventrolateral grooves in the juvenile and pre-adult stage. Suture line with wide external lobe, high median saddle, lanceolate  $E_2$  lobe, V-shaped lateral lobe and acute or rounded umbilical lobes. Suture line formula formula ( $E_2$   $E_1$   $E_2$ ) L  $U_2$   $U_4$   $U_6$   $U_8$ : $U_7$   $U_5$   $U_3$   $U_1$  I.

### Included species

*Pharciceras taouzensis* Termier & Termier, 1950, Anti-Atlas; *Taouzites acutus* Matern, 1931, Rhenish Mountains; *Eobeloceras palentinum* Yatskov, 1990, Cantabrian Mountains.

### Remarks

*Taouzites* presents the morphological end member of an evolutionary series in the Givetian, which, starting from simple gephuoceratids, is characterised by a flattening of the conch with a sharpening venter and simultaneous proliferation of the umbilical lobes (Korn 2001).

*Taouzites acutus* (Matern, 1931)

Fig. 15

*Pharciceras acutum* Matern, 1931: 88, pl. 2 fig. 8.

*Taouzites acutus* – Korn & Klug 2002: 99.

**Diagnosis**

Species of *Taouzites* reaching about 60 mm conch diameter with extremely discoidal, involute conch at 30 mm dm (ww/dm ~ 0.30; uw/dm ~ 0.10); coiling rate very high (WER ~ 2.40). Whorl profile strongly compressed (ww/wh ~ 0.55); umbilical wall oblique and flattened, venter sharply acute. Growth lines very fine, strongly biconvex. Suture line with wide external lobe, high, narrow median saddle, pointed  $E_2$  and  $E_4$  lobes and rounded lateral and umbilical saddles and lobes.

**Material examined****Holotype**

GERMANY • Rhenish Mountains, Oberscheld (“Tiefe Grube”); late Givetian (Red Ironstone); Etzold 1910 Coll.; MB.C.3664. Illustrated by Matern (1931: pl. 2 fig. 8), re-illustrated here in Fig. 15A.

**Paratype**

GERMANY • Rhenish Mountains, Oberscheld (“Tiefe Grube”); late Givetian (Red Ironstone); Etzold 1910 Coll.; MB.C.30430.

**Additional material**

GERMANY • 1 specimen; Rhenish Mountains, Oberscheld (Grube Königszug); late Givetian (Red Ironstone); Krecke 1903 Coll.; MB.C.22193.

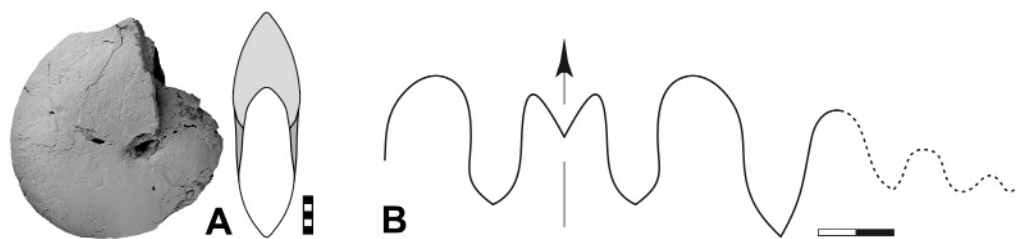
**Description**

Two specimens are selected for description and illustration:

Holotype MB.C.3664: slightly deformed specimen with 29 mm conch diameter in tuffitic ironstone (Fig. 15A).

MB.C.22193: fragmentary specimen with 56 mm diameter in haematitic, micritic limestone.

Holotype MB.C.3664 has a thinly discoidal and involute conch with very high coiling rate (Fig. 15A). The whorl profile strongly compressed; the umbilical wall is very shallow and the flanks converge towards the acute venter that possesses a fine keel. Rather coarse growth lines with biconvex course are visible on the flanks; they extend with a low dorsolateral projection and a high, narrow ventrolateral projection. The suture line possesses a wide, parallel-sided external lobe, a V-shaped lateral lobe, a small and V-shaped  $U_2$  lobe and a shallow, rounded  $U_4$  lobe (Fig. 15B).



**Fig. 15.** *Taouzites acutus* (Matern, 1931). Holotype MB.C.3664 (Etzold 1910 Coll.) from Oberscheld (“Tiefe Grube”). **A.** Lateral view and dorsal projection. **B.** Suture line, at dm ca 9 mm, ww = 3.0 mm, wh = 4.5 mm. Scale bar units = 1 mm.



**Table 6.** Conch dimensions and ratios of *Taouzites acutus* (Matern, 1931).

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.3664	28.7	9.0	16.3	3.1	10.2	0.31	0.55	0.11	2.41	0.37

### Remarks

*Taouzites acutus* resembles *T. taouzensis* from the Anti-Atlas but, at a comparable diameter (30 mm) the conch dimensions are different in *T. taouzensis* with  $ww/dm = 0.25$ ,  $uw/dm = 0.15$ ,  $ww/wh = 0.45$ ,  $WER = 2.60$ .

Family **Koenenitidae** Becker & House, 1993

### Diagnosis

Family of the superfamily Gephuroceratoidea with discoidal conch with moderately narrow to closed umbilicus; rounded venter in early species but acute venter in late species. Growth lines with high ventrolateral projection. Sutural evolution with proliferation of umbilical lobes during phylogeny. Sutural formula  $(E_2 E_1 E_2) L U_2 : U_1 I$  to  $(E_2 E_1 E_2) L U_2 : U_3 U_1 I$ ; lateral lobe simple, usually V-shaped.

### Included genera

*Koenenites* Wedekind, 1913; *Hoeninghausia* Gürich, 1896; *Timanites* Mojsisovics, 1882; *Protimanites* Ljaschenko, 1956 (synonym of *Hoeninghausia*); *Komioceras* Bogoslovsky, 1958.

Genus **Koenenites** Wedekind, 1913

### Type species

*Goniates lamellosus* Sandberger & Sandberger, 1851 (original designation).

### Diagnosis

Genus of the family Koenenitidae with extremely discoidal, subinvolute to involute conch; venter rounded in all stages. Suture line with wide external lobe, moderately high median saddle, narrowly V-shaped  $E_2$  lobe, U-shaped or V-shaped lateral lobe and rounded umbilical lobes. Suture line formula  $(E_2 E_1 E_2) L U_2 : U_1 I$ .

### Included species

*Goniates lamellosus* Sandberger & Sandberger, 1851, Rhenish Mountains; *Koenenites baoshanensis* Yang, 1984, Yunnan; *Koenenites cooperi* Miller, 1938, Michigan; *Koenenites lamellosus kirchgasseri* House, 1978, West Virginia; *Manticoceras Pattersopni* var. *styliophilus* Clarke, 1899, New York; *Goniates sublamellosus* Sandberger & Sandberger, 1851, Rhenish Mountains (synonym of *Koenenites lamellosus* (Sandberger & Sandberger, 1851)); *Koenenites uralensis* Bogoslovsky, 1969, North Urals.

### Remarks

*Koenenites* is the only genus of the family Koenenitidae in which the conch has a rounded venter. *Koenenites*, along with *Hoeninghausia*, also has the simplest suture line in the family with only two umbilical lobes.

***Koenenites lamellosus*** (Sandberger & Sandberger, 1851)

Figs 16–18

*Goniatites lamellosus* Sandberger & Sandberger, 1851: 88, pl. 8 fig. 1, 1a–d.

? *Goniatites Höninghausi* – von Buch 1832: 40, pl. 2 figs 3–4. — Bronn 1835: 107, pl. 1 fig. 1.

*Goniatites sublamellosus* Sandberger & Sandberger 1851: 87, pl. 2 fig. 2, 2a–c.

*Koenenites lamellosus* – Wedekind 1913: 42; 1918: 126. — Matern 1931: 74, pl. 2 fig. 7. — House 1978: 48, pl. 7 figs 3, 5. — Dzik 2002: text-figs 50a–e, 56c–h. — Korn & Klug 2002: 118, text-fig. 118a–b.

*Koenenites sublamellosus* – Wedekind 1918: 126. — Matern 1931: 74. — Korn & Klug 2002: 118, text-fig. 118c.

non *Koenenites lamellosus* – Petter 1959: 157, pl. 10 fig. 14, text-fig. 41a.

**Diagnosis**

Species of *Koenenites* reaching about 90 mm conch diameter with thickly discoidal, evolute conch at 5 mm dm (ww/dm ~ 0.50; uw/dm ~ 0.45); coiling rate moderate (WER ~ 1.85); with thinly discoidal, subinvolute conch at 20 mm dm (ww/dm ~ 0.40; uw/dm ~ 0.28); with extremely discoidal, subinvolute conch at 75 mm dm (ww/dm ~ 0.25; uw/dm ~ 0.23); coiling rate moderate at 5 mm dm (WER ~ 1.85) and very high above 30 mm dm (WER ~ 2.40). Whorl profile compressed (ww/wh ~ 0.50) in the adult stage; umbilical wall steep and rounded, venter rounded. Growth lines lamellar, strongly biconvex with very narrow, high ventrolateral projection. Suture line simple, with V-shaped external lobe, high median saddle, pointed asymmetrical prongs of the E lobe, slightly asymmetrically rounded lateral saddle and pointed L lobe.

**Material examined**

**Lectotype**

GERMANY • Rhenish Mountains, Nanzenbach; early Frasnian (Red Ironstone); Wiesb. 40a. Illustrated by Sandberger & Sandberger (1850–1856: pl. 8 fig. 1) and Korn & Klug (2002: text-fig. 108a), re-illustrated here in Fig. 16A.

**Paralectotype**

GERMANY • Rhenish Mountains, Nanzenbach; early Frasnian (Red Ironstone); Wiesb. 40b. Illustrated by Sandberger & Sandberger (1850–1856: pl. 8 fig. 1a–c) and Korn & Klug (2002: text-fig. 108b), re-illustrated here in Fig. 16D.

**Additional material**

GERMANY • 4 specimens; Rhenish Mountains, Oberscheld (Grube Anna); early Frasnian (Red Ironstone); Koch Coll.; MB.C.4306.1, MB.C.34306.2, MB.C.4306.3, MB.C.22184 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Königszug, 120 m-Sohle); early Frasnian (Red Ironstone); MB.C.22201 • 2 specimens; Rhenish Mountains, Oberscheld (Grube Rinkenbach); early Frasnian (Red Ironstone); Dannenberg Coll.; MB.C.22183, MB.C.22189a–b • 1 specimen; Rhenish Mountains, Oberscheld (Sessacker); early Frasnian (Red Ironstone); Dannenberg Coll.; MB.C.30431 • 2 specimens; Rhenish Mountains, Oberscheld (Staatliche Grube); early Frasnian (Red Ironstone); Hubach 1913 Coll.; MB.C.4303.2, MB.C.4303.3.

**Description**

Eight specimens are selected for description and illustration:

Lectotype Wiesb. 40a: incomplete specimen with 65 mm conch diameter in haematitic ironstone (Fig. 16A).

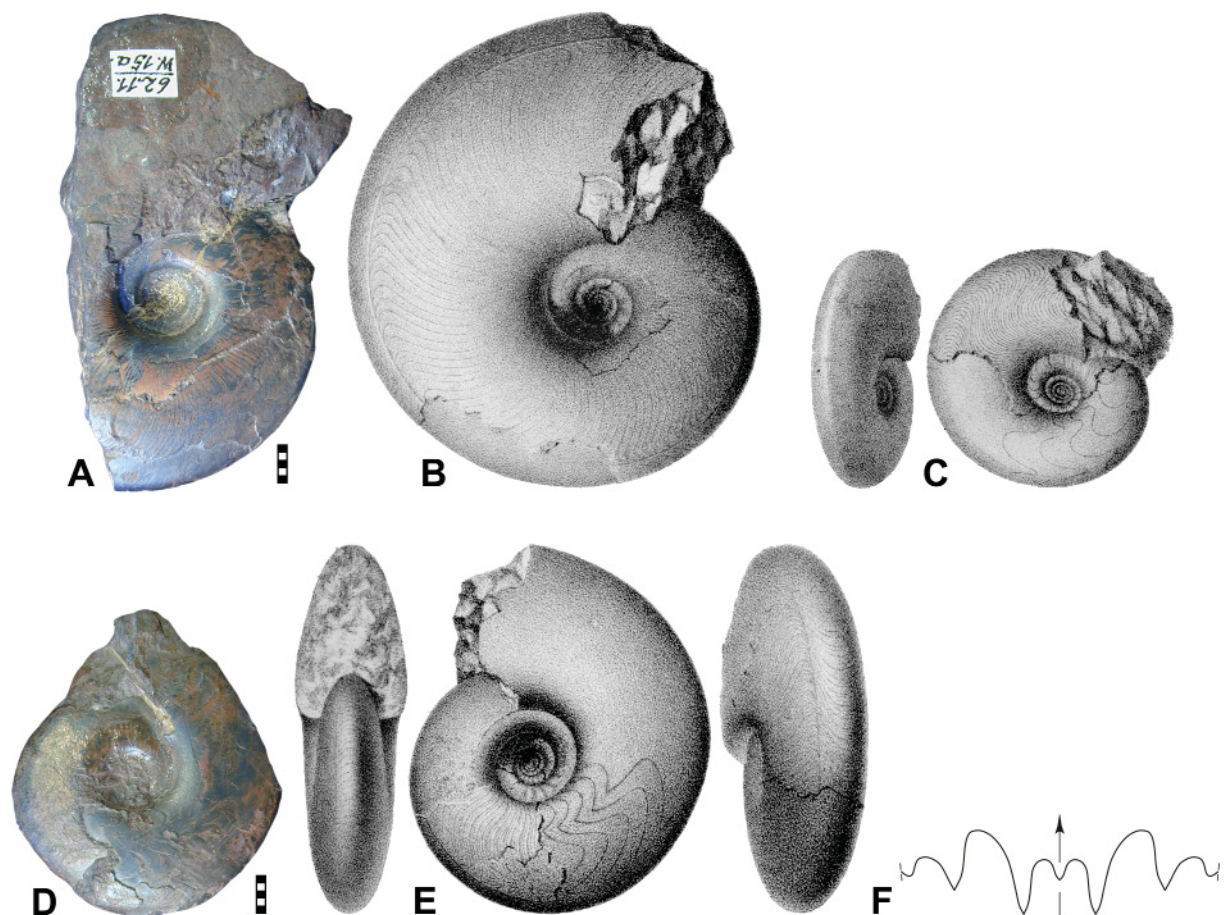
Paratype Wiesb. 40b: incomplete specimen with about 50 mm conch diameter in haematitic ironstone (Fig. 16D).

MB.C.22184: incomplete specimen with 73 mm conch diameter in haematitic iron ore, the last whorl is partly crushed (Fig. 17A).

MB.C.22183: incomplete specimen with 53 mm conch diameter in haematitic ironstone (Fig. 17B).

MB.C.22201: sectioned specimen with 77 mm conch diameter in haematite ore (Fig. 18A).

MB.C.4306.1: well-preserved, complete steinkern specimen with 36 mm conch diameter in haematitic ironstone (Fig. 17C).



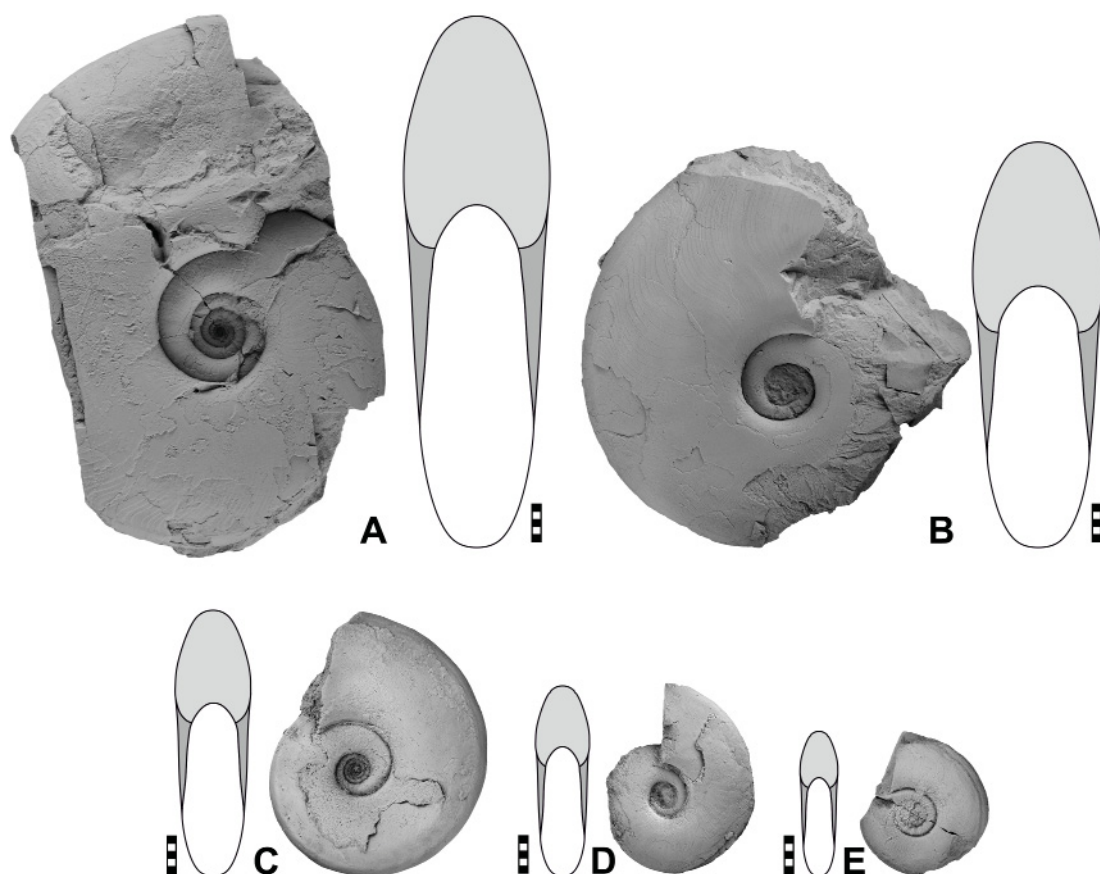
**Fig. 16.** *Koenenites lamellosus* (Sandberger & Sandberger, 1851). **A.** Lectotype 40a in the Wiesbaden collection from Nanzenbach. **B.** Lectotype 40a, reproduction of the figure of Sandberger & Sandberger (1850–1856: pl. 8 fig. 1). **C.** Probably lost specimen, original of “*Goniatites sublamellosus*”, reproduction of the figure of Sandberger & Sandberger (1850–1856: pl. 6 fig. 2, 2a). **D.** Paratype 40b in the Wiesbaden collection from Nanzenbach. **E.** Paratype 40b, reproduction of the figure of Sandberger & Sandberger (1850–1856: pl. 8 fig. 1a–1c). **F.** Suture line of paratype 40b, reproduction of the figure of Sandberger & Sandberger (1850–1856: pl. 8 fig. 1d). Scale bar units = 1 mm.

MB.C.4306.2: well-preserved, complete specimen with 25 mm conch diameter in haematitic ironstone, ornament perfectly preserved (Fig. 17D).

MB.C.4306.3: well-preserved, complete specimen with 20 mm conch diameter in haematitic ironstone, ornament perfectly preserved (Fig. 17E).

The three specimens MB.C.4306.1, MB.C.4306.2 and MB.C.4306.3 allow the study of conch proportions and ornament between 19 and 36 mm diameter (Fig. 17C-E). They are similar in shape with a weak ontogenetic trend towards a slenderer conch (ww/dm decreasing from 0.35 to 0.29). They show an oblique, broadly convex umbilical wall and flanks that converge slowly towards the narrowly rounded venter. The ornament shows lamellar growth lines, which in the two smaller specimens MB.C.4306.2 and MB.C.4306.3 are particularly well-preserved; they extend with a low dorsolateral projection, a deep and wide lateral sinus and a very narrow, very high linguiform ventrolateral projection across the flanks and then turn back to form a narrow, very deep ventral sinus.

The larger specimens MB.C.22183 (53 mm dm) and MB.C.22184 (73 mm dm) are thinly discoidal and subinvolute with a compressed whorl profile; the umbilical wall is steep and the flanks converge towards the narrowly rounded venter (Fig. 17A–B). The ornament shows biconvex growth lines,



**Fig. 17.** *Koenenites lamellosus* (Sandberger & Sandberger, 1851). A. Specimen MB.C.22184 (Koch Coll.) from Oberscheld (Anna Mine). B. Specimen MB.C.22183 (Dannenberg Coll.) from Oberscheld (Rinkenbach Mine). C. Specimen MB.C.4306.1 (Koch Coll.) from Oberscheld (Anna Mine). D. Specimen MB.C.4306.2 (Koch Coll.) from Oberscheld (Anna Mine). E. Specimen MB.C.4306.3 (Koch Coll.) from Oberscheld (Anna Mine). Scale bar units = 1 mm.

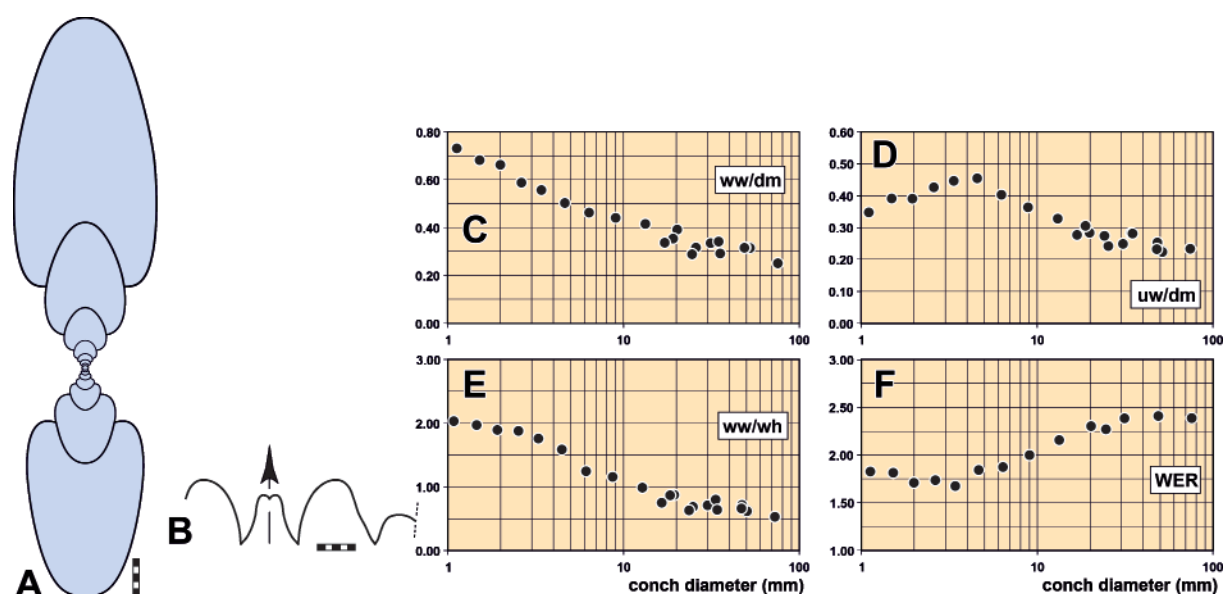


**Table 7.** Conch dimensions and ratios of selected specimens of *Koenenites lamellosus* (Sandberger & Sandberger, 1851).

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.22183	53.0	16.5	26.6	11.8	—	0.31	0.62	0.22	—	—
MB.C.4306.1	36.0	10.4	16.1	10.1	12.6	0.29	0.64	0.28	2.37	0.22
MB.C.4306.2	24.9	7.1	11.2	6.8	8.4	0.29	0.63	0.27	2.28	0.28
MB.C.4306.3	19.4	6.8	7.8	5.9	—	0.35	0.87	0.30	—	—
MB.C.22201	76.36	18.85	35.50	17.71	27.02	0.25	0.53	0.23	2.39	0.24
MB.C.22201	31.74	10.54	14.79	7.85	11.22	0.33	0.71	0.25	2.39	0.24
MB.C.22201	13.50	5.56	5.62	4.42	4.33	0.41	0.99	0.33	2.17	0.23
MB.C.22201	6.48	2.98	2.38	2.61	1.75	0.46	1.25	0.40	1.88	0.26
MB.C.22201	3.47	1.93	1.09	1.55	0.80	0.55	1.77	0.45	1.68	0.27
MB.C.22201	2.03	1.34	0.71	0.79	0.48	0.66	1.90	0.39	1.72	0.32
MB.C.22201	1.15	0.84	0.41	0.40	0.30	0.73	2.04	0.35	1.83	0.27

which are fine on the inner flank and lamellar on the outer flank. They extend with a moderately high dorsolateral projection and a high and subangular ventrolateral projection. The external sinus is deep and semicircular. The suture line is partly visible in specimen MB.C.22184, showing a V-shaped lateral lobe on the inner flank (Fig. 18B).

The sectioned specimen MB.C.22201 (Fig. 18A) shows significant ontogenetic changes in the conch parameters: (1) the ww/dm ratio has a nearly monophasic ontogeny with a rather continuous decrease from 0.75 at 1 mm dm to = 0.25 at 77 mm dm. (2) The ww/wh ratio has a similar course (from 2.05 to 0.50) but with more accelerated decrease between 3 and 10 mm dm. (3) The uw/dm ratio is conspicuously biphasic with a juvenile increase from 0.35 to 0.45 at 5 mm dm and an adult decrease to 0.23. (4) The coiling rate is also biphasic, but not parallel to the uw/dm ratio; the WER shows a juvenile decrease



**Fig. 18.** *Koenenites lamellosus* (Sandberger & Sandberger, 1851). **A.** Cross section of specimen MB.C.22201 from Oberscheld (Königszug Mine). **B.** Suture line of specimen MB.C.22184 (Koch Coll.) from Oberscheld (Anna Mine), at dm = 29.0 mm, ww = 7.4 mm, wh = 11.1 mm. **C–F.** Ontogenetic trajectories of the cardinal conch parameters. Scale bar units = 1 mm.



to 1.68 at 3.5 mm dm, followed by a decelerated increase with asymptotic approximation of a value of 2.40 at 30 mm dm (Fig. 18C–F). The ontogeny of the whorl profile is rather simple with a continuous transformation of a depressed shape into a compressed shape; the value falls below a value of 1.00. Above this diameter, the whorl profile has a steep umbilical wall, a broadly rounded umbilical margin, moderately strong converging flanks and a rounded venter.

### Remarks

Matern (1931: 74, pl. 2 fig. 7) proposed a neotype from the Senckenberg Collection (specimen XI329a) and stated that the original specimen is missing. However, two syntypes figured by Sandberger & Sandberger (1850–1856) are preserved (specimens 40a = old 62.11./W.15a and 40b = old 62.11./W.15b) in the Sandberger collection, which is stored at the Wiesbaden Museum. House (1978: 48, pl. 7 fig. 5) designated specimen 40a as the lectotype; it was illustrated by Sandberger & Sandberger (1850–1856: pl. 8 fig. 1) and is re-illustrated here (Fig. 16A).

Sandberger & Sandberger (1850–1856) described the two new species “*Goniatites sublamellosus*” and “*Goniatites lamellosus*”, which apparently are conspecific. Of these two, mostly “*G. lamellosus*” was re-figured and is therefore here used as the valid species (despite the page priority of “*G. sublamellosus*”).

Superfamily Belocerataceae Hyatt, 1884

Family **Acanthoclymeniidae** Schindewolf, 1955

### Diagnosis

Family of the superfamily Beloceratoidea with sutural formula ( $E_2 E_1 E_2$ ) L U : I; lateral saddle narrow, narrowly rounded to subacute; lateral lobe simple, rounded.

### Included genera

*Acanthoclymenia* Hyatt, 1900; *Prochorites* Clausen, 1969; *Eidoproboloceras* Kirchgasser, 1968 (nomen nudum; synonym of *Prochorites*); *Proboloceras* Clarke, 1899.

Genus ***Acanthoclymenia*** Hyatt, 1900

### Type species

*Clymenia* (*Cyrtoclymenia*) *Neapolitana* Clarke, 1892 (original designation).

### Diagnosis

Genus of the family Acanthoclymeniidae with extremely discoidal, subinvolute to subevolute conch; venter flattened or concave. Suture line with relatively narrow wide lobe, moderately high median saddle, V-shaped  $E_2$  lobe, shallow and rounded lateral lobe. Suture line formula ( $E_2 E_1 E_2$ ) L : U I.

### Included species

*Clymenia* (*Cyrtoclymenia*) *Neapolitana* Clarke, 1892, New York; *Goniatites forcipifer* Sandberger & Sandberger, 1851, Rhenish Mountains; *Goniatites Genundewa* Clarke, 1879, New York; *Goniatites Planorbis* Sandberger & Sandberger, 1851, Rhenish Mountains.

### Remarks

In the description of the type species as well as its assignment to a genus, it was erroneously assumed that it was a clymeniid; this error was corrected by House (1961) and the species was classified among the gephuroceratids, although in the genus *Manticoceras*.

*Acanthoclymenia* is considered the stratigraphically earliest and morphologically simplest genus of the superfamily Beloceratoidea (Korn & Klug 2002). It still has a suture line of the early gephuroceratids (for example *Ponticeras*), consisting of a divided external lobe and a lateral, umbilical and internal lobe each. The genus is distinguished from the ponticeratids by the concave venter; a character that persists in subsequent forms of the Beloceratoidea.

*Acanthoclymenia forcipifera* (Sandberger & Sandberger, 1851)

Figs 19–20

*Goniatites forcipifer* Sandberger & Sandberger, 1851: 81, pl. 6 fig. 3.

*Gephyroceras forcipiferum* – Wedekind 1913: 51; 1918: 122, text-fig. 28f.

*Ponticeras forcipiferum* – Matern 1931: 84.

*Probeloceras forcipiferum* – House in House & Ziegler 1977: 80, pl. 3 figs 28–29.

*Acanthoclymenia forcipifer* – Korn & Klug 2002: 119, text-fig. 123d.

*Acanthoclymenia genundewa* – Dzik 2002: text-fig. 50f–i.

non *Probeloceras forcipiferum* – Petter 1959: 155, pl. 11 figs 11–12, text-fig. 40e. — Ruan 1981: 42, pl. 9 figs 1–5, 8, text-fig. 16.

### Diagnosis

Species of *Acanthoclymenia* reaching about 40 mm conch diameter with extremely discoidal, subinvolute conch between 12 and 28 mm dm ( $ww/dm = 0.20\text{--}0.25$ ;  $uw/dm \sim 0.28$ ); coiling rate very high (WER increasing from 2.25 to 2.60). Whorl profile strongly compressed ( $ww/wh \sim 0.50$ ); umbilical wall shallow and rounded, whorl profile pear-shaped, ventrolateral margin angular, venter flat or slightly concave. Growth lines very fine, strongly biconvex.

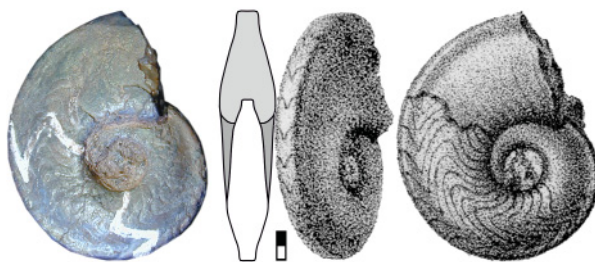
### Material examined

#### Lectotype

GERMANY • Rhenish Mountains, Oberscheld; early Frasnian (Red Ironstone); Wiesb. 36a. Illustrated by Sandberger & Sandberger (1850–1856: pl. 6 fig. 3), re-illustrated by House in House & Ziegler (1977: pl. 3 figs 28–29) and here (Fig. 19).

#### Additional material

GERMANY • 1 specimen; Rhenish Mountains, Oberscheld (Eiserne Hand, Betagrube); early Frasnian (Red Ironstone); Trempel Coll.; MB.C.30432 • 1 specimen; Rhenish Mountains, Oberscheld (Eiserne Hand, Grube Friedrich); early Frasnian (Red Ironstone); Kegel Coll.; MB.C.3669 • 9 specimens; Rhenish



**Fig. 19.** *Acanthoclymenia forcipifera* (Sandberger & Sandberger, 1851); lectotype 36a in the Wiesbaden collection from Oberscheld; photograph, dorsal reconstruction and reproduction of the figure of Sandberger & Sandberger (1850–1856: pl. 6 fig. 3, 3a). Scale bar units = 1 mm.

Mountains, Oberscheld (Grube Anna); early Frasnian (Red Ironstone); Koch Coll.; MB.C.22199.1, MB.C.22199.2, MB.C.22199.3, MB.C.22200, MB.C.30433.1, MB.C.30433.2, MB.C.30433.3 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Sahlgrund, 205 m-Sohle); early Frasnian (Red Ironstone); MB.C.30434 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Stillingseisenzug); early Frasnian (Red Ironstone); Möbus 1901 Coll.; MB.C.30435 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Ypsilanta); early Frasnian (Red Ironstone); Etzold 1910 Coll.; MB.C.30436 • 1 specimen; Rhenish Mountains, Oberscheld (Grube Ypsilanta); early Frasnian (Red Ironstone); Lotz 1901–1902 Coll.; MB.C.30437.

### Description

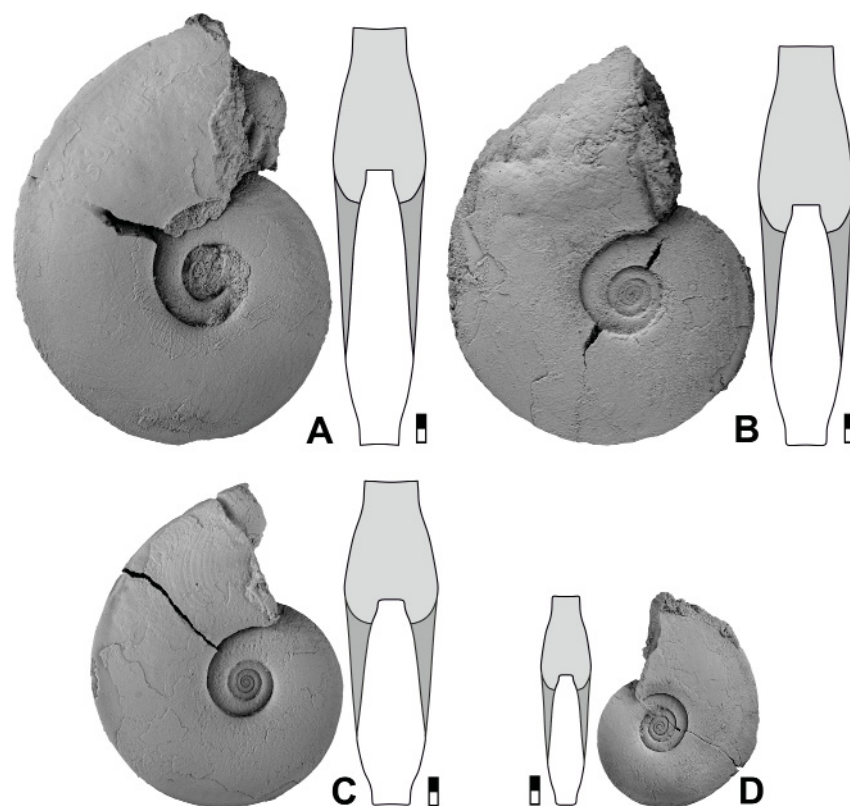
Six specimens are selected for description and illustration:

Lectotype Wiesb. 36a: fully septate specimen with 16 mm conch diameter in haematitic ironstone (Fig. 19).

MB.C.22199.1: rather well-preserved specimen with 28 mm conch diameter in haematitic iron ore; largely covered with shell (Fig. 20A).

MB.C.22199.2: well-preserved, slightly deformed specimen with 14 mm conch diameter in haematitic iron ore; largely covered with shell (Fig. 20D).

MB.C.30433.1: well-preserved, slightly deformed specimen with 27 mm conch diameter in haematitic iron ore; largely covered with shell (Fig. 20B).



**Fig. 20.** *Acanthoclymenia forcipifera* (Sandberger & Sandberger, 1851), all Koch Coll from Oberscheld (Anna Mine). **A.** Specimen MB.C.22199.1. **B.** Specimen MB.C.30433.1. **C.** Specimen MB.C.30433.2. **D.** Specimen MB.C.22199.2. Scale bar units = 1 mm.

**Table 8.** Conch dimensions and ratios of selected specimens of *Acanthoclymenia forcipifera* (Sandberger & Sandberger, 1851).

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.22199.1	27.5	6.2	11.7	7.4	10.4	0.22	0.52	0.27	2.60	0.11
MB.C.30433.1	26.3	6.3	12.2	6.6	10.0	0.24	0.51	0.25	2.61	0.18
MB.C.30433.2	21.4	5.0	9.6	5.6	7.9	0.23	0.52	0.26	2.53	0.17
MB.C.22199.2	13.6	3.2	6.0	3.9	4.6	0.24	0.54	0.29	2.27	0.24

MB.C.30433.2: well-preserved, slightly deformed specimen with 22 mm conch diameter in haematitic iron ore; largely covered with shell (Fig. 20C).

MB.C.30433.3: fragmentary specimen co-occurring in a block of haematitic iron ore together with a specimen *Crickites* Wedekind, 1913.

The specimens MB.C.22199.2 (14 mm dm), MB.C.30433.2 (22 mm dm), MB.C.30433.1 (27 mm dm) and MB.C.22199.1 (28 mm dm) show that, during this growth interval, no significant changes in the conch proportions can be recognised (Fig. 20). The conchs are extremely discoidal and subinvolute with very high coiling rate; the whorl profile is compressed. The umbilical wall is very shallow; the flanks converge towards the angular ventrolateral shoulder, the outer flanks are weakly incurved and the venter is flat. The ornament consists of fine growth lines with biconvex course; they extend with a very low dorsolateral projection on the umbilical margin and a high and narrow ventrolateral projection across the flanks. Faint short riblets are present around the umbilicus.

### Remarks

When Sandberger & Sandberger (1850–1856) described the new species *Goniatites forcipifer*, they did not make it clear whether the species name (“carrying a fire tong”) was a noun or an adjective. Since such species names are usually considered adjectives, we here decline it to the feminine form.

*Acanthoclymenia forcipifera* differs from the second species of the genus from Oberscheld, *A. planorbis* (Sandberger & Sandberger, 1851), in the much narrower umbilicus at 12 mm conch diameter ( $uw/dm \sim 0.30$  in *A. forcipifera* but  $\sim 0.50$  in *A. planorbis*).

### *Acanthoclymenia planorbis* (Sandberger & Sandberger, 1851) Figs 21–22

*Goniatites planorbis* Sandberger & Sandberger, 1851: 96, pl. 9 fig. 3.

*Gephyroceras planorbis* – Wedekind 1918: 122.

*Ponticeras planorbis* – Matern 1931: 83.

*Acanthoclymenia planorbis* – Korn & Klug 2002: 119, text-fig. 123h.

### Diagnosis

Species of *Acanthoclymenia* reaching about 30 mm conch diameter with small, extremely discoidal, evolute conch between 12 and 32 dm ( $uw/dm$  decreasing from  $\sim 0.50$  to  $\sim 0.45$ ). Whorl profile compressed; umbilical wall shallow and rounded, whorl profile pear-shaped, ventrolateral margin angular, venter flat. Growth lines very fine, strongly biconvex.

**Material examined****Lectotype**

GERMANY • Rhenish Mountains, Oberscheld; middle Frasnian (Red Ironstone); Wiesb. 46a. Illustrated by Sandberger & Sandberger (1850–1856: pl. 9 fig. 3a); re-illustrated here (Fig. 21A).

**Paralectotype**

GERMANY • 1 specimen; Rhenish Mountains, Oberscheld; middle Frasnian (Red Ironstone); Wiesb. 46b. Illustrated by Sandberger & Sandberger (1850–1856: pl. 9 fig. 3) re-illustrated here (Fig. 21B).

**Additional material**

GERMANY • 1 specimen; Rhenish Mountains, Oberscheld (Grube Königszug); middle Frasnian (Red Ironstone); Kauth Coll.; MB.C.30438 • 1 specimen; Rhenish Mountains, Oberscheld; middle Frasnian (Red Ironstone); Koch Coll.; MB.C.30439.

**Description**

Four specimens are selected for description and illustration:

Lectotype Wiesb. 46a: incomplete specimen with 32 mm conch diameter in haematitic ironstone (Fig. 21A).

Paralectotype Wiesb. 46b: incomplete specimen with 22 mm conch diameter in haematitic ironstone (Fig. 21B).

MB.C.30438: slab and counterslab with two specimens (13 and 7 mm conch diameter) co-occurring with *Mesobeloceras kayseri* in haematite ore (Fig. 22A).

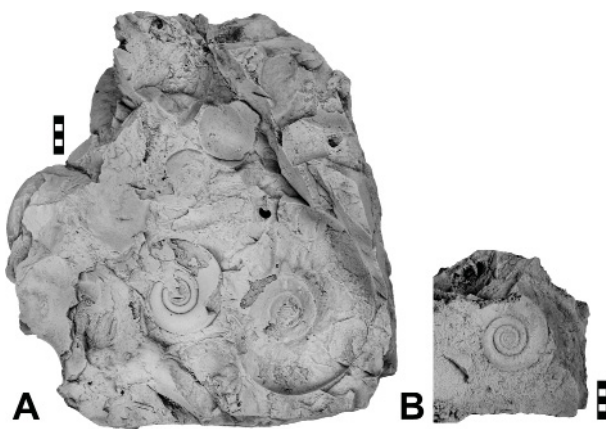
MB.C.30439: moderately well-preserved specimen with 12 mm conch diameter in haematitic iron ore (Fig. 22B).

The specimens contribute only little to our knowledge of the species. All are embedded on rock slabs (Fig. 22), which prevents precise measurement of the whorl width, but it is clear that the conch is extremely discoidal. It is also clear that the whorl profile is pear-shaped with a rounded umbilical wall, convex flanks, a subangular ventrolateral shoulder and a flattened venter. The umbilicus has nearly exactly half the value of the conch diameter.



**Fig. 21.** *Acanthochymenia planorbis* (Sandberger & Sandberger, 1851). **A.** Lectotype 46a in the Wiesbaden collection from Oberscheld; photograph and reproduction of the figure of Sandberger & Sandberger (1850–1856: pl. 9 fig. 3a). **B.** Paratype 46b in the Wiesbaden collection from Oberscheld; photograph and reproduction of the figure of Sandberger & Sandberger (1850–1856: pl. 9 fig. 3). **C.** Probably lost specimen; photograph and reproduction of the figure of Sandberger & Sandberger (1850–1856: pl. 9 fig. 3d, e). Scale bar units = 1 mm.





**Fig. 22.** *Acanthoclymenia planorbis* (Sandberger & Sandberger, 1851). **A.** Specimen MB.C.30438 (Koch Coll.) from Oberscheld. **B.** Specimen MB.C.30439 (Kauth Coll.) from Oberscheld (Königszug Mine). Scale bar units = 1 mm.

### Remarks

*Acanthoclymenia planorbis* differs from the other species of the genus from Oberscheld, *A. forcipifera*, in the much wider umbilicus at 12 mm conch diameter ( $uw/dm \sim 0.50$  in *A. planorbis* but  $\sim 0.30$  in *A. forcipifera*).

### Discussion

The red ironstone of Dillenburg has been considered of great importance in the study of the late Middle Devonian and early Late Devonian ammonoids. Already in the 19<sup>th</sup> century (von Buch 1832; Beyrich 1837; d'Archiac & de Verneuil 1842; Sandberger & Sandberger 1850–1856) and at the beginning of the 20<sup>th</sup> century (Wedekind 1918) further species were described. Afterwards, the decline of ore mining also led to a decrease in palaeontological work.

Time-equivalent ammonoid assemblages were then studied from the Anti-Atlas of Morocco (Petter 1959; Bensaïd 1974; Bockwinkel *et al.* 2009, 2013a, 2015, 2017). Finally, monographs on new finds at various localities in the Rhenish Mountains (Bockwinkel *et al.* 2013b; Bockwinkel & Korn 2015, 2017) were published.

In the meantime, two monographs on the ammonoids of the Red Ironstone have been published; these dealt with the suborders Pharciceratina (Korn & Bockwinkel 2021) and Tornoceratina (Korn & Bockwinkel 2022). In a third step of the revision, we here present the re-description of the ammonoids of the suborder Gephuroceratina, of which eight species are described. All belong to genera that are also known from other regions; the greatest similarity at the generic level is with the Anti-Atlas of Morocco. However, there is apparently no agreement concerning the species.

The species described here come from three stratigraphic intervals, in ascending order: (1) *Pseudoproboloceras pernai* Zone (latest Givetian; genera *Pseudoproboloceras* Bensaïd, 1974, *Ponticeras*, *Darkaoceras* and *Taouzites*) and (2) *Koenenites lamellosus* Zone (early Frasnian; genera *Koenenites* and *Acanthoclymenia*) and (3) *Mesobeloceras kayseri* Zone (middle Frasnian), containing *Acanthoclymenia planorbis*). They can therefore be easily correlated with occurrences in other regions, for example the Anti-Atlas.

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