European Journal of Taxonomy 885: 156–194
https://doi.org/10.5852/ejt.2023.885.2199
CC BY
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2023 · Korn D. & Klug C.

This work is licensed under a Creative Commons Attribution License (CC BY 4.0).

**Research article**

urn:lsid:zoobank.org:pub:8432EEFF-391F-4778-81F6-14F3F6ECAA5F

# Early Carboniferous coiled nautiloids from the Anti-Atlas (Morocco)

Dieter KORN[1,*] & Christian KLUG[2]

[1] Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity, Invalidenstraße 43, 10115 Berlin, Germany.
[2] Paläontologisches Institut und Museum, Universität Zürich, Karl-Schmid-Strasse 4, 8006 Zürich, Switzerland.

[*] Corresponding author: dieter.korn@mfn.berlin
[2] Email: chklug@pim.uzh.ch

[1] urn:lsid:zoobank.org:author:286CA4F3-7EBC-4AEF-A66A-B2508D001367
[2] urn:lsid:zoobank.org:author:79F365F0-C05A-42F6-8EBD-CEB60B08381C

**Abstract.** Viséan coiled nautiloids from North Africa are only poorly known. From the Mougoui Ayoun, Zrigat and Hamou-Rhanem formations of the eastern Anti-Atlas, we describe coiled nautiloids, which belong to the genera *Rineceras*, *Stroboceras*, *Temnocheilus*, *Vestinautilus*, *Maccoyoceras*, *Endolobus*, *Epidomatoceras*, *Liroceras*, *Ephippioceras*, and *Solenochilus*. The new species *Temnocheilus imazighenorum* sp. nov., *Temnocheilus aubrechtovae* sp. nov., *Vestinautilus kesslerae* sp. nov., *Endolobus rota* sp. nov., *Epidomatoceras ebbighausenorum* sp. nov., *Liroceras vermis* sp. nov., *Liroceras karaouii* sp. nov., *Ephippioceras pygops* sp. nov., *Solenochilus lucynae* sp. nov. and *Solenochilus pohlei* sp. nov. are described; six taxa are kept in open nomenclature. The assemblage is composed of the three superfamilies Trigonoceratoidea, Clydonautiloidea and Aipoceratoidea and shows a wide spectrum of conch morphologies, ranging from widely umbilicate compressed forms to involute compact forms, reflecting a broad ecological variation.

**Keywords.** Nautiloidea, Nautilida, Early Carboniferous, Morocco, morphology.

Korn D. & Klug C. 2023. Early Carboniferous coiled nautiloids from the Anti-Atlas (Morocco). *European Journal of Taxonomy* 885: 156–194. https://doi.org/10.5852/ejt.2023.885.2199

## Introduction

Coiled nautiloids are rarities in the cephalopod-bearing Carboniferous rocks of the Anti-Atlas of Morocco. While ammonoids have been collected in large quantities from distinct stratigraphic units (Delépine 1941; Korn *et al.* 1999, 2002, 2003, 2007; Klug & Korn 2001; Bockwinkel & Ebbighausen 2006; Klug *et al.* 2006, 2016; Ebbighausen & Bockwinkel 2007), nautiloids appear to occur in only small numbers and were described only once in a short paper (Delépine 1939). In that article, he described two large specimens that he attributed to the species "*Phacoceras oxystomum* (Phillips, 1836)" and "*Domatoceras planotergatum* (M'Coy, 1844)". They were collected by Clariond in the vicinity of Erfoud and co-occurred with ammonoids named "*Goniatites striatus*" and "*Goniatites crenistria*". These two ammonoids were revised (Korn *et al.* 1999, 2005) and attributed to the species *Maxigoniatites saourensis*

(Pareyn, 1961) and *Goniatites lazarus* Korn, Klug & Mapes, 2005. Clariond's material probably came from a locality 12 km south of the Dar Kaoua Oasis (between the roads leading to Hassilabied and Merzouga), which yielded the ammonoid assemblage described by Delépine (1941).

Here, we describe some coiled nautiloids from the eastern Anti-Atlas to contribute to the knowledge about the stratigraphic and geographic distribution of these cephalopods during the Carboniferous. These nautiloids, which amount to only about 50 specimens in total, came from Late Viséan strata and represent only a small part of collections of hundreds of cephalopod specimens. Remarkably, remains of cephalopods with orthoconic conchs are similarly rare, in contrast to the Devonian strata of the area (cf. Pohle & Klug 2018).

We do not claim to provide a complete overview of the diversity of Carboniferous coiled nautiloids of the northern Gondwana Shelf, since outcrops of Carboniferous strata are vast in the greater Sahara region. The experience of the field work in the Tafilalt of Morocco showed that only a very low number of newly discovered specimens lead to a remarkable increase in the number of species exhibiting an impressive morphological disparity. The limiting factor in determining the diversity is the rarity of the specimens of coiled nautiloids. Accordingly, future collections will certainly lead to a further increase in the number of species.

## Material and methods

The nautiloids described in this paper were collected at four places (Fig. 1) from three rock formations (Fig. 2):

(1) 18 km south-east of Rissani; surface collections with co-occurring *Maxigoniatites saourensis* (Pareyn, 1961) (Korn *et al.* 1999, 2007; Klug *et al.* 2016); basal Mougoui Ayoun Formation (Late Viséan). – One specimen of *Solenochilus lucynae* sp. nov. A small suite of specimens from the area east and south-east of Rissani was purchased from Driss Karaoui (Hassilabied). – One specimen of *Rineceras* sp. 2, one specimen of *Stroboceras* sp., one specimen of *Temnocheilus aubrechtovae* sp. nov.,

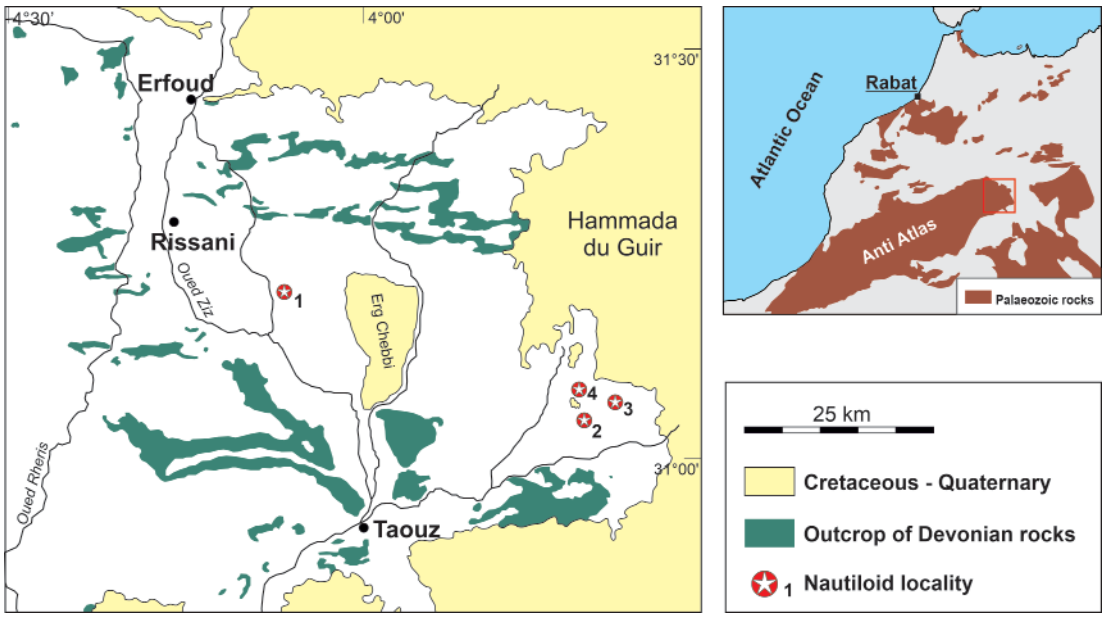


**Fig. 1.** Geographic position of the fossil sites with the nautiloid specimens in the eastern Anti-Atlas of Morocco.

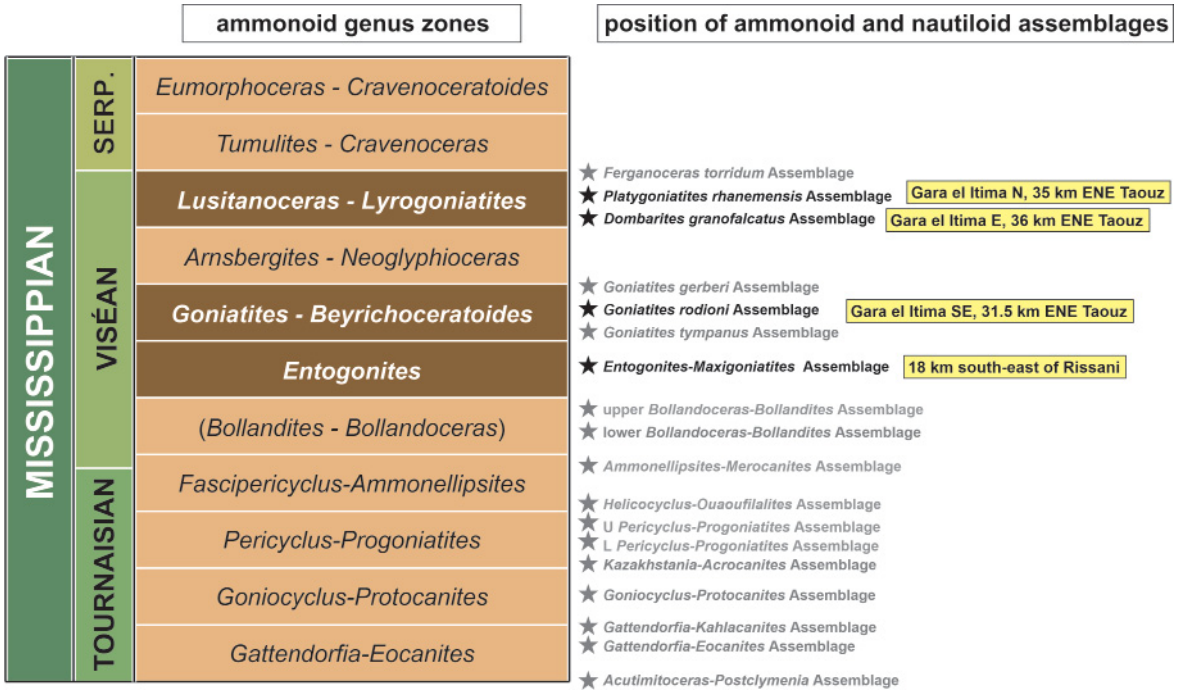


**Fig. 2.** Stratigraphic position of the fossil sites with the nautiloid assemblages described here.

one specimen of *Temnocheilus* sp., one specimen of *Liroceras karaouii* sp. nov., two specimens of *Solenochilus pohlei* sp. nov. and two specimens of *Solenochilus* sp.

(2) South-east of Gara el Itima, 31.5 km east-northeast of Taouz; surface collection with co-occurring *Beyrichoceras* sp.; Zrigat Formation (Late Viséan). – One specimen of *Vestinautilus kesslerae* sp. nov., one specimen of *Maccoyoceras* sp., one specimen of *Endolobus rota* sp. nov. and one specimen of *Endolobus* sp.

(3) East of Gara el Itima, 36 km east-northeast of Taouz; surface collection with co-occurring *Revilloceras granofalcatum* (Kullmann, 1961) (Klug *et al.* 2006); uppermost part of the Zrigat Formation (Viséan–Serpukhovian boundary interval). – One specimen of *Temnocheilus imazighenorum* sp. nov. and one specimen of *Ephippioceras pygops* sp. nov.

(4) North of Gara el Itima, 35 km east-northeast of Taouz; surface collection from one single horizon with co-occurring *Platygoniatites rhanemensis* Korn & Ebbighausen, 2006 (Klug *et al.* 2006); basal Hamou-Rhanem Formation (Viséan–Serpukhovian boundary interval). – Two specimens of *Rineceras* sp. 1, nineteen specimens of *Epidomatoceras ebbighausenorum* sp. nov. and five specimens of *Liroceras vermis* sp. nov.

The description of the specimens follows the terminology of conch, ornament and suture line proposed by Korn (2010) and Klug *et al.* (2015) for the description of ammonoids (Fig. 3). The terminology of conch geometry used here largely corresponds to that proposed by Teichert (1964). The only differences are in the following terms: umbilical angle or shoulder (= umbilical margin) and umbilical area (= umbilical width).

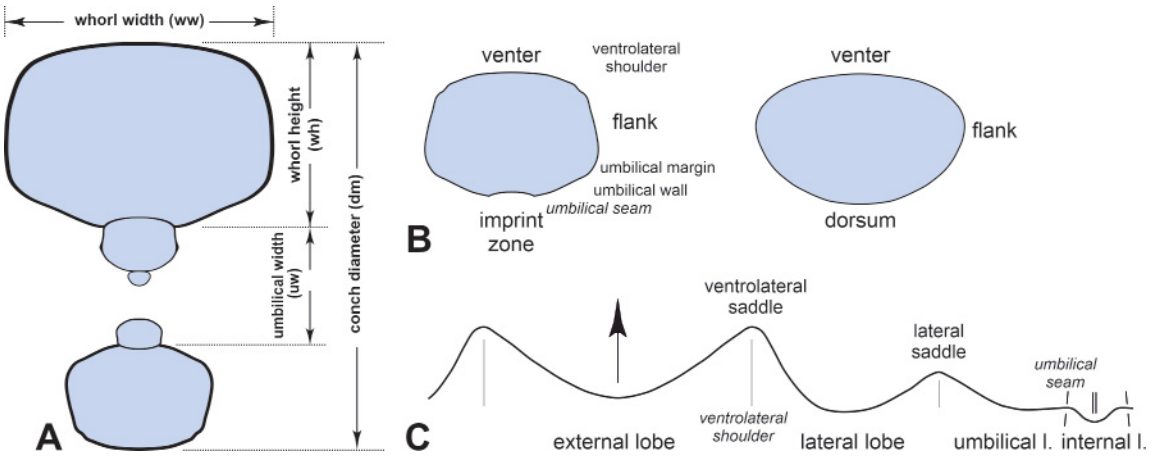


**Fig. 3.** The conch and suture line parameters used in the taxonomic descriptions. **A**. Conch parameters. **B**. Descriptive terms of whorl profiles. **C**. Suture line terminology.

**Abbreviations used in the species descriptions:**

| | | |
|---|---|---|
| ah | = | apertural height |
| dm | = | conch diameter |
| IZR | = | imprint zone rate |
| MB.C. | = | Fossil cephalopod collection of the Museum für Naturkunde, Berlin |
| PIMUZ | = | Fossil invertebrate collection of the Paläontologisches Institut, Zürich |
| uw | = | umbilical width |
| WER | = | whorl expansion rate |
| wh | = | whorl height |
| ww | = | whorl width |

## Results

Order Nautilida Agassiz, 1847
Suborder Tainoceratina Shimansky, 1957
Superfamily Trigonoceratoidea Hyatt, 1884

Family **Trigonoceratidae** Hyatt, 1884

**Remarks**

The extent and content of genera in the family Trigonoceratidae has been repeatedly debated over the past few decades, and several very different views have been expressed (e.g., Flower & Kummel 1950; Shimansky 1957, 1967; Kummel 1964; Dzik 1984; Histon 1999). Differences of opinion are partly related to the treatment and evaluation of the poorly understood family Koninckioceratidae Hyatt in Zittel, 1900. In this context, two genera (*Temnocheilus* M'Coy, 1844 and *Endolobus* Meek & Worthen, 1865) are particularly problematic and have been assigned to different families by different authors. For example, *Temnocheilus* has been placed in the families Temnocheilidae Mojsisovics, 1902, Koninckioceratidae, and Tainoceratidae Hyatt, 1883. However, the great resemblance to *Vestinautilus* Ryckholt, 1852 and other members of the family Trigonoceratidae suggests that *Temnocheilus* should also be included in this family.

Genus ***Rineceras*** Hyatt, 1893

**Type species**

*Gyroceras propinquum* de Koninck, 1880; subsequent designation by Foord (1900).

**Diagnosis**

Genus of the family Trigonoceratidae with usually discoidal subevolute to evolute conch; whorls detached or slightly in contact; whorl profile elliptical or rounded triangular with broad venter. Conch moderately to rapidly increasing in height with a high coiling rate (WER usually higher than 2.00). Ornament with coarse growth lines and coarse spiral ridges; coarse granulation at the crossing points of growth lines and spiral ridges. Septa without inflexions, rather deeply concave. Suture line with shallow external and lateral lobes. Siphuncle small with subcentral position (after Kummel 1964; Shimansky 1967; emended).

**Included Early Carboniferous species**

Early Carboniferous species of *Rineceras* are known from a number of regions such as:

North America (Meek & Worthen 1860; Miller & Garner 1953): *Nautilus* (*Discus*) *digonus* Meek & Worthen, 1860, Indiana; *Rineceras ohioense* Miller & Garner, 1953, Ohio.

Northern and Central Europe (Fleming 1828; de Koninck 1844, 1880; Holzapfel 1889; Schmidt 1951; Turner 1954): *Nautilus Luidii* Fleming, 1828, Derbyshire; *Gyroceras Meyerianum* de Koninck, 1844, Belgium; *Gyroceras propinquum* de Koninck, 1880, Belgium; *Nautilus rhenanus* Holzapfel, 1889, Rhenish Mountains; *Triboloceras patteiskyi* Schmidt, 1951, Rhenish Mountains; *Pararineceras balladoolense* Turner, 1954, Isle of Man.

North Africa (Korn & Bockwinkel 2022; Korn *et al.* 2022): *Rineceras multituberculatum* Korn, Miao & Bockwinkel, 2022, Algeria; *Rineceras rectangulatum* Korn, Miao & Bockwinkel, 2022, Algeria; *Rineceras tenerum* Korn & Bockwinkel, 2022, Algeria.

Western Russia, Urals and Kazakhstan (Eichwald 1857; Kruglov 1933; Shimansky 1967): *Nautilus canaliculatus* von Eichwald, 1857, South Urals; *Nautilus carinatus* von Eichwald, 1857, Western Russia; *Rhineceras alapaevskensis* Kruglov, 1933, Urals; *Rineceras carinatiforme* Shimansky, 1967, Kazakhstan.

**Remarks**

For a discussion of the composition and limits of the genus, see Korn *et al.* (2022) and Korn & Bockwinkel (2022).

***Rineceras*** sp. 1
Fig. 4A

**Material examined**

MOROCCO • 2 specimens; Anti-Atlas, north of Gara el Itima, 35 km east-northeast of Taouz; basal Hamou-Rhanem Formation; Ebbighausen & Korn 2004 Coll.; MB.C.31293.1–2.

**Description**

Specimen MB.C.31293.1 is a fragment of about a quarter of a whorl of the body chamber (Fig. 4A); it has a whorl width of 23 mm, which may correspond to a conch diameter of 60 mm. The weakly

depressed whorl profile (ww/wh ~ 1.25) is rounded-trapezoidal with a flattened venter, a broadly rounded ventrolateral shoulder and a broadly rounded umbilical wall. The whorl overlap zone is very small (IZR ~ 0.10).

The fragment shows the well-preserved shell ornament with 14 spiral ridges on each side from the midventer to the umbilical seam; the ridges are irregularly spaced on the venter but almost equally spaced on the ventrolateral margin and umbilical wall. The growth lines, which extend with a deep, rounded V-shaped sinus across the venter, are much finer than the spiral ridges. They are occasionally strengthened to form a conspicuous granulation; at the crossing with the spiral ridges, they form slightly elongate spines.

***Rineceras*** sp. 2
Fig. 4B

**Material examined**

MOROCCO • 1 specimen; Anti-Atlas, region south-west of Rissani; basal Mougoui Ayoun Formation; Karaoui Coll.; PIMUZ 39510.

**Description**

Specimen PIMUZ 39510 is mostly an internal mould (Fig. 4B), which has a conch diameter of 42.5 mm and is 14 mm wide with an umbilicus 20.5 mm wide (uw/dm ~ 0.40). The body chamber and last three chambers are partly embedded in a sideritic nodule. It has a depressed rounded-triangular whorl profile with flattened venter. Flanks and venter bear longitudinal equidistant ridges (5 on the umbilical wall, 3 to 4 on the flank and 2 between the ventrolateral ridges); a granulation is visible at some places at the crossing points of spiral ridges and growth lines.

Genus ***Stroboceras*** Hyatt, 1884

**Type species**

*Gyroceras Hartii* Dawson, 1868; original designation.

**Diagnosis**

Genus of the family Trigonoceratidae with discoidal, subevolute to evolute conch; whorls slightly embracing, outer whorl may lose contact to the penultimate whorl. Adult conch with a polygonal whorl

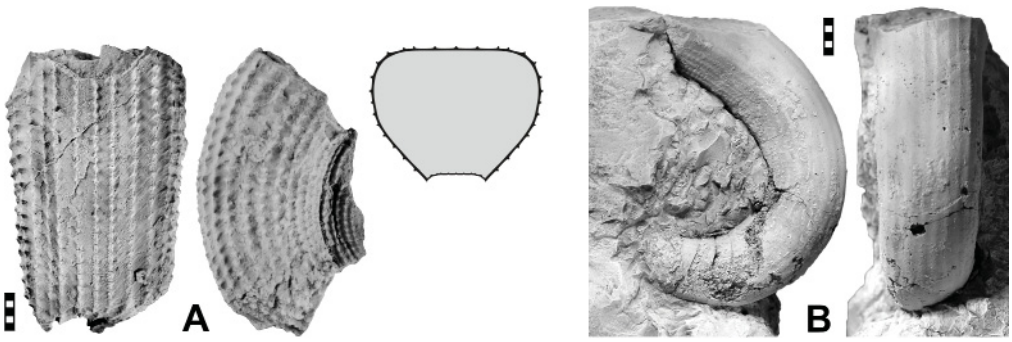


**Fig. 4.** Specimens of *Rineceras* Hyatt, 1893. **A**. *Rineceras* sp. 1; specimen MB.C.31293.1 (Ebbighausen & Korn 2004 Coll.) from Gara el Itima N; ventral and lateral views, and whorl profile. **B**. *Rineceras* sp. 2; specimen PIMUZ 39510 (Karaoui Coll.) from south-east of Rissani; lateral and ventral views. Scale bar units = 1 mm.

profile; venter slightly convex, flattened, less often slightly concave, flanks almost flat or irregularly concave, dorsum slightly concave. Conch moderately to rapidly increasing in height with a high coiling rate (WER usually higher than 2.00). Prominent longitudinal keels usually well developed, separated by concave zones. Suture line with small lobes and saddles reflecting keels and longitudinal grooves on the surface of the conch. Siphuncle small with subcentral position between septum centre and venter (after Shimansky 1967; emended).

**Included species**

A review of the species belonging to *Stroboceras* has been given by Korn & Bockwinkel (2022). Species of the genus have been described from the following regions:

North America (Dawson 1868; Miller & Garner 1953; Niko & Mapes 2005): *Gyroceras Hartii* Dawson, 1868, Nova Scotia; *Stroboceras intermedium* Miller & Garner, 1953, Michigan; *Stroboceras gordoni* Niko & Mapes, 2005, Arkansas.

Northern and Central Europe (Hyatt 1893; Schmidt 1951; Ramsbottom & Moore 1961): *Stroboceras anglicum* Hyatt, 1893, Yorkshire; *Coelonautilus humerosus* Schmidt, 1951, Rhenish Mountains; *Stroboceras trifer* Schmidt, 1951, Silesia; *Stroboceras evansi* Ramsbottom & Moore, 1961, Ireland.

North Africa (Korn & Bockwinkel 2022): *Stroboceras mane* Korn & Bockwinkel, 2022, Algeria; *Stroboceras ancilis* Korn & Bockwinkel, 2022, Algeria.

Western Russia and Urals (Murchison *et al.* 1845; Eichwald 1857; Shimansky 1967): *Nautilus bicarinatus* de Verneuil in Murchison *et al*., 1845, South Urals; *Nautilus ammoneus* Eichwald, 1857, South Urals; *Stroboceras mstense* Shimansky, 1967, Moscow Basin.

**Remarks**

For a discussion of the composition and limits of the genus, see Korn & Bockwinkel (2022).

***Stroboceras*** sp.
Fig. 5

**Material examined**

MOROCCO • 1 specimen; Anti-Atlas, region south-west of Rissani; basal Mougoui Ayoun Formation; Karaoui Coll.; PIMUZ 39512.

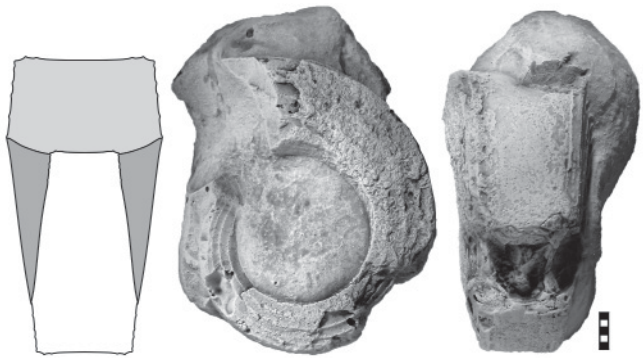

**Fig. 5.** *Stroboceras* sp., specimen PIMUZ 39512 (Karaoui Coll.) from south-east of Rissani; reconstruction of apertural view, lateral and ventral views. Scale bar units = 1 mm.

**Description**

The single specimen PIMUZ 39512 has a conch diameter of 42 mm and is embedded in a siderite nodule (Fig. 5). Less than a whorl of the evolute conch (uw/dm ~ 0.47 to 0.54) is available for study; this shows an angular and depressed whorl profile (ww/wh ~ 1.40) with flattened, weakly convergent flanks and a flattened, slightly concave venter. The ventrolateral shoulder and umbilical margin are subangular. There are six longitudinal ridges on the flank, the outer ones forming the umbilical margin and the ventrolateral shoulder, respectively. Additionally, there are two ridges on the outside of each venter, followed by some much finer lines towards the plane of symmetry. A slight granulation is produced on the ridges by the growth lines, which are somewhat reinforced here.

Genus ***Temnocheilus*** M'Coy, 1844

**Type species**

*Nautilus* (*Temnocheilus*) *coronatus* M'Coy, 1844; subsequent designation by Hyatt (1883–1884).

**Diagnosis**

Genus of the family Trigonoceratidae with discoidal to pachyconic, usually subevolute conch. The first whorl is about 30 mm in diameter with an umbilical foramen about 12 mm wide; the conch is rapidly increasing in height with a high coiling rate (WER usually higher than 2.00). Whorls weakly embracing, their profile triangular with more or less angular umbilical margin. Sculpture with longitudinal tubercles along the ventral margin. Septa usually without inflexions, rather deeply concave. Suture line with shallow ventral and deeper lateral, rounded internal lobe. The siphuncle has a position between the centre of the aperture and the venter (after Shimansky 1967).

**Included Early Carboniferous species**

Most of the species of *Temnocheilus* are known from Late Carboniferous and Permian strata (Shimansky 1967: 98). Early Carboniferous species are known from three regions:

British Isles (Sowerby 1821; M'Coy 1844; Hind 1914; Platt 1938): *Nautilus tuberculatus* Sowerby, 1821, Scotland; *Nautilus* (*Temnocheilus*) *coronatus* M'Coy, 1844, Ireland; *Temnocheilus derbiensis* Hind, 1914, England; *Temnocheilus ventro-concavus* Platt, 1938, Scotland.

South Urals (Shimansky 1967): *Temnocheilus coronatiformae* Shimansky, 1967; South Urals.

North Africa (this paper): *Temnocheilus imazighenorum* sp. nov., Anti-Atlas; *Temnocheilus aubrechtovae* sp. nov., Anti-Atlas.

**Remarks**

For a discussion of the composition and limits of the genus, see Korn & Bockwinkel (2022).

***Temnocheilus imazighenorum*** sp. nov.
urn:lsid:zoobank.org:act:84E662FC-B0AB-4F6C-A69D-FD82103B2127
Fig. 6; Table 1

**Diagnosis**

Species of *Temnocheilus* with thinly pachyconic, subevolute conch (ww/dm ~ 0.65; uw/dm ~ 0.38); whorl profile moderately depressed, trapezoidal (ww/wh ~ 1.85), venter flattened, ventrolateral shoulder angular with elongated longitudinal nodes. Whorls very weakly embracing. Shell surface almost smooth.

**Etymology**

Named after the Imazighen, the ethnic group indigenous to the Maghreb region of North Africa.

**Material examined**

**Holotype**

MOROCCO • Anti-Atlas, east of Gara el Itima, 36 km east-northeast of Taouz; uppermost Zrigat Formation; Ebbighausen & Korn 2004 Coll.; illustrated in Fig. 6; MB.C.31291.

**Description**

Holotype MB.C.31291 is a somewhat weathered specimen 105 mm in diameter, allowing the study of two whorls (Fig. 6). The conch is barrel-shaped, thinly pachyconic and subevolute (ww/dm = 0.64; uw/dm = 0.38) with a very high coiling rate (WER = 2.28) and weakly embracing whorls. The whorl profile is trapezoidal with a flattened venter, an angular ventrolateral shoulder and flattened flanks plus umbilical wall. On the penultimate whorl, the ventrolateral shoulder bears eight longitudinally elongate nodes per half volution; they are much weaker on the last volution. The shell surface appears to be smooth.

**Remarks**

*Temnocheilus imazighenorum* sp. nov. is similar to *T. coronatus* but differs in the more compressed conch (ww/dm ~ 0.65 in *T. imazighenorum* but ~ 0.75 in *T. coronatus*), in the less depressed whorl profile (ww/wh ~ 1.85 in *T. imazighenorum* but ~ 2.25 in *T. coronatus*) and in the more flattened venter, which is broadly arched in *T. coronatus*. *Temnocheilus coronatiformae* differs in the slightly convex venter.

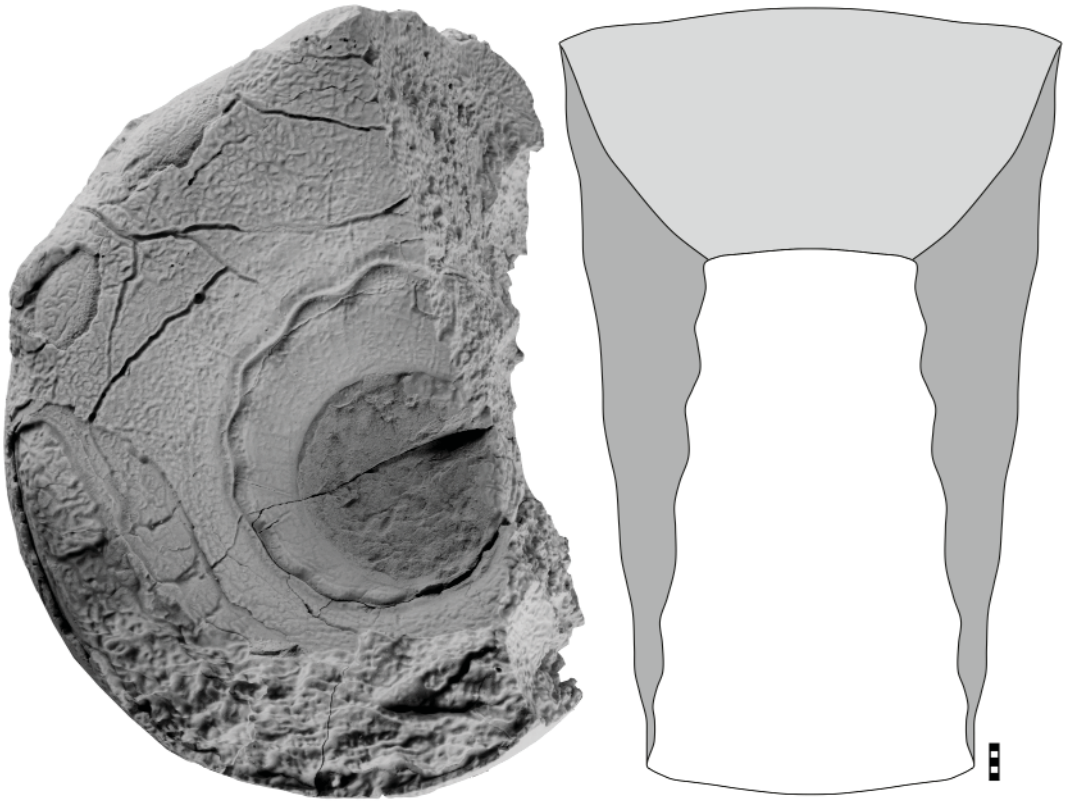

**Fig. 6.** *Temnocheilus imazighenorum* sp. nov., holotype MB.C.31291 (Ebbighausen & Korn 2004 Coll.) from E of Gara el Itima; lateral view and reconstruction of apertural view. Scale bar units = 1 mm.

**Table 1.** Conch dimensions (in mm) and ratios of the holotype of *Temnocheilus imazighenorum* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| MB.C.31291 | 105.5 | 67.8 | 37.1 | 40.5 | 35.6 | 0.64 | 1.83 | 0.38 | 2.28 | 0.04 |

***Temnocheilus aubrechtovae*** sp. nov.
urn:lsid:zoobank.org:act:51FDC5C3-01AA-47F6-B678-F67E2C360F4A
Fig. 7; Table 2

**Diagnosis**

Species of *Temnocheilus* with thickly pachyconic, subevolute conch (ww/dm ~0.80; uw/dm ~0.35); whorl profile strongly depressed, rounded-trapezoidal (ww/wh ~2.05), venter broadly rounded, ventrolateral shoulder angular with large, elongated longitudinal nodes (about 10 per whorl). Whorls weakly embracing. Shell surface almost smooth.

**Etymology**

Named after Martina Aubrechtová, in honour of her studies on Palaeozoic nautiloids.

**Material examined**

**Holotype**

MOROCCO • Anti-Atlas, region south-west of Rissani; basal Mougoui Ayoun Formation; Karaoui Coll.; illustrated in Fig. 7; PIMUZ 39511.

**Description**

Holotype PIMUZ 93511 is a slightly deformed but otherwise rather well-preserved specimen with a conch diameter of 54 mm (Fig. 7). The last quarter of the last preserved whorl belongs to the body chamber. The conch is thickly pachyconic to cadiconic and subevolute with a high coiling rate (WER = 2.04–2.21). The whorl profile is broadly trapezoidal (ww/wh 1.88 to 2.14) with a very broadly and continuously rounded venter; the ventrolateral shoulder is narrowly rounded. The nodes are about twice as long as they are wide and their spacing is equal to their length. There are ten such nodes on the last whorl, giving the ventrolateral shoulder a conspicuous coronate appearance.

**Fig. 7.** *Temnocheilus aubrechtovae* sp. nov.; holotype PIMUZ 39511 (Karaoui Coll.) from south-east of Rissani; reconstruction of apertural view, dorsal, lateral and ventral views. Scale bar units = 1 mm.

**Table 2.** Conch dimensions (in mm) and ratios of the holotype of *Temnocheilus aubrechtovae* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| PIMUZ 93511 | 54.2 | 41 | 19.2 | 20.5 | 16.5 | 0.76 | 2.14 | 0.38 | 2.21 | 0.14 |
| PIMUZ 93511 | 36.5 | 23.9 | 12.7 | 13.5 | 10.9 | 0.65 | 1.88 | 0.37 | 2.04 | 0.14 |

### Remarks

*Temnocheilus aubrechtovae* sp. nov. differs from the other Early Carboniferous species of the genus in the shape of the venter, which is either nearly flat (e.g., *T. coronatus*, *T. imazighenorum* sp. nov.) or slightly concave (e.g., *T. ventroconcavum*). *Temnocheilus coronatiformae* has a similar conch shape but differs from *T. aubrechtovae* in the much smaller and more numerous ventrolateral nodes (about 15 per volution).

## ***Temnocheilus*** sp.

Fig. 8

### Material examined

MOROCCO • 1 specimen; Anti-Atlas, region south-west of Rissani; basal Mougoui Ayoun Formation; Karaoui Coll.; PIMUZ 39516.

### Description

The fragmentary specimen PIMUZ 39516 has a conch diameter of 80 mm (Fig. 8A). It shows the coronate, strongly depressed whorl profile (ww/wh ~ 1.80), the flat area of flank and umbilical wall, the narrowly rounded ventrolateral shoulder and the flattened but convex venter (Fig. 8B). The ventrolateral shoulder is decorated with about 10 rounded tubercles on half a volution. The internal suture line possesses a deep, V-shaped rectangular internal lobe (Fig. 8C) caused by an inflexion of the strongly concave septum.

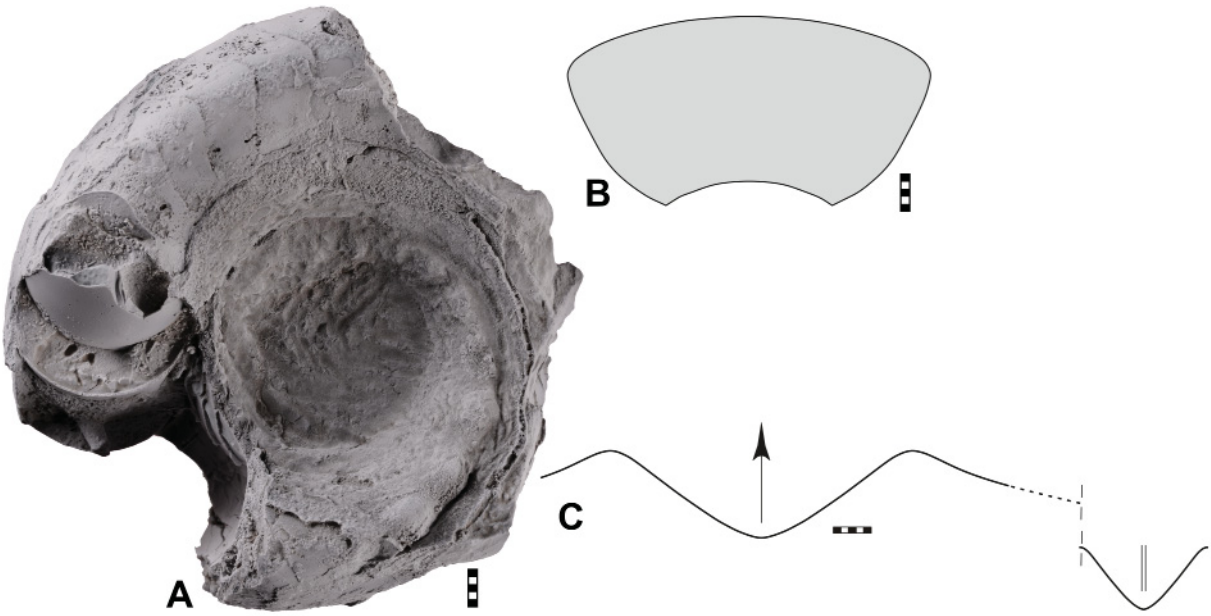


**Fig. 8.** *Temnocheilus* sp.; specimen PIMUZ 39516 (Karaoui Coll.) from south-east of Rissani. **A**. Lateral view. **B**. Whorl profile. **C**. Suture line, at ww ~ 43 mm, wh ~ 23 mm. Scale bar units = 1 mm.

Genus ***Vestinautilus*** Ryckholt, 1852

**Type species**

*Nautilus Koninckii* d'Orbigny, 1850; subsequent designation by Hyatt (1884).

**Diagnosis**

Genus of the family Trigonoceratidae with usually thickly discoidal to pachyconic evolute conch; whorls slightly impressed or without contact; whorl profile rounded triangular or trapezoidal with flattened or weakly concave venter and pronounced ventrolateral shoulder. Conch rapidly increasing in height with a high coiling rate (WER usually higher than 2.20). Ornament with fine lines and very coarse spiral ridges around the ventrolateral shoulder, sometimes also on the venter. Septa without inflexions, moderately concave. Suture line slightly sinuous with small external lobes, sometimes with lateral and internal lobes. Siphuncle small with subcentral position (after Kummel 1964; Shimansky 1967; emended).

**Included species**

Reviews of the species belonging to *Vestinautilus* have been given by Histon (1999), Korn *et al.* (2022) and Korn & Bockwinkel (2022). Species of the genus have been described from the following regions:

North America (Winchell 1862): *Nautilus* (*Trematodiscus*) *altidorsalis* Winchell, 1862, Michigan.

Northern and Central Europe (Sowerby 1825; d'Orbigny 1842–1851; de Koninck 1844; Foord 1891, 1900; Turner 1954): *Nautilus biangulatus* Sowerby, 1825, Southwest England; *Nautilus cariniferus* Sowerby, 1825, Ireland; *Vestinautilus crassimarginatus* Foord, 1900, Ireland; *Vestinautilus crateriformis* Foord, 1900, Ireland; *Triboloceras formosum* Foord, 1900, Ireland; *Nautilus Koninckii* d'Orbigny, 1850, Belgium; *Nautilus multicarinatus* Sowerby, 1825, Ireland; *Coelonautilus paucicarinatus* Foord, 1891, Ireland; *Nautilus pinguis* de Koninck, 1844, Belgium; *Vestinautilus semiglaber* Foord, 1900, Ireland; *Vestinautilus semiplicatus* Foord, 1900, Ireland; *Subvestinautilus simulans* Turner, 1954, Isle of Man.

North Africa (Korn & Bockwinkel 2022; Korn *et al.* 2022): *Vestinautilus angulatus* Korn & Bockwinkel, 2022, Algeria; *Vestinautilus bicristatus* Korn & Bockwinkel, 2022, Algeria; *Vestinautilus concinnus* Korn, Miao & Bockwinkel, 2022, Algeria; *Vestinautilus inflexus* Korn & Bockwinkel, 2022, Algeria; *Vestinautilus padus* Korn, Miao & Bockwinkel, 2022, Algeria; *Vestinautilus papilio* Korn & Bockwinkel, 2022, Algeria; *Vestinautilus kesslerae* sp. nov., Anti-Atlas.

West Russia, Urals and Kazakhstan (Tsvetaeva 1898; Shimansky 1967): *Subvestinautilus maritimus* Shimansky, 1967, Middle Urals; *Subvestinautilus rector* Shimansky, 1967, Kazakhstan; *Coelonautilus znamenskianus* Tzwetaeva, 1898, West Russia.

**Remarks**

Turner (1954) revised *Vestinautilus* and specifically restricted the genus "to forms resembling the type-species in possessing a venter concave or channelled at some stage of growth, a broad, depressed whorl-section, and a conch ornamented with spiral ribs, lirae and sulci." At the same time, he introduced the new genus *Subvestinautilus*, which he classified in the family Temnocheilidae. He stated that "the genus much resembles *Vestinautilus* … in shape but lacks a concave or channelled venter at any stage of development." However, since he regarded *Vestinautilus* as belonging to the family Triboloceratidae, he indirectly saw the close morphological similarity with it as the result of convergent evolution. This opinion was followed by Shimansky (1967) and Histon (1999), albeit with a different family attribution. However, Dzik (1984) rejected this concept, treating *Subvestinautilus* as a synonym of *Vestinautilus*.

We do not accept the separation of the two genera. The variable shape of the venter, which changes in some species during ontogeny, can hardly be regarded as a distinguishing criterion for these genera. We therefore assign species with coarse spiral ridges and a broad trapezoidal whorl profile, whether with a concave or convex venter, to *Vestinautilus*.

***Vestinautilus kesslerae*** sp. nov.
urn:lsid:zoobank.org:act:73A42507-23FD-4390-9DEE-8FC07C72A7BC
Fig. 9; Table 3

**Diagnosis**

Species of *Vestinautilus* with thickly pachyconic, subevolute conch (ww/dm ~0.68; uw/dm ~0.38); whorl profile moderately depressed, oval (ww/wh ~1.75), venter broadly arched, ventrolateral shoulder subangular with three weak spiral ridges. Whorls not embracing, just touching the preceding one. Ornament with coarse growth-lines forming a moderately deep, broadly arched ventral sinus.

**Etymology**

Named after Birgit Kessler (Berlin), who found the holotype.

**Material examined**

**Holotype**

MOROCCO • Anti-Atlas, South-east of Gara el Itima, 31.5 km east-northeast of Taouz; Zrigat Formation; Kessler 2007 Coll.; illustrated in Fig. 9; MB.C.31287.

**Description**

Holotype MB.C.31287 is an entirely chambered steinkern specimen with 41 mm phragmocone diameter; it comprises one and a quarter whorl (Fig. 9). At the largest diameter of the specimen, the conch shape is thinly pachyconic and subevolute (ww/dm ~0.68; uw/dm ~0.38). The whorl profile is depressed (ww/wh ~1.74) and has the shape of a symmetric oval. The coiling rate is very high (WER ~2.72) and the last whorl just touches the preceding one. The umbilical window has a diameter of 11.5 mm.

**Fig. 9.** *Vestinautilus kesslerae* sp. nov. from SE of Gara el Itima; holotype MB.C.31287 (Kessler 2007 Coll.); dorsal, lateral and ventral views. Scale bar units = 1 mm.

**Table 3.** Conch dimensions (in mm) and ratios of *Vestinautilus kesslerae* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| MB.C.31287 | 41.2 | 28.2 | 16.2 | 15.7 | 16.2 | 0.68 | 1.74 | 0.38 | 2.72 | 0.00 |

The initial chamber is bluntly cone-shaped with a length of 0.6 mm, a height of 2.0 mm and a width of about 4 mm. Very early in ontogeny, the whorl profile becomes depressed and already immediately after the protoconch, an angular ventrolateral shoulder is formed. This angular shoulder becomes more pronounced to form a spiral ridge, which is, at a conch diameter of 25 mm, accompanied by one less well-developed ridge on each side. The outer of these ridges fades out and is only barely visible at a conch diameter of 42 mm. Only some traces of the shell ornament are visible in the dorsal portion. They show coarse growth lines and three of them are arranged at a millimetre distance. They form a broadly arched ventral sinus.

The siphuncle has a subcentral position with a slight shift towards the venter. The suture line forms a wide and shallow external lobe, a very shallow and wide lateral lobe and a small, rounded internal lobe.

**Remarks**

*Vestinautilus kesslerae* sp. nov. has a somewhat marginal position in the morphological spectrum of the genus. It differs from the other species because of the combination of a number of conch and sculpture characters: the advolute conch shape even at a conch diameter of 40 mm, the comparatively weak development of only a few longitudinal ridges and the convex venter.

Genus ***Maccoyoceras*** Miller, Dunbar & Condra, 1933

**Type species**

*Nautilus* (*Discites*) *discors* M‘Coy, 1844; original designation.

**Diagnosis**

Genus of the family Trigonoceratidae with discoidal, usually evolute conch; whorls slightly impressed; whorl profile hexagonal or pentagonal with flattened or slightly concave venter and narrowly rounded umbilical margin. Conch moderately increasing in height with a high coiling rate (WER usually higher than 2.00). Ornament in the adult stage with coarse growth lines, in the preadult stage with fine spiral lines. Suture line with shallow external and lateral lobes. Siphuncle small with subcentral position (after Kummel 1964; emended).

**Included species**

North America (Winchell 1862): *Nautilus* (*Trematodiscus*) *discoidalis* Winchell, 1862, Michigan.

Northern and Central Europe (de Koninck 1844; M‘Coy 1844; Foord 1900): *Nautilus* (*Discites*) *discors* M‘Coy, 1844, Ireland; *Nautilus Leveilleanus* de Koninck, 1844, Belgium; *Discitoceras Wrightii* Foord, 1900, Ireland.

North Africa (Korn & Bockwinkel 2022; Korn *et al.* 2022): *Maccoyoceras concavum* Korn & Bockwinkel, 2022, Algeria; *Maccoyoceras habadraense* Korn & Bockwinkel, 2022, Algeria; *Maccoyoceras pentagonum* Korn, Miao & Bockwinkel, 2022, Algeria; *Maccoyoceras saharensis* Korn & Bockwinkel, 2022, Algeria.

**Remarks**

For a discussion of the composition and limits of the genus, see Korn *et al.* (2022) and Korn & Bockwinkel (2022).

***Maccoyoceras*** sp.
Fig. 10

**Material examined**

MOROCCO • 1 specimen; Anti-Atlas, southeast of Gara el Itima, 31.5 km east-northeast of Taouz; Zrigat Formation; Korn & Ebbighausen 2007 Coll.; MB.C.31288.

**Description**

Specimen MB.C.31288 is a weathered fragment of about a quarter of a whorl of the body chamber. It belongs to a specimen with a conch diameter of about 100 mm. Shell ornament is not preserved. The conch is evolute (uw/dm is about 0.50); the whorl profile is subquadratic with a slightly concave venter, subangular ventrolateral shoulders, sinuous flanks with a broadly rounded umbilical margin and a convex dorsum (Fig. 10).

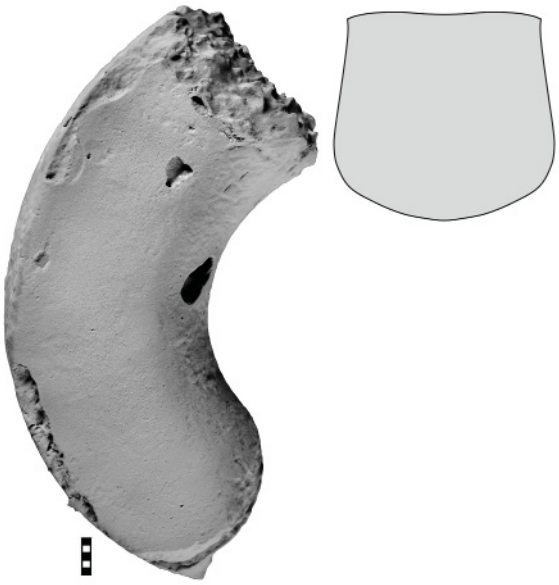

**Fig. 10.** *Maccoyoceras* sp. from Gara el Itima SE. Specimen MB.C.31288 (Ebbighausen & Korn 2004 Coll.); lateral view and whorl profile. Scale bar units = 1 mm.

Genus ***Endolobus*** Meek & Worthen, 1865

**Type species**

*Nautilus* (*Endolobus*) *peramplus* Meek & Worthen, 1865 (= *Nautilus spectabilis* Meek & Worthen, 1860); original designation.

**Diagnosis**

Genus of the family Trigonoceratidae with usually pachyconic, subinvolute or evolute conch; whorls usually slightly impressed, whorl profile compressed with broadly rounded or slightly flattened venter

and rounded umbilical margin. Conch very rapidly increasing in height with a high coiling rate (WER usually higher than 2.50). Sculpture with broad, rounded nodes on the flanks. Septa without inflexions, moderately concave. Suture line nearly straight with very shallow external lobe and usually with an internal lobe; some species with an annular lobe. Siphuncle with subcentral position.

**Included Early Carboniferous species**

North America (Meek & Worthen 1860, 1865; Miller & Gurley 1897; Miller & Collins 1947; Youngquist 1949; Collinson 1955; Sweet & Brookley 1956): *Nautilus spectabilis* Meek & Worthen, 1860, Illinois; *Nautilus* (*Endolobus*) *peramplus* Meek & Worthen, 1865 (synonym of *Nautilus spectabilis*); *Temnochilus greenense* Miller & Gurley, 1897, Indiana; *Endolobus greenbrierensis* Miller & Collins, 1947, Pennsylvania; *Solenochilus occidens* Youngquist, 1949, Nevada; *Endolobus clorensis* Collinson, 1955; Kentucky; *Endolobus indianensis* Sweet & Brookley, 1956, Indiana.

North Africa (this paper): *Endolobus rota* sp. nov., Anti-Atlas.

**Remarks**

*Endolobus* is a genus in need of revision both in its definition and possible phylogenetic position. For example, according to Gordon (1965), the annular lobe belongs to the diagnosis of the genus, whereas Shimansky (1967) did not consider this a necessary character. The assignment of the material from the Anti-Atlas can therefore only be tentative. Early Carboniferous species are known mainly from North America (for a species list, see Gordon 1965). Most of them are very large specimens, which makes a comparison with considerably smaller specimens difficult. The material from the Anti-Atlas is not very typical for *Endolobus* and occupies a marginal position within the genus.

***Endolobus rota*** sp. nov.
urn:lsid:zoobank.org:act:6E9B29A6-1308-4860-B96A-1C2E1B414621
Fig. 11; Table 4

**Diagnosis**

Species of *Endolobus* with pachyconic, subinvolute conch (ww/dm ~ 0.75; uw/dm ~ 0.25), whorl profile moderately compressed (ww/wh ~ 1.60) with slightly flattened venter and broadly rounded ventrolateral shoulder. Coiling rate extremely high (WER ~ 3.45), whorls not embracing. Ventrolateral shoulder with very low nodes. Suture line with very broad and shallow lobe on the venter and without internal lobe.

**Etymology**

From the Latin '*rota*', meaning 'wheel', because of the conch shape.

**Material examined**

**Holotype**

MOROCCO • Anti-Atlas, southeast of Gara el Itima, 31.5 km east-northeast of Taouz; Zrigat Formation; Korn & Ebbighausen 2007 Coll.; illustrated in Fig. 11; MB.C.31289.

**Description**

Specimen MB.C.31289 is a fragment of a specimen with about 85 mm conch diameter, consisting of three chambers and a short part of the body chamber with about 63 mm whorl width (Fig. 11A). At a whorl height of 39 mm, it has a ww/wh ratio of 1.60, but this ratio increases markedly during the previous half volution. The whorl profile is rounded-triangular with a broad venter, a broadly rounded ventrolateral shoulder and a nearly semicircular area consisting of flanks and dorsum (Fig. 11A).

**Table 4.** Conch dimensions (partly reconstructed, in mm) and ratios of *Endolobus rota* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| MB.C.31289 | 84.5 | 62.5 | 39.0 | 22.5 | 39.0 | 0.74 | 1.60 | 0.27 | 3.45 | 0.00 |

A concave dorsal whorl zone does not exist. One large and very low ventrolateral node is visible on the fragment. The suture line extends with a wide and shallow lobe across the venter; it forms a low saddle on the flank and does not possess an internal lobe (Fig. 11B).

**Remarks**

*Endolobus rota* differs from the other Early Carboniferous species of the genus mainly in the very low and broad nodes on the ventrolateral margin. Another criterion is the lack of whorl overlap, but this may be due to the relatively small size of the holotype when compared with the North American species of *Endolobus*.

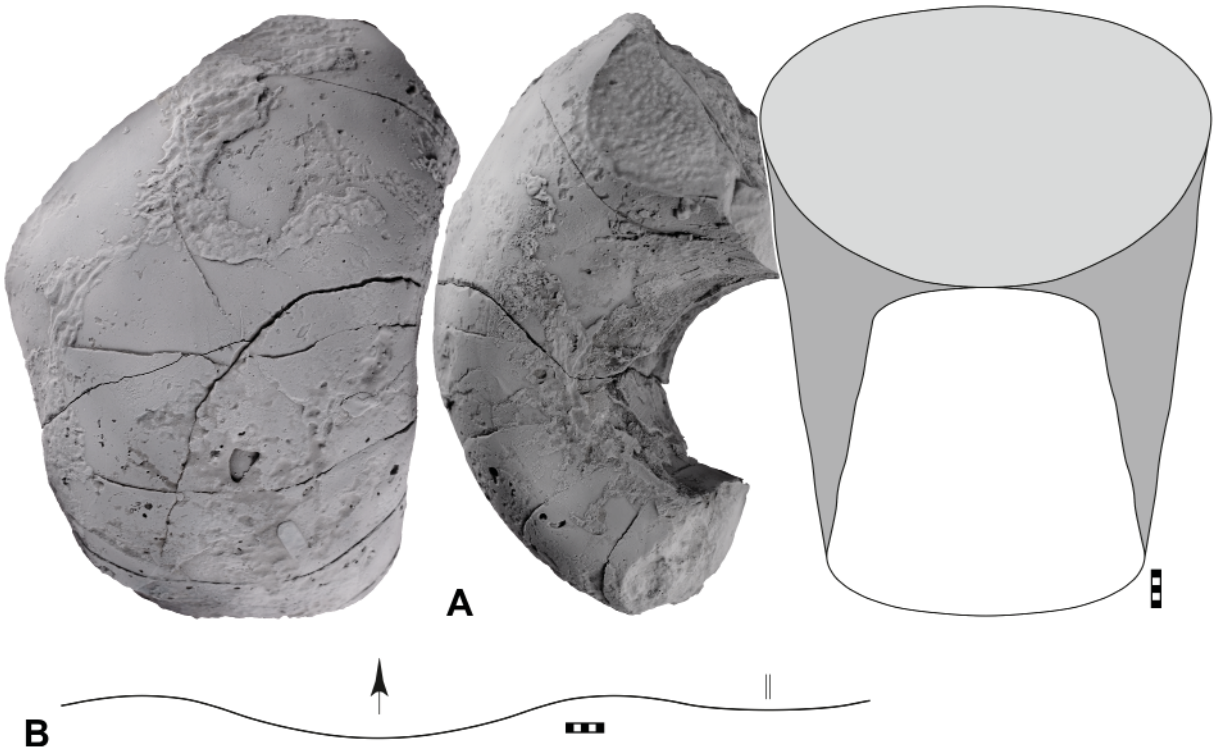


**Fig. 11.** *Endolobus rota* sp. nov. from SE of Gara el Itima; holotype MB.C.31289 (Ebbighausen & Korn 2004 Coll.). **A**. Ventral and lateral views, reconstruction of apertural view. **B**. Suture line, at ww = 53.0 mm, wh = 27.0 mm. Scale bar units = 1 mm.

***Endolobus*** sp.
Fig. 12

**Material examined**

MOROCCO • 1 specimen; Anti-Atlas, southeast of Gara el Itima, 31.5 km east-northeast of Taouz; Zrigat Formation; Korn & Ebbighausen 2007 Coll.; MB.C.31290.

**Description**

Specimen MB.C.31290 is a phragmocone fragment of a little less than a quarter of a whorl (Fig. 12) and consisting of seven chambers. It has a whorl height of 15 mm and a ww/wh ratio of 1.90. The venter is broadly rounded and separated from the rounded umbilical wall by a narrowly rounded umbilical margin. There is a shallow dorsal imprint zone (IZR ~ 0.20). The suture lines are rather densely arranged; they show a very wide and shallow lobe on the flanks and venter and a shallow, broadly rounded internal lobe.

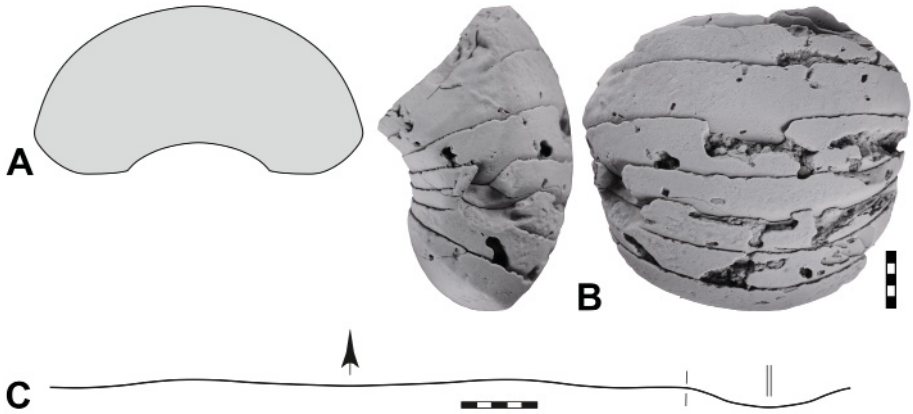


**Fig. 12.** *Endolobus* sp. from SE of Gara el Itima; specimen MB.C.31290 (Ebbighausen & Korn 2004 Coll.). **A**. Whorl profile. **B**. Lateral and ventral views. **C**. Suture line, at ww = 28.0 mm, wh = 14.5 mm. Scale bar units = 1 mm.

Family Grypoceratidae Hyatt in Zittel, 1900

Genus ***Epidomatoceras*** Turner, 1954

**Type species**

*Nautilus planotergatus* M'Coy, 1844; original designation.

**Diagnosis**

Genus of the family Trigonoceratidae with discoidal to pachyconic, usually subevolute conch. The first whorl is 12–20 mm in diameter with an umbilical foramen about 4–8 mm wide; the conch is rapidly increasing in height with a high coiling rate (WER usually higher than 2.50). Whorls weakly embracing, their profile is rectangular with more or less angular umbilical margin and ventrolateral shoulder. Sculpture with faint longitudinal ridges around the ventrolateral shoulder. Septa without inflexions, moderately concave. Suture line with moderately deep ventral and lateral lobes. The siphuncle has a position between the centre of the aperture and the venter (after Shimansky 1967).

**Included species**

British Isles (Phillips 1836; M'Coy 1844; Foord 1900; Turner 1954, 1965): *Nautilus Doohylensis* Foord, 1900, Ireland; *Epidomatoceras maccoyi* Turner, 1954, Derbyshire; *Nautilus planotergatus* M'Coy, 1844, Ireland; *Epidomatoceras neilsoni* Turner, 1965, Scotland; *Epidomatoceras flemingi* Turner, 1965, Scotland; *Nautilus subsulcatus* Phillips, 1836, Yorkshire.

Urals and Kazakhstan (Shimansky 1967): *Epidomatoceras aemulum* Shimansky, 1967, Kazakhstan; *Epidomatoceras vivum* Shimansky, 1967, South Urals.

North Africa (this paper): *Epidomatoceras ebbighausenorum* sp. nov., Anti-Atlas.

**Remarks**

*Epidomatoceras* belongs to a group of Early Carboniferous nautiloids of which the phylogenetic and taxonomic relationships are far from being solved (Dzik & Korn 1992). Unlike most other late Tournaisian and Viséan evolute nautiloids, it shows the formation of a distinct umbilical margin.

The genus has a wide distribution across facies boundaries; it occurs in both shallow and deep shelf strata. For this reason, it is often found together with ammonoids.

***Epidomatoceras ebbighausenorum*** sp. nov.
urn:lsid:zoobank.org:act:E0A17693-5DCD-463E-B266-0D4AFE16AB29
Figs 13–14; Table 5

**Diagnosis**

Species of *Epidomatoceras* with thickly pachyconic, subevolute conch (ww/dm ~ 0.68; uw/dm ~ 0.32); whorl profile moderately depressed, rounded-rectangular (ww/wh ~ 1.65), venter flattened, ventrolateral shoulder subangular, in the middle growth stages marked by a spiral ridge. Whorls very weakly embracing. Ornament with very fine growth lines. Septa simply concave towards the venter, suture line with shallow lobes on venter and flanks.

**Etymology**

Named after Volker Ebbighausen (1941–2011) and Rodion Ebbighausen, who collected the majority of the type material.

**Material examined**

**Holotype**

MOROCCO • Anti-Atlas, north of Gara el Itima, 35 km east-northeast of Taouz; basal Hamou-Rhanem Formation; Ebbighausen, Ebbighausen & Korn 2004 Coll.; illustrated in Fig. 13A; MB.C.31294.1.

**Paratypes**

MOROCCO • 18 specimens; same collection data as for holotype; Ebbighausen, Ebbighausen & Korn 2004 Coll.; MB.C.31294.2–31295.19.

**Description**

Holotype MB.C.31294.1 is a nearly complete but somewhat corroded specimen with a conch diameter of 67 mm; it allows the study of two whorls (Fig. 13A). The conch is widely wheel-shaped with a moderately wide umbilicus (ww/dm = 0.68; uw/dm = 0.33). The profile of the last whorl is depressed (ww/wh = 1.64) and subtrapezoidal with a nearly flat, steep umbilical wall, a subangular umbilical margin, slightly flattened, weakly converging flanks, a broadly rounded ventrolateral shoulder and a

flattened venter with a shallow concave depression. Half a volution earlier, at 41 mm dm, the venter is weakly convex and the ventrolateral shoulders are marked by three longitudinal ridges, of which the inner one is the most prominent and separated from the middle one by a distinct groove. The outer of the three ridges is the weakest and located on the venter. The shell surface appears to be smooth. The internal mould of the inner whorls is visible in the umbilicus; they show a pronounced umbilical margin and a rather steep, flattened umbilical wall.

Paratypes MB.C.31294.2 (Fig. 13B) and MB.C.31294.3 (Fig. 13C) have a conch morphology that is very similar to that of the holotype. Specimen MB.C.31294.3 is less well preserved in the outer whorl but provides a good insight of the earlier growth stage. Already at 15 mm diameter, an angular and slightly raised umbilical margin is developed, on which the growth lines are strengthened and form delicate plications.

Paratype MB.C.31294.4 yielded a conch cross section that allows the study of two and a half volutions ranging from 9 mm to 46 mm conch diameter (Fig. 14A). It is not clear from the specimen whether

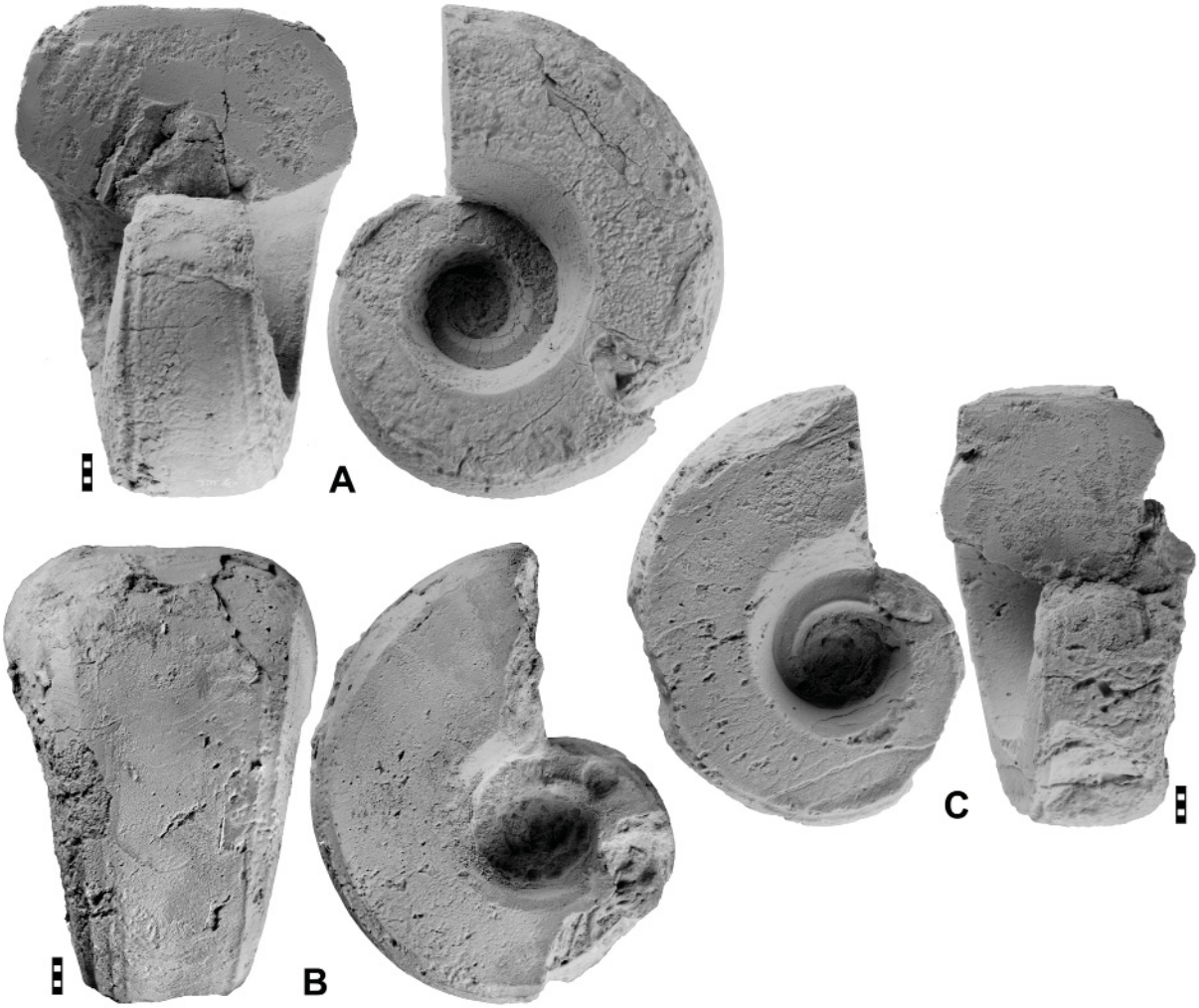


**Fig. 13.** *Epidomatoceras ebbighausenorum* sp. nov. from N of Gara el Itima (all Ebbighausen, Ebbighausen & Korn 2004 Coll.). **A**. Holotype MB.C.31294.1; dorsal and lateral views. **B**. Paratype MB.C.31294.2; ventral and lateral views. **C**. Paratype MB.C.31294.3; lateral and apertural views. Scale bar units = 1 mm.

some parts of the inner whorls are dissolved; the umbilical opening appears to have a width of 3.7 mm. The earliest preserved whorl profile (1.66 mm high, 2.53 mm wide) is rounded triangular with a flattened venter, but half a volution later (9 mm dm), a pronounced, subangular ventrolateral shoulder is developed and the nearly parallel, weakly converging flanks are bordered umbilically by a broadly rounded umbilical margin. From this growth stage, the whorl profile is rounded pentangular. Half a volution later, at 15 mm dm, this whorl profile is still present, but the umbilical margin is sharpened by a longitudinal crest formed by the shell. This whorl does not embrace the preceding one. Another half of a whorl later, at 26 mm dm, the umbilical wall is flattened and steep, while the umbilical margin is rounded. In this stage, the ventrolateral shoulder is characterised by a longitudinal groove accompanied by weak crests on both sides. Finally, at 46 mm dm, the ventrolateral and umbilical shoulders are narrowly rounded; venter, flanks and umbilical wall are flattened. The cross section demonstrates that the conch proportions do not change significantly during ontogeny. There is, between 9 and 46 mm conch diameter, a slight increase of the ww/dm ratio (from 0.58 to 0.66) paralleled by a slight decrease of the uw/dm ratio (from 0.43 to 0.29). The coiling rate increases from about 2.65 to 3.10 (Fig. 14C–E).

It appears that intraspecific variation ranges within rather narrow limits and ontogenetic changes are small. Specimens between 36 and 67 mm conch diameter, for instance, range in their ww/dm ratio between 0.60 and 0.70 with a weak tendency to become stouter with increasing diameter. In the same growth interval, the umbilical width ratio shows a very weak decrease. Only the coiling rate appears to decrease more significantly from a WER value of about 3.15 at 50 mm dm to 2.70 at 67 mm dm (Fig. 14C–E).

Paratype MB.C.31294.5 is a rather poorly preserved fragment of a large specimen (37 mm whorl width), but it shows the surface of a septum. This is continuously domed; the lobes in the suture line (Fig. 14B) are thus cut-out shapes of the septum and are not caused by septal inflexions. The siphuncle has a subcentral position and is slightly shifted from the centre towards the venter.

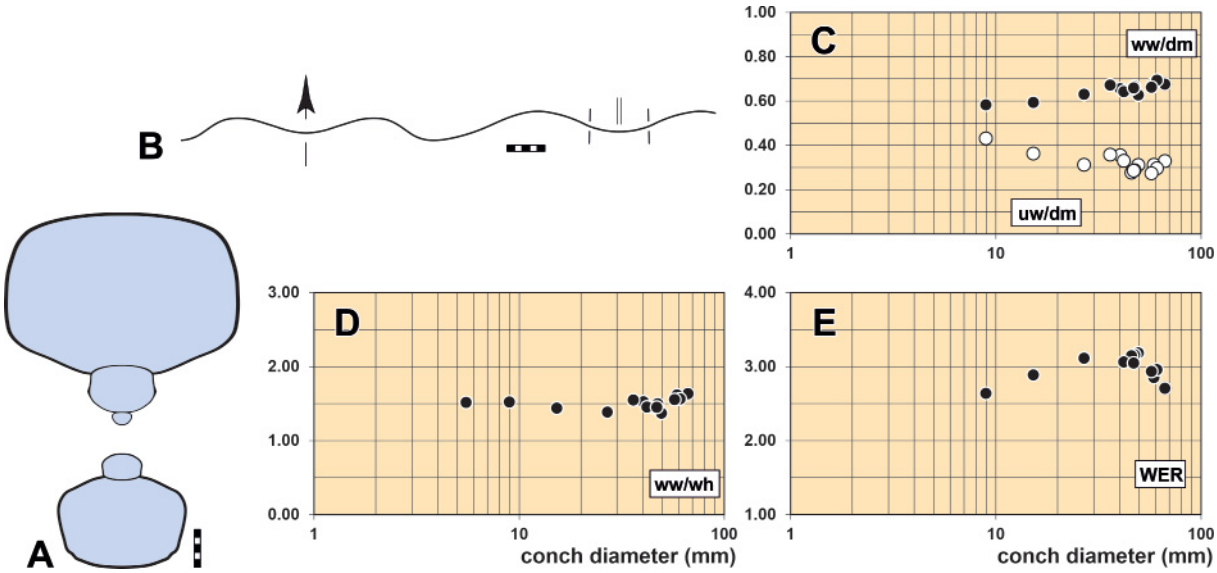


**Fig. 14.** *Epidomatoceras ebbighausenorum* sp. nov. from N of Gara el Itima (all Ebbighausen, Ebbighausen & Korn 2004 Coll.). **A**. Cross section of paratype MB.C.31294.4. **B**. Suture line of paratype MB.C.31294.5, at ww = 30.5 mm, wh = 22.5 mm. **C–E**. Ontogenetic trajectories of the cardinal conch parameters. Scale bar units = 1 mm.

**Table 5.** Conch dimensions (in mm) and ratios of *Epidomatoceras ebbighausenorum* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| MB.C.31294.1 | 66.5 | 45.0 | 27.5 | 21.9 | 26.1 | 0.68 | 1.64 | 0.33 | 2.71 | 0.05 |
| MB.C.31294.2 | 60.9 | 42.3 | 27.0 | 18.1 | 25.5 | 0.69 | 1.57 | 0.30 | 2.96 | 0.06 |
| MB.C.31294.3 | 58.8 | 40.0 | 24.7 | 18.4 | 24.0 | 0.68 | 1.62 | 0.31 | 2.85 | 0.03 |
| MB.C.31294.6 | 57.3 | 37.9 | 24.3 | 15.7 | 23.8 | 0.66 | 1.56 | 0.27 | 2.94 | 0.02 |
| MB.C.31294.7 | 49.4 | 31.0 | 22.6 | 15.4 | 21.7 | 0.63 | 1.37 | 0.31 | 3.18 | 0.04 |
| MB.C.31294.4 | 47.3 | 31.6 | 21.0 | 13.6 | 20.7 | 0.67 | 1.50 | 0.29 | 3.16 | 0.02 |
| MB.C.31294.8 | 45.7 | 29.9 | 20.6 | 12.6 | 19.9 | 0.65 | 1.45 | 0.28 | 3.15 | 0.03 |
| MB.C.31294.9 | 42.0 | 26.0 | 18.6 | 13.9 | 18.0 | 0.62 | 1.40 | 0.33 | 3.06 | 0.03 |

**Remarks**

*Epidomatoceras ebbighausenorum* sp. nov. differs from the other species of the genus in its stout conch and depressed whorl profile and the narrower umbilicus. The type species of the genus, *Epidomatoceras planotergatum*, for instance, has a nearly quadratic whorl profile (ww/wh ~ 1.05), while it is depressed in *E. ebbighausenorum* (ww/wh ~ 1.60). The umbilicus is rather wide in *E. planotergatum* (uw/dm ~ 0.37) but narrower in *E. ebbighausenorum* (uw/dm ~ 0.30). Similar differences occur when *E. ebbighausenorum* is compared with other species of *Epidomatoceras*, although *E. doohylense* possesses a slightly depressed whorl profile (ww/wh ~ 1.10).

Superfamily Clydonautiloidea Hyatt in Zittel, 1900
Family Liroceratidae Miller & Youngquist, 1949

Genus ***Liroceras*** Teichert, 1940

**Type species**

*Coloceras liratum* Girty, 1911; original designation.

**Diagnosis**

Genus of the family Liroceratidae with pachyconic to globular, involute or subinvolute conch; umbilicus closed by a plug in some species. The first whorl is 10–20 mm in diameter with a very small umbilical foramen; the conch is rapidly increasing in height with a high coiling rate (WER usually higher than 2.50). Whorls weakly embracing, their profile ranges from reniform to nearly circular. Juvenile conch with longitudinal ridges; adult ornament with growth lines with a fairly deep ventral sinus and spiral lines around the umbilicus in some species. Septa without inflexions, slightly concave. Suture line simple, nearly straight to straight with a shallow, broadly rounded internal lobe. The siphuncle has a position between the centre of the aperture and the venter (after Gordon 1965; Shimansky 1967).

**Included Early Carboniferous species**

Species of *Liroceras* are known from the Early Carboniferous to the Late Permian. Shimansky (1967: 194) and Gordon (1965: 156) provided species lists of the genus, several of which are also known from the Early Carboniferous:

Northern and Central Europe (Trenkner 1868; Miller *et al.* 1933; Schmidt 1951; Turner 1954; Ramsbottom & Moore 1961): *Nautilus Grundensis* Trenkner, 1868, Harz Mountains; *Coloceras hyatti* Miller, Dunbar & Condra, 1933, Belgium; *Liroceras occlusor* Schmidt, 1951, Harz Mountains; *Liroceras*

*schaelkense* Schmidt, 1951, Rhenish Mountains; *Liroceras lunense* Turner, 1954, Yorkshire; *Liroceras leitrimense* Ramsbottom & Moore, 1961, Ireland.

North Africa (this paper): *Liroceras vermis* sp. nov.; Anti-Atlas; *Liroceras karaouii* sp. nov., Anti-Atlas.

Western Russia and Urals (Eichwald 1857; Shimansky 1967): *Nautilus excentricus* von Eichwald, 1857, western Russia; *Liroceras fornicatum* Shimansky, 1967, western Russia; *Liroceras praelunense* Shimansky, 1967, North Urals; *Liroceras ruzhencevi* Shimansky, 1967, South Urals.

North China (Ruan & Zhou 1987): *Liroceras reniforme* Ruan & Zhou, 1987, Ningxia.

**Remarks**

*Liroceras* is a genus with a wide stratigraphic range, extending from the Viséan to the latest Permian. Gordon (1965) and Shimansky (1967) compiled species lists; these demonstrate the wide stratigraphic and geographic distribution. In contrast, the morphological range within the genus is small; the conchs of all species are very similar and differ mainly in the width of the umbilicus and in the formation of spiral lines. The most similar genus is *Bistrialites* Turner, 1954, but in this genus the umbilical margin is more angular, in contrast to *Liroceras* with a rounded or subangular umbilical margin.

***Liroceras vermis*** sp. nov.
urn:lsid:zoobank.org:act:AE14647B-7469-4BFC-91E3-99F7A8791CDD
Figs 15–16; Table 6

**Diagnosis**

Species of *Liroceras* with thickly pachyconic, subinvolute conch (ww/dm ~0.82; uw/dm ~0.20), whorl profile moderately depressed (ww/wh ~1.75) with broadly rounded venter and broadly rounded umbilical margin. Coiling rate very high (WER ~2.85), whorls very weakly embracing (IZR ~0.15). Suture line nearly straight.

**Etymology**

From the Latin '*vermis*', meaning 'maggot', because of the appearance of the holotype.

**Material examined**

**Holotype**

MOROCCO • Anti-Atlas, north of Gara el Itima, 35 km east-northeast of Taouz; basal Hamou-Rhanem Formation; Ebbighausen & Korn 2004 Coll.; illustrated in Fig. 15C; MB.C.31295.1.

**Paratypes**

MOROCCO • 4 specimens; same collection data as for holotype; Ebbighausen & Korn 2004 Coll.; MB.C.31295.2–31295.5.

**Description**

Specimen MB.C.31295.1 (Fig. 15C) was chosen as the holotype because it is the only one that shows traces of the shell ornament. It is, with 34 mm conch diameter, thickly pachyconic and subinvolute (ww/dm ~0.82; uw/dm ~0.21) with a strongly depressed, reniform whorl profile (ww/wh ~1.77), a very small whorl overlap zone (IZR ~0.12) and a very high coiling rate (WER ~2.85). The whorl profile has a broadly parabolic outline. The venter is broadly arched; the conch is widest at the umbilical margin from where the broadly rounded flanks converge towards the venter. The umbilical margin is continuously rounded and the umbilical wall is convex. The suture line extends almost straight across the umbilical

wall, flanks and venter. Shell remains on the umbilical wall show that four fine and sharp, wide-standing spiral lines are located on the outer portion of the umbilical wall. These spirals are entirely formed by the shell; they are not visible on the internal mould.

Paratype MB.C.31295.3 (Fig. 15B) is also a desert-corroded specimen, with 42 mm conch diameter, of which the last quarter of a whorl belongs to the body chamber. It has a geometry very similar to that of the holotype (ww/dm ~ 0.81; uw/dm ~ 0.20; ww/wh ~ 1.76; WER ~ 2.89; IZR ~ 0.11) The suture line extends almost straight across the umbilical wall, flanks and venter (Fig. 16A).

The second paratype, MB.C.31295.2 (Fig. 15A), has about 49 mm in conch diameter and is less strongly corroded than the other two specimens. It is an internal mould that appears to be completely smooth without any traces of ornament. Its conch proportions are almost exactly corresponding to those of the other two specimens.

The three specimens show that ontogenetic changes of the conch geometry and variation between the specimens is low (Fig. 16B–D), at least in the examined size-range. Between 20 and 49 mm in conch diameter, the ww/dm ratio ranges between 0.81 and 0.88, the uw/dm ratio between 0.20 and 0.25 and the whorl expansion rate between 2.83 and 2.89.

**Remarks**

*Liroceras vermis* sp. nov. belongs to the thickly pachyconic to globular species of the genus like *L. excentricum* and *L. lunense*, while the other species possess more compressed conchs. The new species differs from *L. lunense* and *L. concentricus* in the wider umbilicus (uw/dm ~ 0.20 in *L. vermis* and ~ 0.12 in the other two species) and from *L. praelunense* in the more slender conch (ww/dm ~ 0.82 in contrast to ~ 0.92).

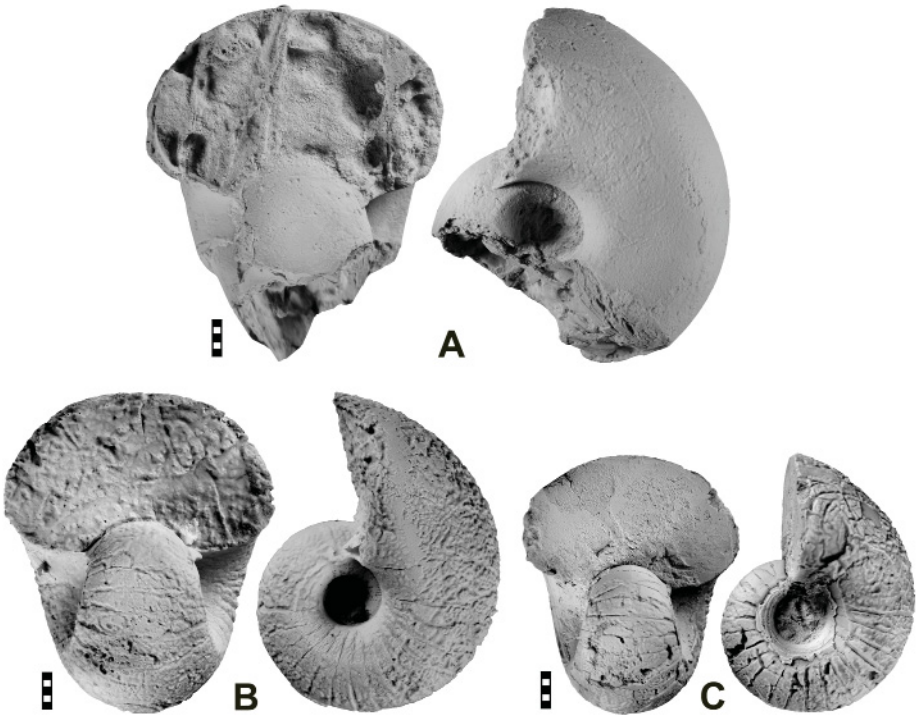


**Fig. 15.** *Liroceras vermis* sp. nov. from N of Gara el Itima (all Ebbighausen & Korn 2004 Coll.). **A**. Paratype MB.C.31295.2; dorsal and lateral views. **B**. Paratype MB.C.31295.3; dorsal and lateral views. **C**. Holotype MB.C.31295.1; dorsal and lateral views. Scale bar units = 1 mm.

**Table 6.** Conch dimensions (in mm) and ratios of *Liroceras vermis* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| MB.C.31295.2 | 48.8 | 40.6 | 23.9 | 10.4 | 19.8 | 0.83 | 1.70 | 0.21 | 2.83 | 0.17 |
| MB.C.31295.3 | 42.1 | 34.3 | 19.4 | 8.4 | 17.3 | 0.81 | 1.76 | 0.20 | 2.89 | 0.11 |
| MB.C.31295.1 | 34.3 | 28.2 | 15.9 | 7.2 | 14.0 | 0.82 | 1.77 | 0.21 | 2.85 | 0.12 |

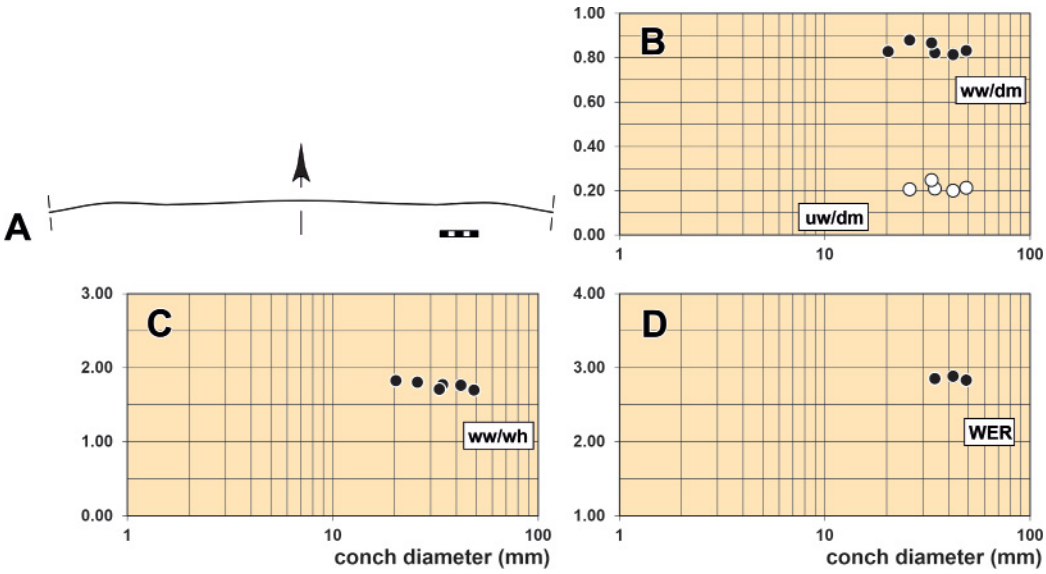


**Fig. 16.** *Liroceras vermis* sp. nov. from N of Gara el Itima. **A**. Suture line of paratype MB.C.31295.3 (Ebbighausen & Korn 2004 Coll.), at dm = 32.0 mm, ww = 29.5 mm, wh = 15.0 mm. **B–D**. Ontogenetic trajectories of the cardinal conch parameters. Scale bar units = 1 mm.

***Liroceras karaouii*** sp. nov.
urn:lsid:zoobank.org:act:2EDCD119-FDE9-426A-9547-A89E8AA520F4
Fig. 17; Table 7

**Diagnosis**

Species of *Liroceras* with thickly pachyconic, subinvolute conch (ww/dm ~ 0.75; uw/dm ~ 0.25), whorl profile moderately depressed (ww/wh ~ 1.65) with broadly rounded venter and subangular umbilical margin. Coiling rate very high (WER ~ 2.65), whorls very weakly embracing (IZR ~ 0.17). Suture line nearly straight.

**Etymology**

Named after Driss Karaoui (Hassilabied), the collector of the specimen.

**Material examined**

**Holotype**

MOROCCO • Anti-Atlas, region south-west of Rissani; basal Mougoui Ayoun Formation; Karaoui Coll.; illustrated in Fig. 17; PIMUZ 39515.

**Table 7.** Conch dimensions (in mm) and ratios of the holotype of *Liroceras karaouii* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| PIMUZ 39515 | 45.9 | 35.5 | 21.5 | 11.4 | 17.8 | 0.77 | 1.65 | 0.25 | 2.67 | 0.17 |

**Description**

Holotype PIMUZ 39515 is a corroded, desert-polished specimen with a phragmocone diameter of about 46 mm (Fig. 17). It is fully septate and has about 22 chambers in the last volution. It is, at 46 mm in conch diameter, thickly pachyconic and subinvolute (ww/dm = 0.77; uw/dm = 0.25) with a strongly depressed, reniform whorl profile (ww/wh = 1.65), a very small whorl overlap zone (IZR = 0.17) and a very high coiling rate (WER ~ 2.65). The whorl profile is crescent-shaped and widest at the subangular umbilical margin. The umbilical wall is flattened and slightly oblique. The suture line extends nearly linearly across the flanks and venter.

**Remarks**

*Liroceras karaouii* sp. nov. differs from *L. vermis* sp. nov. in the subangular umbilical margin and in the slightly wider umbilicus (uw/dm ~ 0.25 in *L. karaouii* but only uw/dm ~ 0.20 in *L. vermis*). This shape of the umbilicus is also the most important distinguishing character from the other species of the genus. The pronounced umbilical margin in *L. karaouii* can be seen as a plesiomorphic character, which transforms from the possible evolutionary lineage from *Bistrialites* to *Liroceras*.

**Fig. 17.** *Liroceras karaouii* sp. nov.; dorsal projection, dorsal and lateral views of holotype PIMUZ 39515 (Karaoui Coll.) from the region south-east of Rissani; reconstruction of apertural view, dorsal and lateral views. Scale bar units = 1 mm.

Family Ephippioceratidae Miller & Youngquist, 1949

Genus ***Ephippioceras*** Hyatt, 1884

**Type species**

*Nautilus ferratus* Cox, 1858; original designation.

**Diagnosis**

Genus of the family Ephippioceratidae with pachyconic to globular, involute conch. The first whorl is about 10 mm in diameter; the conch is rapidly increasing in height with a high coiling rate (WER usually

higher than 2.50). Whorls weakly embracing, with reniform profile. Shell surface smooth, sometimes with fine spiral lines. Septa bipartite by a median inflexion and two strongly concave lateral sides. Suture line with subtriangular external saddle, shallow lobes on flanks and umbilical wall and rounded internal saddle. The siphuncle has a position between the centre of the aperture and the venter (after Gordon 1965; Shimansky 1967).

**Included Early Carboniferous species**

North America (Cox 1858): *Nautilus ferratus* Cox, 1858, Kentucky.

British Isles (Sowerby 1821; Ramsbottom & Moore 1961): *Nautilus bilobatus* Sowerby, 1821, Scotland; *Ephippioceras spirale* Ramsbottom & Moore, 1961, Ireland.

North Africa (this paper): *Ephippioceras pygops* sp. nov.; Anti-Atlas.

West Russia and Urals (Hyatt 1891; Fredericks 1915; Shimansky 1967): *Ephippioceras Verneuili* Hyatt, 1891, South Urals; *Ephippioceras mosquense* Fredericks, 1915, Moscow Basin; *Ephippioceras sphaericum* Shimansky, 1967, South Urals.

**Remarks**

*Ephippioceras* is a genus of which several of the species are known from only a few specimens; furthermore, the very different sizes of the described specimens make a comparison difficult. Another problem is the often fragmentary preservation of the material.

***Ephippioceras pygops*** sp. nov.
urn:lsid:zoobank.org:act:498203A9-1F48-441C-B413-35C683103AE1
Fig. 18; Table 8

**Diagnosis**

Species of *Ephippioceras* with thickly pachyconic, subinvolute conch, whorl profile moderately depressed (ww/wh ~ 1.60) with broadly rounded venter and rounded umbilical margin. Impressed zone deep (IZR ~ 0.37). Suture line with high, subangular ventral saddle.

**Etymology**

Named after the brachiopod genus *Pygope*, because of the shape of the septal surface.

**Material examined**

**Holotype**

MOROCCO • Anti-Atlas, east of Gara el Itima, 36 km east-northeast of Taouz; uppermost Zrigat Formation; Ebbighausen & Korn 2004 Coll.; illustrated in Fig. 18; MB.C.31292.

**Description**

Specimen MB.C.31292 (Fig. 18A) is a fragment of a specimen with a phragmocone diameter of about 80 mm. The whorl profile is crescent-shaped with a broadly rounded venter that continues onto the flanks, a rounded umbilical margin and a convex umbilical wall. The whorl section is moderately depressed (ww/wh = 1.60) and the whorl embraces the preceding one to a rather high degree (IZR = 0.37). The septal surface shows the striking bilobate shape with a median ridge that separates the septum in two concave bulges. The suture line forms a narrow, subangular saddle on the venter, a wide, broadly rounded lobe on the flank and another smaller lobe on the umbilical wall (Fig. 18C).

**Table 8.** Conch dimensions (in mm) and ratios of *Ephippioceras pygops* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| MB.C.31292 | – | 77.7 | 48,6 | – | 30.7 | – | 1.60 | – | – | 0.37 |

**Remarks**

*Ephippioceras pygops* sp. nov. has a far less depressed whorl profile when compared with the other species of the genus. While the ww/wh ratio is only 1.60 in *E. pygops*, it is close to a value of 2.00 or even higher in *E. clitellarium* and *E. sphaericum* (Shimansky 1967). In *E. bilobatum*, *E. ferratum* and *E. verneuili*, the whorl overlap is much lower (IZR ~ 0.20) than in *E. pygops* (IZR ~ 0.37). *Ephippioceras spirale* is difficult to compare because of the small size (19 mm dm) of the only one specimen.

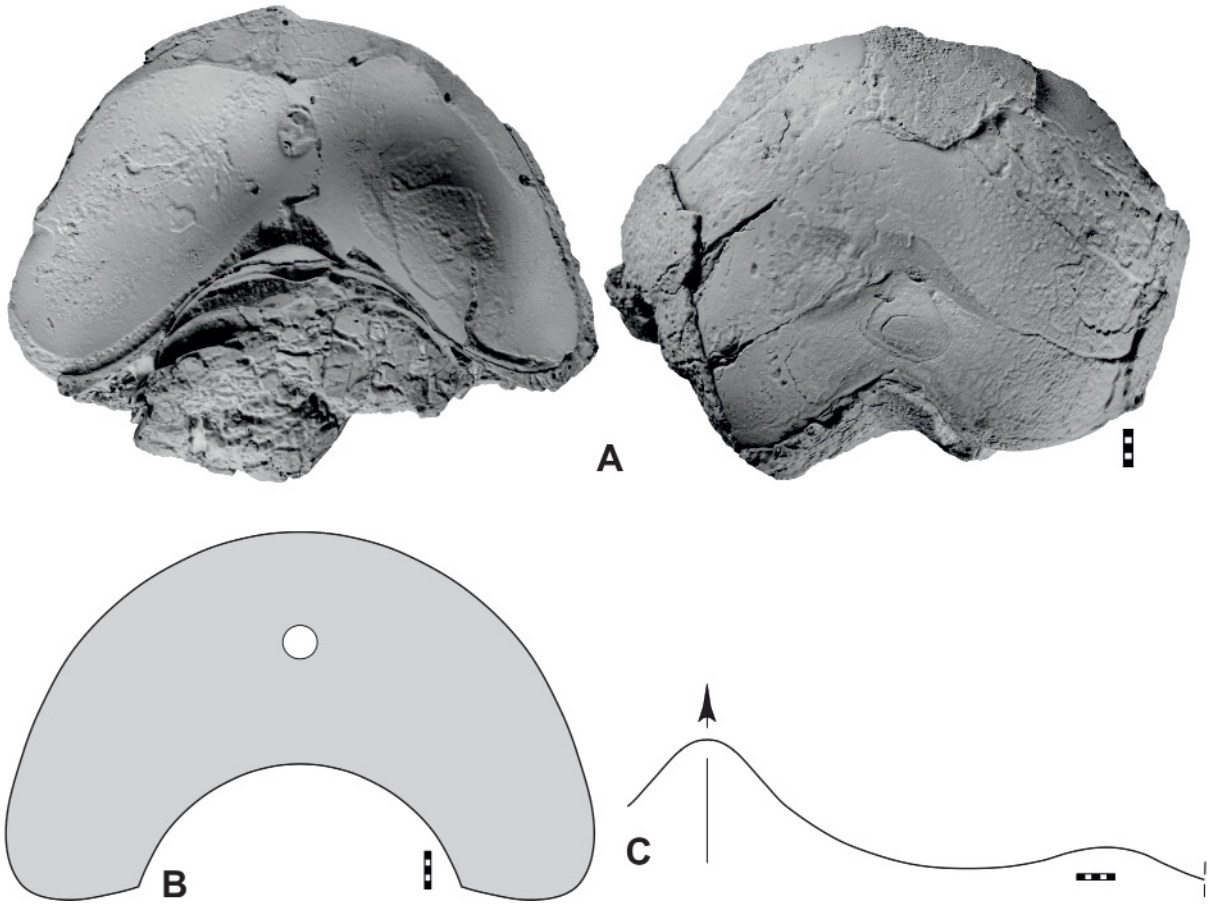


**Fig. 18.** *Ephippioceras pygops* sp. nov.; holotype MB.C.31292 (Korn 1999 Coll.) from N of Gara el Itima. **A**. Dorsal and ventral views. **B**. Whorl profile. **C**. Suture line, at ww = 76 mm, wh = 53 mm. Scale bar units = 1 mm.

Superfamily Aipoceratoidea Hyatt, 1883
Family Solenochilidae Hyatt, 1893

Genus ***Solenochilus*** Meek & Worthen, 1870

**Type species**

*Nautilus* (*Cryptoceras*) *Springeri* White & St. John, 1868; original designation.

**Diagnosis**

Genus of the family Solenochilidae with pachyconic to globular, involute or subinvolute conch. The conch is very rapidly increasing in height with an extremely high coiling rate (WER usually higher than 4.00). Adult body chamber with long lateral outgrowths. Whorls weakly without contact or embracing, their profile ranges from reniform to nearly circular. Suture line simple, nearly straight with a small annular lobe. The siphuncle has a position adjacent to the venter (after Gordon 1965; Shimansky 1967).

**Included Early Carboniferous species**

Gordon (1965: 152) gave an overview of the previously described species of *Solenochilus*. He listed 24 species (some with question marks), most of which are known from Late Carboniferous strata of North America.

So far, only a few Early Carboniferous species are known from two regions:

British Isles (Phillips 1836; Foord 1891, 1901): *Nautilus dorsalis* Phillips, 1836, Yorkshire; *Solenocheilus Hibernicus* Foord, 1891, Ireland; *Solenocheilus clausus* Foord, 1901, Ireland.

North Africa (this paper): *Solenochilus lucynae* sp. nov., Anti-Atlas; *Solenochilus pohlei* sp. nov., Anti-Atlas.

**Remarks**

*Solenochilus* is a genus whose species are mainly known from late Carboniferous strata of North America. Gordon (1965) published an identification key for these species, in which the species described from Europe can also be included. However, it is clear that this key does not represent a phylogenetic scheme and that it contains species with different ontogenetic stages.

Most occurrences of specimens of the genus are in sediments of the shallow shelf; therefore, *Solenochilus* is usually only rarely found together with ammonoids. For example, the genus is apparently absent from the assemblages of the Dalle à *Merocanites* of Timimoun (Korn *et al.* 2022) and Gara el Itima N; both are occurrences characterised by a high number of ammonoid specimens. The comparatively frequent occurrence of the genus in layers with many ammonoids at Rissani is therefore an exception.

***Solenochilus lucynae*** sp. nov.
urn:lsid:zoobank.org:act:C87D7BC3-B511-48C4-922B-FCF319D97534
Fig. 19; Table 9

**Diagnosis**

Species of *Solenochilus* with thickly pachyconic, involute conch (ww/dm ~0.80; umbilicus closed), whorl profile weakly depressed (ww/wh ~1.25) with broadly rounded venter and broadly rounded umbilical margin. Coiling rate extremely high (WER ~3.90), whorls moderately embracing (IZR ~0.25). Suture line on flanks and venter nearly straight, in dorsal area with deep, V-shaped internal lobe.

**Etymology**

Named after Lucyna Leda, who found the holotype.

**Material examined**

**Holotype**

MOROCCO • Anti-Atlas, 18 km south-east of Rissani; basal Mougoui Ayoun Formation; Leda 2011 Coll.; illustrated in Fig. 19; MB.C.31286.

**Paratypes**

MOROCCO • 2 specimens; Anti-Atlas, region south-east of Rissani; basal Mougoui Ayoun Formation; Karaoui Coll.; PIMUZ 39509, PIMUZ 39514.

**Description**

Holotype MB.C.31286 is a steinkern specimen with a 72 mm conch diameter, of which the last 120 degrees belong to the body chamber (Fig. 19). The peculiar conch shape with extremely high coiling rate (WER = 3.92) can be described as thickly pachyconic (ww/dm = 0.82); the whorl profile is characterised by the nearly circular, weakly depressed shape (ww/wh ~ 1.25) with venter, flanks, umbilical margin and umbilical wall broadly rounded. The embraced area of the preceding whorl is very small, the imprint zone depth is ~ 0.25. The internal mould is smooth, without traces of ornament. The suture line possesses a very shallow, broadly rounded lateral lobe and a very shallow external lobe.

Paratype PIMUZ 39509 is much smaller at 27 mm dm. The initial chamber is conical with a diameter of ca 4.8 mm. Half of it has broken off, exposing the first septum. The whorl height increase is extreme, while the umbilical width and whorl overlap are very low. The whorl cross section is nearly circular. The first four sutures are nearly straight with a very small and shallow external lobe. Following the fourth septum (ca 14 mm dm), a few weak radial ridges are visible on the flank, which fade out after a few millimetres. Parts of the growth lines are visible on the broadest part of the whorl, where they form a projection (at 15 mm dm).

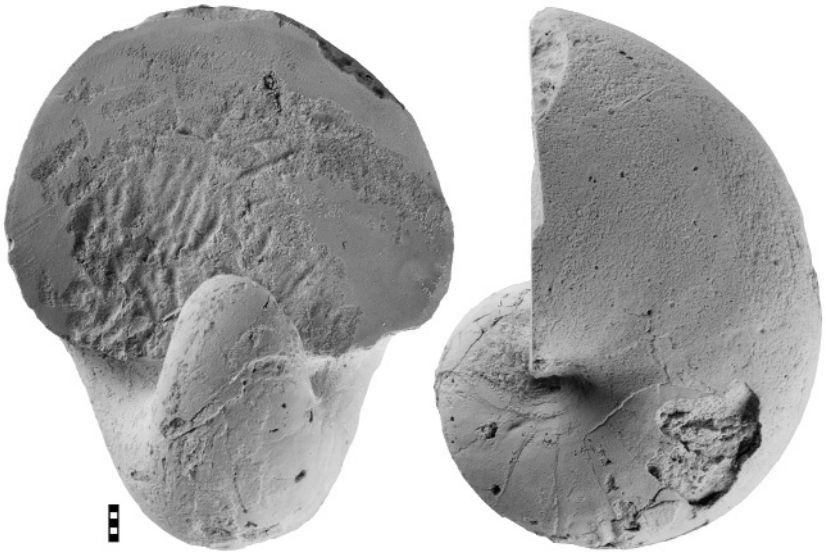

**Fig. 19.** *Solenochilus lucynae* sp. nov.; holotype MB.C.31286 (Leda 2011 Coll.) from 18 km SE of Rissani; dorsal and lateral views. Scale bar units = 1 mm.

**Table 9.** Conch dimensions (in mm) and ratios of *Solenochilus lucynae* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| MB.C.31286 | 71.9 | 59.2 | 46.8 | 0.0 | 35.6 | 0.82 | 1.26 | 0.00 | 3.92 | 0.24 |
| PIMUZ 39509 | 27.0 | 21.2 | 19.7 | 1.0 | 14.0 | 0.79 | 1.08 | 0.04 | 5.33 | 0.29 |

### Remarks

*Solenochilus lucynae* sp. nov. differs from the other Early Carboniferous species of the genus as follows: *S. dorsale* and *S. hibernicum* possess, in contrast to the new species, a slightly opened umbilicus. *Solenochilus clausum* has an almost closed umbilicus but differs in the more slender conch and hence a narrower whorl profile (ww/wh ~ 0.70) from *S. lucynae* (ww/wh ~ 1.25).

## ***Solenochilus pohlei*** sp. nov.

urn:lsid:zoobank.org:act:7C35A00D-0C45-43E5-A3F0-B7A2811164D6

Fig. 20; Table 10

### Diagnosis

Species of *Solenochilus* with thickly pachyconic, involute conch (ww/dm ~ 0.80; uw/dm ~ 0.15), whorl profile weakly compressed (ww/wh ~ 1.40) with broadly rounded venter and rounded umbilical margin. Development of a distinct ridge in the centre of the umbilical wall. Coiling rate extremely high (WER higher than 5.50), whorls not embracing. Suture line nearly straight.

### Etymology

Named after Alexander Pohle, in honour of his studies on Palaeozoic nautiloids.

### Material examined

#### Holotype

MOROCCO • Anti-Atlas, region south-east of Rissani; basal Mougoui Ayoun Formation; Karaoui Coll.; illustrated in Fig. 20B; PIMUZ 39513.

#### Paratype

MOROCCO • 1 specimen; same collection data as for holotype; Karaoui Coll.; PIMUZ 39508.

### Description

Holotype PIMUZ 39513 is an almost completely septate fragment of a conch with a constructed diameter of about 78 mm (Fig. 20A–B). It has an oval, slightly depressed whorl profile (ww/wh ~ 1.40) with a broadly rounded area consisting of flanks and venter. The whorl profile is widest near the rounded umbilical margin. The umbilical wall shows a rapid change from a simple convex shape to a biconcave shape in the segment of the last third volution. This is produced by the rapid protrusion of a narrowly rounded ridge, which would probably develop into a longer umbilical spine at a later ontogenetic stage. The dorsum is flattened and slightly incurved, but there is no sign of a preceding whorl; the coiling rate is extremely high (WER ~ 5.60). The specimen shows an oval, slightly depressed whorl profile in the penultimate half volution (Fig. 20A). The specimen does not provide evidence of the size of the protoconch. Areas of the shell surface are preserved on the umbilical wall and the inner flanks, although heavily corroded. They show fine growth lines that are already strongly curved backwards from the umbilical ridge, show a weak projection on the umbilical margin and extend backwards on the inner flank.

Paratype PIMUZ 39508 is also corroded and measures 73 mm in diameter (Fig. 20C). It exposes two thirds of the last whorl including parts of the body chamber. This specimen shows no whorl overlap and an extreme whorl expansion rate of over 6.00. The umbilicus is opened (uw/dm = 0.16); the umbilicus is oblique and convex. It displays the characteristic bulge, which rises from the umbilical seam and climbs toward the umbilical shoulder over the last half volution. The terminal spine is not preserved, since the terminal aperture is missing. It shows the nearly straight suture line. It shows that the siphuncle has a nearly ventral position but does not affect the suture line.

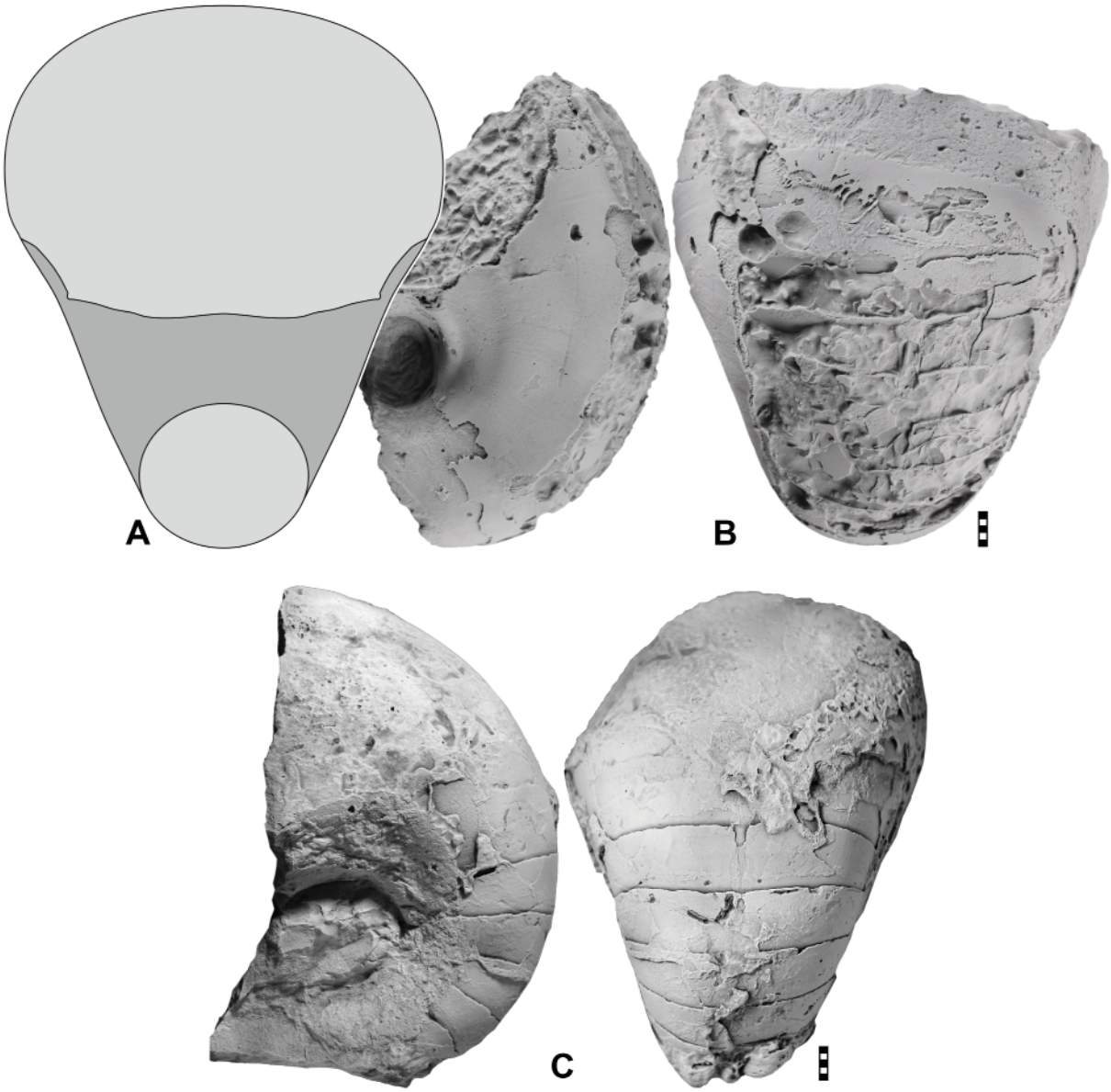


**Fig. 20.** *Solenochilus pohlei* sp. nov. from the region south-east of Rissani, both Karaoui Coll. **A**. Holotype PIMUZ 39513; cross section, partly reconstructed. **B**. Holotype PIMUZ 39513; lateral and ventral views. **C**. Paratype PIMUZ 39508; lateral and ventral views. Scale bar units = 1 mm.

**Table 10.** Conch dimensions (partly reconstructed; in mm) and ratios of *Solenochilus pohlei* sp. nov.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| PIMUZ 39513 | 78 | 63 | 45 | 12 | 45 | 0.81 | 1.40 | 0.15 | 5.59 | 0 |
| PIMUZ 39508 | 73.3 | 57.7 | 43.7 | 11.5 | 43.7 | 0.79 | 1.32 | 0.16 | 6.13 | 0 |

### Remarks

*Solenochilus pohlei* sp. nov. differs from *S. lucynae* sp. nov. in the presence of a ridge in the centre of the umbilical wall. Furthermore, *S. lucynae* has embracing whorls, while in *S. pohlei* the whorls, at least at a conch diameter of about 78 mm, do not show a concave whorl zone.

A very similar specimen was illustrated by Sturgeon & Miller (1948) as *Solenochilus greenensis*; however, it has a Moscovian age. According to the authors, is has a "relatively narrow" impressed zone and differs thus from *S. pohlei* sp. nov., without an impressed zone.

## ***Solenochilus*** sp.

Fig. 21; Table 11

### Material examined

MOROCCO • 2 specimens; Anti-Atlas, region south-east of Rissani; basal Mougoui Ayoun Formation; Karaoui Coll.; PIMUZ 39509, PIMUZ 39514.

### Description

Specimen PIMUZ 39509 is a phragmocone fragment of a quarter of a whorl (Fig. 21A). It has a whorl height of 49 mm and has a weakly depressed whorl profile (ww/wh = 1.32). The fragment suggests that the whorls were growing very rapidly; the imprint zone is very small. It is likely that the umbilicus is

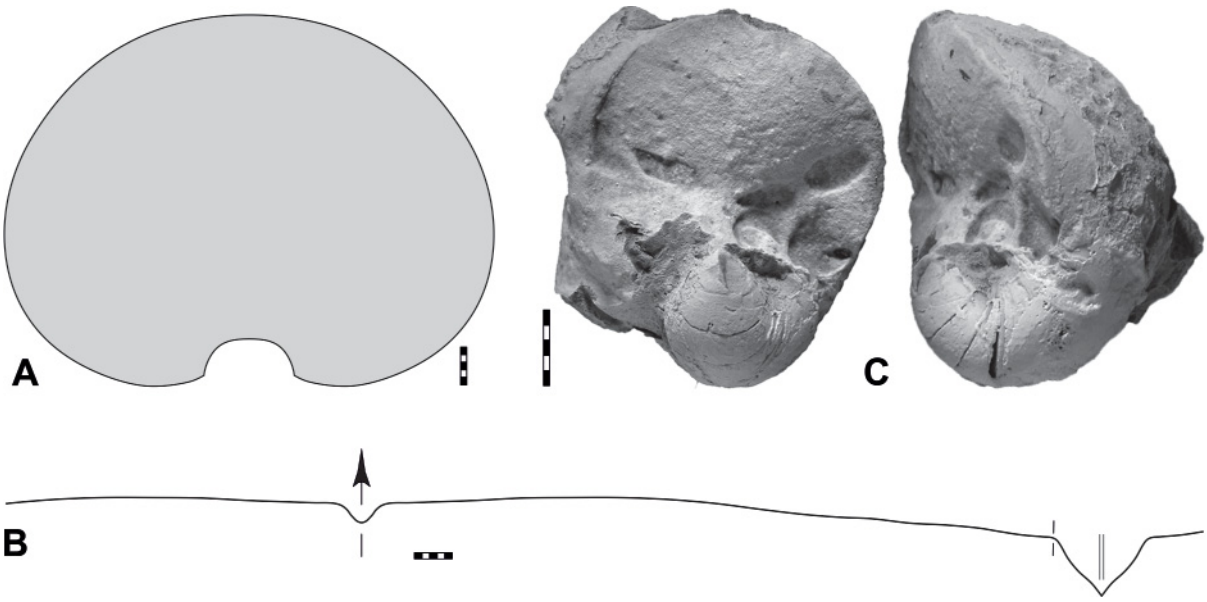


**Fig. 21.** *Solenochilus* sp., both Karaoui Coll. **A**. Specimen PIMUZ 39509; whorl profile. **B**. Specimen PIMUZ 39509; suture line at ww = 61.6 mm, wh = 46.3 mm. **C**. Specimen PIMUZ 39514; dorsal and lateral views. Scale bar units = 1 mm.

**Table 11.** Conch dimensions (partly reconstructed; in mm) and ratios of *Solenochilus* sp.

| specimen | dm | ww | wh | uw | ah | ww/dm | ww/wh | uw/dm | WER | IZR |
|---|---|---|---|---|---|---|---|---|---|---|
| PIMUZ 39509 | – | 64.6 | 49.0 | – | 37.0 | – | 1.32 | – | – | 0.10 |
| PIMUZ 39514 | 24.8 | 18.5 | 12.3 | 4.5 | 12.3 | 0.75 | 1.50 | 0.18 | 3.94 | 0.00 |

slightly opened. The suture line is almost straight with a small external lobe and a V-shaped internal lobe (Fig. 21B) created by a funnel-like indentation of the septum.

Specimen PIMUZ 39514 is a juvenile specimen with 25 mm conch diameter; it consists of less than one whorl. It is pachyconic with an umbilical window of about 6 mm diameter. The preserved protoconch is 3 mm long and 3.5 mm wide.

**Remarks**

It is not certain that the two specimens described here belong to the same species. The fragment of the larger specimen shows a slightly open navel in contrast to *Solenochilus lucynae* sp. nov. The difference to *S. pohlei* sp. nov. lies in the configuration of the umbilical wall, which forms a longitudinal ridge in *S. pohlei*.

## Discussion

We describe 16 taxa of coiled nautiloids, of which six are kept in open nomenclature. All come from two regions, namely the Gara el Itima northeast of Taouz and the great plain between Dar Kaoua, Hassilabied, Merzouga and the Oued Ziz (Fig. 1). The specimens were loosely collected from mostly fine clastic successions of the Mougoui Ayoun, Zrigat and Hamou-Rhanem formations. As listed in the Material section, these nautiloids are usually significantly scarcer than contemporaneous ammonoids. Nevertheless, the diversity and disparity are remarkably high in comparison to the co-occurring ammonoids (Korn *et al.* 1999, 2002, 2003, 2007, 2022; Klug & Korn 2001; Bockwinkel & Ebbighausen 2006; Klug *et al.* 2006, 2016; Ebbighausen & Bockwinkel 2007; Korn & Bockwinkel 2022).

Conch forms of the Viséan nautiloids from the Anti-Atlas range from very involute with closed umbilicus to advolute, from moderate to extremely high whorl expansion rates and from smooth to strongly ornamented. Following Tendler *et al.* (2015), this disparity in conch forms reflects specializations for certain tasks. While some of the Viséan nautiloid species have rather compact conchs, they were not optimized for hydrodynamics (see also Klug *et al.* 2016). It appears like compactness and manoeuvrability (e.g., Peterman & Ritterbush 2022) were the main tasks these nautiloids were positively selected for, while ammonoids occupied other archetypes with mostly more streamlined conchs, although some overlap in conch morphology occurs.

This raises the question of niches occupied by the various species of ammonoids and nautiloids. Overall, abundances of ammonoid species are higher. This might indicate that the nautiloids were either primarily less common or that their main habitat was situated elsewhere. One ecological factor could be water depth. In any case, in order to draw conclusions on these palaeoecological factors, many more collections from different palaeoenvironments are needed.

## Acknowledgements

We are indebted to Markus Brinkmann (Berlin) for the preparation as well as to Jenny Huang and Oskar Werb (Berlin) for the photography of some of the specimens. Many thanks to Andy King (Taunton) and an anonymous reviewer for reviewing an earlier version of the manuscript and for very helpful suggestions.

## References

Bockwinkel J. & Ebbighausen V. 2006. A new ammonoid fauna from the *Gattendorfia-Eocanites* Genozone of the Anti-Atlas (Early Carboniferous; Morocco). *Fossil Record* 9: 87–129. https://doi.org/10.5194/fr-9-87-2006

Collinson C. 1955. A new species of *Endolobus* (Nautiloidea) from the Clore limestone (Chester) of western Kentucky. *Journal of Paleontology* 29: 178–181.

Cox E.T. 1858. Palaeontological report of Coal Measure Mollusca. *Geological Survey of Kentucky Report* 3: 559–576.

Dawson J.W. 1868. *Acadian Geology: The Geological Structure. Organic Remains and Mineral Resources of Nova Scotia, New Brunswick, and Prince Edward Island*. MacMillan, London. https://doi.org/10.5962/bhl.title.38560

de Koninck L.G.D. 1844. *Description des Animaux fossiles qui se trouvent dans le Terrain carbonifère de la Belgique.* H. Dessain, Brussels.

de Koninck L.G.D. 1880. Faune du Calcaire Carbonifère de la Belgique, deuxième partie, genres *Gyroceras*, *Cyrtoceras*, *Gomphoceras*, *Orthoceras*, *Subclymenia* et *Goniatites*. *Annales du Museé royal d`Histoire naturelle, Belgique* 5: 1–333.

Delépine G. 1939. Nautiloides du Viséen supérieur du Tafilalet (Maroc). *Annales de la Société géologique du Nord* 64: 63–70.

Delépine G. 1941. Les goniatites du Carbonifère du Maroc et des confins Algéro-Marocains du sud (Dinantien-Westphalien). *Notes et Mémoires, Service géologique, Protectorat de la République française au Maroc, Direction de la Production industrielle et des Mines, Division des Mines et de la Géologie Republique française Maroc* 56: 1–111.

d'Orbigny A. 1842–1851. *Paléontologie française. Terrains jurassiques. I. Céphalopodes*. Orbigny, Paris.

Dzik J. 1984. Phylogeny of the Nautiloidea. *Palaeontologia Polonica* 45: 1–219.

Dzik J. & Korn D. 1992. Devonian ancestors of *Nautilus*. *Paläontologische Zeitschrift* 66: 81–98. https://doi.org/10.1007/BF02989479

Ebbighausen V. & Bockwinkel J. 2007. Tournaisian (Early Carboniferous/Mississippian) ammonoids from the Ma'der Basin (Anti-Atlas, Morocco). *Fossil Record* 10: 125–163. https://doi.org/10.1002/mmng.200700003

Eichwald C.E. von. 1857. Beitrag zur geographischen Verbreitung der fossilen Thiere Russlands. Alte Periode. Klasse der Cephalopoden. *Moskovskoe Obshchestvo Lyubiteley Prirody* 30: 192–212.

Fleming J. 1828. *A History of British Animals, Exhibiting the Descriptive Characters and Systematical Arrangement of the Genera and Species of Quadrupeds, Birds, Reptiles, Fishes, Mollusca, and Radiata of the United Kingdom: Including the Indigenous, Extirpated, and Extinct Kinds, together with Periodical and Occasional Visitants*. Bell, Bradfute, Duncan, Edinburgh, London. https://doi.org/10.5962/bhl.title.12859

Flower R.H. & Kummel B. 1950. A classification of the Nautiloidea. *Journal of Paleontology* 24: 604–616.

Foord A.H. 1891. *Catalogue of the Fossil Cephalopoda in the British Museum, Part II. Containing the Remainder of the Suborder Nautiloidea, Consisting of the Families Lituitidae, Trochoceratidae, and Nautilidae, with a Supplement*. Order of the Trustees, London.

Foord A.H. 1900. Monograph on the Carboniferous Cephalopoda of Ireland. Part III. Containing the Families Tainoceratidæ, Trigonoceratidæ, Triboloceratidæ, Rineceratidæ, Coloceratidæ, and Solenocheilidæ (in Part). *Monographs of the Palaeontographical Society* 54: 49–126. https://doi.org/10.1080/02693445.1900.12035492

Foord A.H. 1901. Monograph of the Carboniferous Cephalopoda of Ireland, Part IV. Containing the families Solenocheilidae (concluded) and Glyphioceratidae. *Monographs of the Palaeontographical Society* 55: 127–146. https://doi.org/10.1080/02693445.1901.12035497

Fredericks G. 1915. Fauna verkhnepaleozoyskoy tolstshy okrestnosty g. Krasnoufimska Permskoy guberniy. *Memoires du Comité géologique* 109: 1–117.

Gordon M.Jr. 1965. Carboniferous cephalopods of Arkansas. *Professional Papers, U.S. Geological Survey* 460: 1–322. https://doi.org/10.3133/pp460

Hind W. 1914. *Temnocheilus derbiensis*, sp. nov. *Proceedings of the Yorkshire Geological Society* 19: 18–19. https://doi.org/10.1144/pygs.19.1.18

Histon K. 1999. A revision of A.H. Foord's monograph of Irish Carboniferous nautiloid cephalopods (1897–1901). Part 2. *Monographs of the Palaeontographical Society* 153 (611): 63–129. https://doi.org/10.1080/25761900.2022.12131791

Holzapfel E. 1889. Die Cephalopoden-führenden Kalke des unteren Carbon von Erdbach-Breitscheid bei Herborn. *Palaeontologische Abhandlungen, Neue Folge* 5: 1–74.

Hyatt A. 1883–1884. Genera of fossil cephalopods. *Proceedings of the Boston Society of Natural History* 22: 253–338.

Hyatt A. 1891. Carboniferous cephalopods. *Annual Report of the Geological Survey of Texas* 2: 327–356.

Hyatt A. 1893. Carboniferous cephalopods, second paper. *Annual Report of the Geological Survey of Texas* 4: 327–356, 379–474.

Klug C. & Korn D. 2001. Epizoa and post-mortem epicoles on cephalopod shells – Devonian and Carboniferous examples from Morocco. *Berliner geowissenschaftliche Abhandlungen, E* 36: 145–155.

Klug C., Döring S., Korn D. & Ebbighausen V. 2006. The Viséan sedimentary succession at the Gara el Itima (Anti-Atlas, Morocco) and its ammonoid faunas. *Fossil Record* 9: 3–60. https://doi.org/10.5194/fr-9-3-2006

Klug C., Korn D., Landman N.H., Tanabe K., De Baets K. & Naglik C. 2015. Describing ammonoid conchs. *In*: Klug C., Korn D., De Baets K., Kruta I. & Mapes R.H. (eds) *Ammonoid Paleobiology: from Anatomy to Ecology. Topics in Geobiology 43*: 3–24. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9630-9_1

Klug C., De Baets K. & Korn D. 2016. Exploring the limits of morphospace: ontogeny and ecology of late Visean ammonoids from the Tafilalt, Morocco. *Acta Palaeontologica Polonica* 61: 1–14. https://doi.org/10.4202/app.00220.2015

Korn D. 2010. A key for the description of Palaeozoic ammonoids. *Fossil Record* 13 (1): 5–12. https://doi.org/10.1002/mmng.200900008

Korn D. & Bockwinkel J. 2022. Early Carboniferous nautiloids from the Central Sahara, southern Algeria. *European Journal of Taxonomy* 831: 67–108. https://doi.org/10.5852/ejt.2022.831.1871

Korn D., Klug C. & Mapes R.H. 1999. Visean and Early Namurian Ammonoids from the Tafilalt (Eastern Anti-Atlas, Morocco). *Abhandlungen der Geologischen Bundesanstalt* 54: 345–375.

Korn D., Klug C., Ebbighausen V. & Bockwinkel J. 2002. Palaeogeographical meaning of a Middle Tournaisian ammonoid fauna from Morocco. *Geologica et Palaeontologica* 36: 79–86.

Korn D., Bockwinkel J., Ebbighausen V. & Klug C. 2003. Palaeobiogeographic and evolutionary meaning of an early Late Tournaisian ammonoid fauna from the Tafilalt of Morocco. *Acta Palaeontologica Polonica* 48: 71–92.

Korn D., Klug C. & Mapes R.H. 2005. The Lazarus ammonoid family Goniatitidae, the tetrangularly coiled Entogonitidae, and Mississippian biogeography. *Journal of Paleontology* 79 (2): 356–365. https://doi.org/ff6g8v

Korn D., Bockwinkel J. & Ebbighausen V. 2007. Tournaisian and Visean ammonoid stratigraphy in North Africa. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 243: 127–148. https://doi.org/10.1127/0077-7749/2007/0243-0127

Korn D., Miao L. & Bockwinkel J. 2022. The nautiloids from the Dalle à *Merocanites* of Timimoun (Tournaisian-Viséan boundary, Algeria). *European Journal of Taxonomy* 789: 104–129. https://doi.org/10.5852/ejt.2022.789.1635

Kruglov M.V. 1933. Verkhnepermskie nautilidy basseynov rek Pinegi i Kuloya (The Upper Permian Nautilida of the Pinega and Kuloi River Basins). *Trudy geologicheskogo Instituta Akademiya Nauk SSSR* 3: 185–208.

Kummel B. 1964. Nautiloidea-Nautilida. *In*: Moore R.C. (ed.) *Treatise on Invertebrate Paleontology*: K383–K466. The Geological Society of America and The University of Kansas Press, Lawrence, KS.

M'Coy F. 1844. *A Synopsis of the Characters of the Carboniferous Fossils of Ireland*. University Press, Dublin. https://doi.org/10.5962/bhl.title.11559

Meek F.B. & Worthen A.H. 1860. Descriptions of new Carboniferous fossils from Illinois and other western States. *Proceedings of the Academy of Natural Sciences of Philadelphia* 12: 447–472.

Meek F.B. & Worthen A.H. 1865. Contributions to the palaeontology of Illinois and other western states. *Proceedings of the Academy of Natural Sciences of Philadelphia* 17: 245–273.

Miller A.K. & Collins L.R. 1947. *Endolobus* from the Greenbrier limestone of Pennsylvania. *Journal of Paleontology* 21: 239–241.

Miller A.K. & Garner H. 1953. Lower Mississippian cephalopods of Michigan. Part II. Coiled nautiloids. *Contributions from the Museum of Paleontology* 11 (6): 111–151.
Available from http://hdl.handle.net/2027.42/48279 [accessed 21 Jun. 2023].

Miller A.K., Dunbar C. & Condra G.E. 1933. The nautiloid cephalopods of the Pennsylvanian system in the Mid-Continent region. *Nebraska Geological Survey Bulletin* 9: 1–240.

Miller S.A. & Gurley W.F.E. 1897. New species of crinoids, cephalopods and other Palaeozoic fossils. *Bulletin of the Illinois State Museum of Natural History* 12: 48–53.

Murchison R.I., De Verneuil É. & Keyserling A.G. 1845. *Géologie de la Russie d'Europe et des Montagnes de l'Oural. Vol. II. Troisième Partie. Paléontologie*. Murray, London, Paris.

Niko S. & Mapes R.H. 2005. Early Carboniferous trigonoceratid nautilids from the Pitkin Formation of Arkansas, Midcontinent North America. *Paleontological Research* 9: 233–241. https://doi.org/10.2517/prpsj.9.233

Peterman D.J. & Ritterbush K.A. 2022. Resurrecting extinct cephalopods with biomimetic robots to explore hydrodynamic stability, maneuverability, and physical constraints on life habits. *Scientific Reports* 12: e11287. https://doi.org/10.1038/s41598-022-13006-6

Phillips J. 1836. *Illustrations of the Geology of Yorkshire, Part II. The Mountain Limestone District.* John Murray, London.

Platt M.I. 1938. A new species of *Temnocheilus* McCoy from Holy Island, Northumberland. *Geological Magazine* 75: 454–459. https://doi.org/10.1017/S0016756800091895

Pohle A. & Klug C. 2018. Body size of orthoconic cephalopods from the late Silurian and Devonian of the Anti-Atlas (Morocco). *Lethaia* 51: 126–148. https://doi.org/10.1111/let.12234

Ramsbottom W. & Moore E. 1961. Coiled nautiloids from the Viséan of Ireland. *Geological Journal* 2 (4): 630–644. https://doi.org/10.1002/gj.3350020406

Ruan Y. & Zhou Z. 1987. Carboniferous cephalopods in Ningxia Hui Autonomous Region. *In*: *Namurian Strata and Fossils of Ningxia, China*: 55–177. China Scientific Books, Hong Kong.

Schmidt H. 1951. Nautiliden aus deutschem Unterkarbon. *Paläontologische Zeitschrift* 24: 23–57. https://doi.org/10.1007/BF03044551

Shimansky V.N. 1957. Sistematika i filogeniya otryada Nautilida. *Byulleten' moskovskogo Obshchestva Ispytatelei Prirody, Otdel geologicheskiy* 32: 105–120.

Shimansky V.N. 1967. Kamennougol'nye Nautilida. *Trudy paleontologicheskogo Instituta Akademiya Nauk SSSR* 115: 1–244.

Sowerby J. 1821. *The Mineral Conchology of Great Britain; or Coloured Figures and Descriptions of those Remains of Testaceous Animals or Shells, which have been Preserved at Various Times and Depths in the Earth*. Vol. 3. Arding, London.

Sowerby J.D.C. 1825. *The Mineral Conchology of Great Britain; or Coloured Figures and Descriptions of those Remains of Testaceous Animals or Shells, which have been Preserved at Various Times and Depths in the Earth*. Vol. 5. Richard Taylor, London.

Sturgeon M.T. & Miller A.K. 1948. Some additional cephalopods from the Pennsylvanian of Ohio. *Journal of Paleontology* 22: 75–80.

Sweet W.C. & Brookley A.C. 1956. An *Endolobus* from the Beaver Bend Limestone (Chester) of Indiana. *Journal of Paleontology* 30: 101–103.

Teichert C. 1964. Morphology of hard parts. *In*: Moore R.C. (ed.) *Treatise on Invertebrate Paleontology*: K13–K53. The Geological Society of America and The University of Kansas Press, Lawrence, KS.

Tendler A., Mayo A. & Alon U. 2015. Evolutionary tradeoffs, Pareto optimality and the morphology of ammonite shells. *BMC Systems Biology* 9: e12. https://doi.org/10.1186/s12918-015-0149-z

Trenkner W. 1868. Palaeontologische Novitäten vom nordwestlichen Harze. I. Iberger Kalk und Kohlengebirge von Grund. *Abhandlungen der naturforschenden Gesellschaft zu Halle* 10: 123–182.

Tsvetaeva M. 1898. Nautilidy i ammonei nizhnego otdela srednerusskogo kamennougol'nogo izvestnyaka. *Trudy geologicheskogo Komiteta* 8 (4): I–VII, 1–46.

Turner J.S. 1954. On the Carboniferous nautiloids: some Middle Viséan species from the Isle of Man. *Liverpool and Manchester Geological Journal* 1 (3): 298–325. https://doi.org/10.1002/gj.3350010307

Turner J.S. 1965. On the Carboniferous nautiloids: *Nautilus quadratus* Fleming and certain other coiled nautiloids. *Proceedings of the Leeds Philosophical and Literary Society* 9: 223–256.

Winchell A. 1862. Notice of the rocks lying between the Carboniferous limestone of the Lower Peninsula of Michigan and the limestones of the Hamilton group; with descriptions of some cephalopods supposed to be new to science. *American Journal of Science and Arts* 33: 352–366. https://doi.org/10.2475/ajs.s2-33.99.352

Youngquist W. 1949. The cephalopod fauna of the White Pine shale of Nevada. *Journal of Paleontology* 23: 276–305.

*Manuscript received: 22 November 2022*
*Manuscript accepted: 2 January 2023*
*Published on: 2 August 2023*
*Topic editor: Marie-Béatrice Forel*
*Desk editor: Kristiaan Hoedemakers*

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic.

# ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: European Journal of Taxonomy

Jahr/Year: 2023

Band/Volume: 0885

Autor(en)/Author(s): Korn Dieter, Klug Christian

Artikel/Article: Early Carboniferous coiled nautiloids from the Anti-Atlas (Morocco) 156-194