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Research article

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The nautiloids from the Early Carboniferous Dalle à *Merocanites* of Timimoun, western Algeria

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Abstract. Early Carboniferous coiled nautiloids from North Africa are virtually unknown. An assemblage of nine species, all from the family Trigonoceratidae, from the Dalle à *Merocanites* (Tournaisian-Viséan boundary interval) of Timimoun in western Algeria is described, being the most diverse Carboniferous nautiloid assemblage known from North Africa but much less diverse than the time-equivalent assemblages from Belgium and Ireland. The assemblage consists of the species *Maccoyoceras pentagonum* sp. nov., *Lispoceras orbis* sp. nov., *Thrincoceras devolvere* sp. nov., *Rineceras multituberculatum* sp. nov., *Rineceras rectangulatum* sp. nov., *Vestinautilus padus* sp. nov., *Vestinautilus concinnus* sp. nov., *Planetoceras destrictum* sp. nov. and *Planetoceras transforme* sp. nov. A morphometric analysis of *Maccoyoceras pentagonum* sp. nov. and *Lispoceras orbis* sp. nov. shows that the intraspecific variation in these species is within rather narrow limits.

Keywords. Nautiloidea, Early Carboniferous, Algeria, morphology, taxonomy.

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Introduction

The evolutionary history of Carboniferous nautiloids is far less well-studied than that of ammonoids. This is partly due to the mostly much rarer finds; the fossil record of nautiloids is incomplete because of many stratigraphic gaps. For example, little is known about coiled nautiloids at the Devonian–Carboniferous transition, as no earliest Tournaisian representatives are yet known (Dzik 1984; Dzik &

Korn 1992). Only from the middle to late Tournaisian, the assemblages are quite species-rich with a broad morphological spectrum known from several regions.

Coiled nautiloids are often recovered as 'accompanying fauna' when collecting ammonoids, but they are usually far behind the ammonoids in terms of specimen numbers. This is possibly owing to the facies; Palaeozoic ammonoids are particularly common in sedimentary rocks of the deep shelf, while nautiloids tended to prefer shallower areas. Therefore, coiled nautiloids outnumber ammonoids only in certain lithologies and regions, such as in the Carboniferous limestones of Belgium (de Koninck 1844, 1878, 1880; Demanet 1938) and Ireland (Sowerby 1825; Foord 1900, 1901; Histon 1999), which globally yield the most diverse Early Carboniferous nautiloid assemblages. In contrast to the assemblages of Ireland and Belgium, Early Carboniferous coiled nautiloids have only occasionally been collected in greater diversity in other regions. These regions include the American Midwest (e.g., Hyatt 1893; Miller *et al.* 1933; Miller & Garner 1953; Niko & Mapes 2015, 2016) as well as the Ural Mountains (Shimansky 1967) and the Rhenish Mountains (Holzapfel 1889; Schmidt 1951).

Apparently, the considerably poorer fossil record of the Carboniferous nautiloids also had a major impact on the research history of these organisms. In contrast to the ammonoids, which were intensively collected and studied for stratigraphic purposes for much of the 20th century, there was no such need for the coiled nautiloids. It is therefore probably no coincidence that the first revision of nautiloids from Foord's monographs did not take place until a hundred years later (Histon 1999). The nautiloids in the monographs of de Koninck have not yet been revised at all.

Early Carboniferous coiled nautiloids from North Africa are almost unknown; there is only one short study (Delépine 1939) describing two specimens from Erfoud (Morocco). Here, we describe an assemblage of nine species from the Dalle à *Merocanites* (Tournaisian-Viséan boundary interval) of Timimoun in western Algeria. In contrast to the occurrences in Ireland and Belgium, which are closely associated with Waulsortian mudmounds, the new collections come from deposits of the deeper shelf. We compare it in terms of morphological diversity with time-equivalent records from other regions, with a special focus on Ireland and Belgium.

Material and methods

We examined a material consisting of a total of 56 specimens. All specimens are from the Dalle à *Merocanites* (Conrad 1984) of outcrops in the Sebkha de Timimoun (Fig. 1), 14.5 km west-southwest of Timimoun (Gourara, Algeria). The nautiloids occur there together with the species-rich *Ammonellipsites-Merocanites* ammonoid assemblage, which is present in considerably larger numbers of individuals (637 specimens of ammonoids belonging to 16 species were described by Ebbighausen *et al.* 2010).

The Dalle à *Merocanites* is a limestone unit about 1.90 m thick; it consists of a few, mainly sideritic and dolomitised nodular layers separated by strongly weathered shales. Like the ammonoids, the nautiloids from this unit are rather well preserved, although some details have been destroyed by dolomitisation. Several specimens are preserved including the protoconch and the body chamber and show an excellently preserved shell surface with the most delicate details.

The material studied here is kept in the fossil cephalopod collection at the Museum für Naturkunde, Berlin under the catalogue numbers MB.C.30378 to MB.C.30386. The specimens have conch diameters of up to 90 mm; this means that they do not reach the size of some of the Irish and Belgian time equivalent individuals. This is partly due to the composition of the Timimoun assemblage, which exclusively consists of the superfamily Trigonoceratoidea Hyatt, 1884, whereas the assemblages from Ireland and Belgium contain large-sized representatives of the Liroceratoidea Miller & Youngquist, 1949 and Aipoceratoidea Hyatt, 1883.

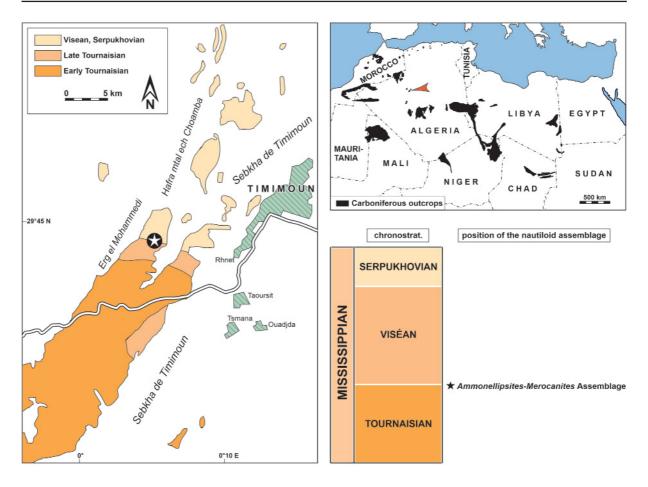


Fig. 1. Geographic and stratigraphic position of the fossil site in the Dalle à *Merocanites* near Timimoun with the nautiloid assemblage described here.

The following species are represented in the Timimoun assemblage:

Maccoyoceras pentagonum sp. nov.	34 specimens
Lispoceras orbis sp. nov.	15 specimens
Thrincoceras devolvere sp. nov.	1 specimen
Rineceras multituberculatum sp. nov.	1 specimen
Rineceras rectangulatum sp. nov.	1 specimen
Vestinautilus padus sp. nov.	1 specimen
Vestinautilus concinnus sp. nov.	1 specimen
Planetoceras destrictum sp. nov.	1 specimen
Planetoceras transforme sp. nov.	1 specimen

The morphological description of the material follows, to the extent possible, the scheme for Palaeozoic ammonoids outlined by Korn (2010) and Klug *et al.* (2015). However, due to the lack of ontogenetic data of some species, some of the descriptions must remain incomplete.

Abbreviations used in the species descriptions

ah = apertural height dm = conch diameter IZR = imprint zone rate

MB.C. = Cephalopod collection of the Museum für Naturkunde, Berlin

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

Genus Maccovoceras Miller, Dunbar & Condra, 1933

Type species

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

Diagnosis

Genus of the family Trigonoceratidae with evolute conch; whorls slightly impressed; whorl profile hexagonal or pentagonal with flattened venter and narrowly rounded umbilical margin. 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

Nautilus (Trematodiscus) discoidalis Winchell, 1862, Michigan; Nautilus (Discites) discors M'Coy, 1844, Ireland; Nautilus Leveilleanus de Koninck, 1844, Belgium; Maccoyoceras pentagonum sp. nov., Algeria; Discitoceras wrightii Foord, 1900, Ireland.

Stratigraphic range

Late Tournaisian to Viséan.

Maccoyoceras pentagonum sp. nov. urn:lsid:zoobank.org:act:5C272A6C-5B23-4D36-B28B-8650C8A6D38B Figs 2–3; Table 1

Diagnosis

Species of Maccoyoceras reaching about 80 mm conch diameter. Conch with weakly compressed to circular whorl profile (ww/wh = 0.80–1.00); venter flattened or completely applanate, ventrolateral shoulder narrowly rounded or subangular. Whorls very weakly embracing or just touching. Ornament in the juvenile stage with spiral lines on the flank and outer area of the venter, in the adult stage without spiral lines. Growth lines with weakly biconvex course with a shallow lateral sinus and a moderately high ventrolateral projection.

Etymology

From the Latin 'pentagon'; referring to the shape of the whorl profile.

Type material

Holotype

ALGERIA • Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); illustrated in Fig. 2A; MB.C.30378.1.

Paratypes

ALGERIA • 33 specimens; Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); MB.C.30378.2– MB.C.30378.34.

Description

Holotype MB.C.30378.1 is the largest specimen available; it has a conch almost 74 mm in diameter (Fig. 2A). It is extremely discoidal and subevolute (ww/dm = 0.31; uw/dm = 0.37) with compressed whorls (ww/wh = 0.80) and a very high coiling rate (WER = 2.65). The inner whorls are loosely coiled with a 6 mm wide umbilical window; the dorsum touches the venter of the previous whorl after one and a quarter whorl. The first whorl and a half are circular in profile. Thereafter, the venter becomes flattened and bordered to the flanks by a subangular shoulder. At 25 mm in diameter, the umbilical margin becomes narrowly rounded. During the last half whorl, the ventrolateral shoulder becomes rounded and the venter is broadly convex in profile (Fig. 3A).

The ornament shows a succession of four developmental stages in the present specimens:

- (1) On slightly more than the first volution, up to a conch diameter of 15 mm, coarse spiral lines and growth lines form a granular surface on the flanks. The growth lines extend backwards on the flank.
- (2) For almost three quarters of a whorl between 15 and 28 mm in diameter, the flanks are ornamented with spiral lines that become strikingly finer during this growth interval. At the beginning of this stage, they are much wider than their interstices, but at the end they are visible as very fine lines separated by interstices ten times wider. Some of the spiral lines granulate out to a diameter of the conch of 23 mm.
- (3) A short segment of a volution (between 28 and 32 mm dm) shows hardly visible spiral lines; biconvex, rather coarse growth lines with a weakly biconvex course are the dominant type of ornament.
- (4) Beyond 32 mm diameter of the conch, the ornament consists only of coarse growth lines. They are weakly biconvex with a very low dorsolateral projection, a shallow lateral sinus, a low ventrolateral projection; the venter is almost smooth.

The other specimens illustrated here largely confirm the ornament development of specimen MB.C.30378.1 or provide additional information. Specimen MB.C.30378.4 (Fig. 2D) has a very well-preserved shell ornament; it clearly shows the sudden change that terminates the second ontogenetic ornament stage at 26 mm diameter. The third stage with clearly weaker spiral lines is only 45 degrees long.

Specimen MB.C.30378.8 (Fig. 2H) shows, up to at least 40 mm conch diameter, spiral lines on the venter. Specimen MB.C.30378.5 (Fig. 2E) possesses, between 15 and 20 mm diameter, rather coarse spiral lines.

Between 20 and 70 mm shell diameter, there are ontogenetic changes in the shell proportions (Fig. 3B–E). These specimens show that the conch becomes more slender (ww/dm decreases from 0.40 to 0.30) and slightly more involute (uw/dm decreases from 0.45 to 0.40). Additionally, the whorl profile becomes more compressed (ww/wh decreases from 1.10 to 0.80). For the first three parameters of the conch, the

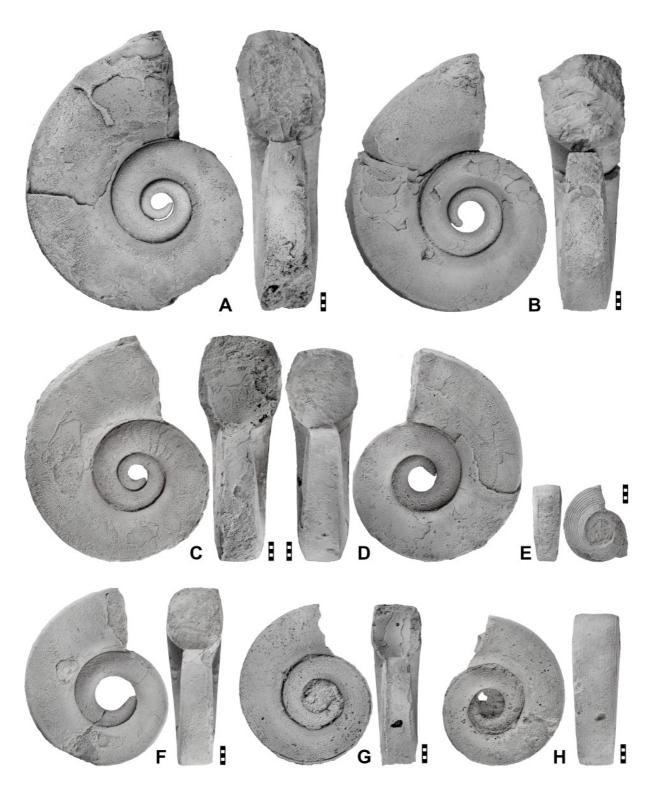


Fig. 2. *Maccoyoceras pentagonum* sp. nov. **A.** Holotype MB.C.30378.1. **B.** Paratype MB.C.30378.2. **C.** Paratype MB.C.30378.3. **D.** Paratype MB.C.30378.4. **E.** Paratype MB.C.30378.5. **F.** Paratype MB.C.30378.6. **G.** Paratype MB.C.30378.7. **H.** Specimen MB.C.30378.8. Scale bar units = 1 mm.

Table 1. Conch dimensions (in mm) and ratios of *Maccoyoceras pentagonum* sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30378.1	73.6	22.7	28.4	27.4	28.4	0.31	0.80	0.37	2.65	0.00
MB.C.30378.2	62.3	20.3	21.5	26.5	21.5	0.33	0.94	0.43	2.33	0.00
MB.C.30378.3	58.8	21.0	21.8	23.4	21.8	0.36	0.96	0.40	2.53	0.00
MB.C.30378.4	54.3	17.5	19.2	21.8	19.2	0.32	0.91	0.40	2.40	0.00
MB.C.30378.6	47.2	14.9	16.3	20.3	16.3	0.32	0.91	0.43	2.33	0.00
MB.C.30378.7	42.4	13.3	13.5	19.5	13.5	0.31	0.99	0.46	2.15	0.00
MB.C.30378.8	39.9	13.0	13.2	17.7	13.2	0.33	0.99	0.44	2.24	0.00
MB.C.30378.5	20.2	7.8	6.9	8.8	6.9	0.39	1.13	0.44	2.31	0.00

intraspecific variation is small (Fig. 3B–D). In contrast, the plasticity of the coiling rate is very striking; the whorl expansion rate ranges from 2.10 to 2.70 between 30 and 40 mm conch diameters (Fig. 3E).

Remarks

Maccoyoceras pentagonum sp. nov. has a similar conch shape and ornament to the other species of the genus already known from Belgium and Ireland. However, the new species differs from M. discors (M°Coy 1844) in the compressed whorl profile, which is approximately quadrate at 80 mm conch diameter in M. discors. Maccoyoceras leveilleanum has a convex venter (de Koninck 1844) and M. wrightii (Foord, 1900) has a convex venter and an even more compressed whorl profile (ww/wh \sim 0.70 at 50 mm dm) (Foord 1900).

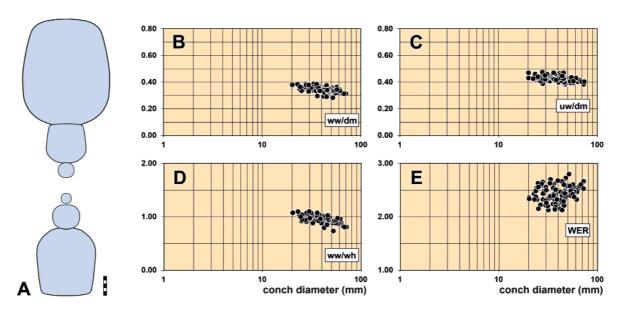


Fig. 3. *Maccoyoceras pentagonum* sp. nov. **A.** Reconstructed cross section of the holotype MB.C.30378.1. **B–E.** Ontogenetic trajectories of the cardinal conch parameters of selected specimens. Scale bar units = 1 mm.

Genus Lispoceras Hyatt, 1893

Type species

Lispoceras trivolve Hyatt, 1893; original designation.

Diagnosis

Genus of the family Trigonoceratidae with evolute conch; whorls just touching each other; whorl profile weakly depressed elliptical or circular. Ornament in the adult stage with fine 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

Lispoceras orbis sp. nov., Algeria; Lispoceras proconsul Shimansky, 1967, Kazakhstan; Lispoceras rotundum Hyatt, 1893, Ireland; Lispoceras trivolve var. simplum Hyatt, 1893, Belgium; Lispoceras trivolve Hyatt, 1893, Belgium.

Remarks

Lispoceras was an insufficiently described and delimited genus; the type species L. trivolve was described by Hyatt (1893: 426) but not illustrated. Kummel (1964: K430) then published a photographic illustration of the type species and Shimansky (1967: 141) provided a more accurate diagnosis of the genus.

Stratigraphic range

Late Tournaisian to Viséan.

Lispoceras orbis sp. nov. urn:lsid:zoobank.org:act:06A766FF-8347-4085-ACB2-39F48B4AD4AE Figs 4–6; Table 2

Diagnosis

Species of *Lispoceras* reaching about 90 mm conch diameter. Conch with nearly circular whorl profile (ww/wh = 1.00-1.10). The outer whorl just touches the preceding ones. Ornament in the juvenile stage with spiral lines on the flank and the venter, in the adult stage without spiral lines. Growth lines with weakly biconvex course with a shallow lateral sinus, a moderately high ventrolateral projection and a deep, semicircular ventral sinus.

Etymology

From the Latin nomen 'orbis', meaning 'circle' and referring to the whorl profile.

Type material

Holotype

ALGERIA • Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); illustrated in Fig. 4A; MB.C.30379.1.

Paratypes

ALGERIA • 14 specimens; Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); MB.C.30379.2– MB.C.30379.15.

Description

Holotype MB.C.30379.1 consists of just over two and a half volutions, in which it reaches a conch diameter of 84 mm (Fig. 4A). Its initial stage is loosely coiled with an 8 mm wide umbilical window; the poorly preserved protoconch has a circular whorl profile of about 2.5 mm diameter. The umbilical window is closed at 26 mm diameter of the conch. The proportions of the conch change only slightly ontogenetically; the whorl profile is circular throughout ontogeny. At a diameter of 84 mm, the conch is thinly discoidal and subevolute (ww/dm = 0.42; uw/dm = 0.39), with a high coiling rate of the conch (WER = 2.66). Near the maximum diameter of the specimen, the whorl width increases (ww/wh = 1.10), which may indicate adulthood of the specimen.

The ornament shows a succession of four developmental stages in the present specimens:

(1) The first volution, up to a conch diameter of 18 mm, possesses a combination of coarse spiral lines (about 50 from middorsum to midventer) and growth lines of the same strength. Together, they

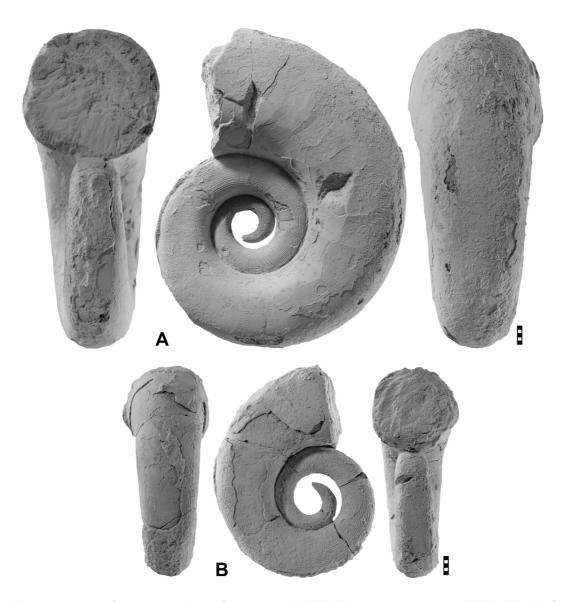


Fig. 4. *Lispoceras orbis* sp. nov. **A.** Holotype MB.C.30379.1. **B.** Paratype MB.C.30379.2. Scale bar units = 1 mm.

- produce a coarse granulation, in which the elements are much wider than their interstices. The growth lines extend backwards on the flank.
- (2) In the three quarters of a whorl between 18 and 36 mm diameter, the ornament is reticulate with a continuous weakening of both the spiral lines and the granulation. At a diameter of 20 mm, the spiral lines are as wide as their interspaces, but at 36 mm diameter, the interspaces are already five times as wide as the spiral lines. The growth line course is rectiradiate and weakly biconvex.
- (3) In a quarter of a volution (between 36 and 44 mm dm), the spiral lines are very weak; the growth lines are also weaker when compared with the preceding stage.

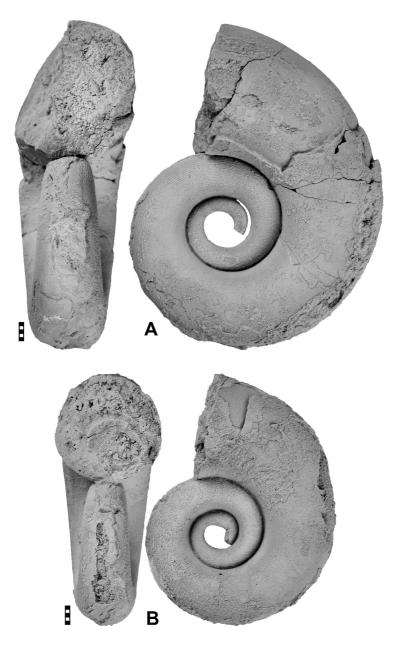


Fig. 5. *Lispoceras orbis* sp. nov. **A.** Paratype MB.C.30379.3. **B.** Paratype MB.C.30379.4. Scale bar units = 1 mm.

Table 2. Conch dimensions (in mm) and ratios of Lispoceras orbis sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30379.1	83.6	35.5	32.3	33.0	32.3	0.42	1.10	0.39	2.66	0.00
MB.C.30379.3	72.5	29.2	28.4	27.4	28.4	0.40	1.03	0.38	2.70	0.00
MB.C.30379.4	65.7	27.6	27.0	24.4	26.0	0.42	1.02	0.37	2.73	0.04
MB.C.30379.2	55.0	21.0	21.4	21.5	21.4	0.38	0.99	0.39	2.67	0.00

(4) The last stage above 44 mm conch diameter is then characterised by the loss of the spiral lines. Very fine growth lines extend across the flank in a weakly biconvex course, forming a deep, semicircular ventral sinus.

Intraspecific variation is limited in the material (Fig. 6B–E), but the cardinal conch parameters show some ontogenetic changes in the growth interval between 20 and 85 mm conch diameter: (1) the ww/dm ratio increases slowly from an average of 0.38 to 0.42 (Fig. 6B), (2) the uw/dm ratio decreases from nearly 0.50 to 0.38 (Fig. 6C), (3) the ww/wh ratio decreases from 1.20 to 1.00 (Fig. 6D) and (4) the whorl expansion rate shows a more prominent increase from 2.20 to 2.80 (Fig. 6E).

Variation in the ornament is also limited. The change from the third to the fourth ornament stage, for instance, takes place between 37 and 42 mm conch diameter in specimens MB.C.30379.4 (Fig. 5B), MB.C.30379.2 (Fig. 4B) and MB.C.30379.3 (Fig. 5A).

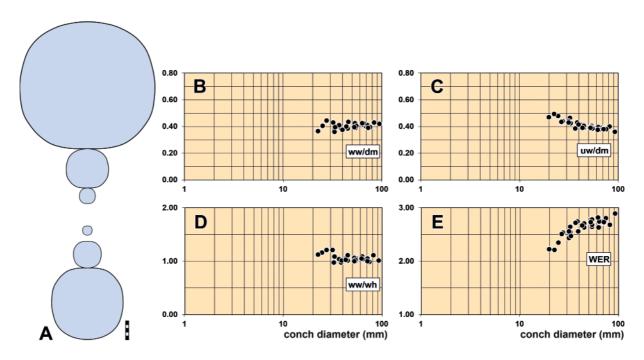


Fig. 6. *Lispoceras orbis* sp. nov. **A.** Reconstructed cross section of holotype MB.C.30379.1. **B–E.** Ontogenetic trajectories of the cardinal conch parameters of selected specimens. Scale bar units = 1 mm.

Remarks

Lispoceras orbis sp. nov. has a circular to very weakly depressed whorl profile (ww/wh = 1.00-1.10) and thus differs from *L. trivolve* with a slightly more depressed whorl profile (ww/wh = 1.25). In addition, *L. trivolve* has much coarser spiral lines (Kummel 1964). *L. proconsul* also has more depressed whorl profile (ww/wh = 1.05-1.25) and whorls that detach from the previous whorl at about 30 mm diameter of the conch (Shimansky 1967).

Genus *Thrincoceras* Hyatt, 1893

Type species

Thrincoceras depressum Hyatt, 1893; subsequent designation by Schmidt (1951).

Diagnosis

Genus of the family Trigonoceratidae with evolute conch; whorls slightly impressed or slightly detached; whorl profile nearly quadrate with flattened venter and narrowly rounded ventrolateral shoulder and umbilical margin. Ornament with fine growth lines and moderately coarse spiral lines. Suture line with shallow external and lateral lobes. Siphuncle small with subcentral position (after Kummel 1964; emended).

Included species

Thrincoceras depressum Hyatt, 1893, Kentucky; Gyroceras Hibernicum Foord, 1891, Ireland; Thrincoceras Hyatti Foord, 1900, Ireland; Thrincoceras kentuckiense Hyatt, 1893, Kentucky; Thrincoceras devolvere sp. nov., Algeria.

Remarks

Several genera with a coarse spiral ornament and granulation on the spirals were introduced within the family Trigonoceratidae; these show a rather continuous morphological variation:

Chouteauceras Miller & Garner, 1953 – whorls compressed, oval, separated by interspaces;

Rineceras Hyatt, 1893 – whorls depressed, oval or rounded triangular, separated by interspaces;

Pararineceras Turner, 1954 – whorls depressed, oval or rounded triangular to rounded-trapezoidal, touching or slightly embracing the preceding one;

Discitoceras Hyatt, 1884 – whorls depressed, subtrapezoidal with narrowly rounded venter, slightly embracing the preceding one;

Thrincoceras Hyatt, 1893 – whorls subquadrate in section and embracing the preceding one. However, one must bear in mind that *Thrincoceras* also developed an adult stage in which the whorl loses contact with the preceding one. The holotype of *T. hyatti*, for instance, uncoils at about 90 mm conch diameter (Foord 1900; Histon 1999).

Stratigraphic range

Late Tournaisian to Late Carboniferous (?).

Thrincoceras devolvere sp. nov. urn:lsid:zoobank.org:act:DFAFE2FC-2688-426E-B543-D0F61D31C354 Fig. 7; Table 3

Diagnosis

Species of *Thrincoceras* with weakly depressed, rounded-trapezoidal whorl profile (ww/wh ~ 1.40), venter slightly flattened, ventrolateral shoulder broadly rounded. Whorls slightly embracing, above

40 mm dm with the tendency for slow uncoiling. Ornament with about 20 spiral lines on the flank and few delicate spiral lines on the outer part of the venter, main area of the venter without spiral lines. Growth lines concavo-convex with shallow lateral sinus and deep, rounded V-shaped ventral sinus.

Etymology

After the Latin verb 'devolvere', meaning 'devolve', referring to the coiling.

Type material

Holotype

ALGERIA • Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); illustrated in Fig. 7; MB.C.30380.

Description

Holotype MB.C.30380 is an incomplete specimen with 43 mm diameter of the conch (Fig. 7). It is thinly discoidal and evolute (ww/dm = 0.44; uw/dm = 0.48), with a weakly depressed, rounded-trapezoidal whorl profile (ww/wh = 1.37) and a high coiling rate (WER = 2.14). It can be seen on the specimen that uncoiling starts at the last quarter of the last whorl, as the depth of the imprint zone decreases slightly.

The ornament consists of about 20 spiral lines on the flank, which are raised to faint ridges in the region of the middle flank and become weaker towards both the umbilicus and the venter. These spirals are crossed by finer growth lines and together form a conspicuous granulation on the penultimate volution. Most part of the venter does not have spiral lines; there are delicate growth lines, which form a deep and wide, rounded V-shaped ventral sinus. It appears that one volution earlier, spirals are also developed on the venter, but the specimen is poorly preserved in this area.

Remarks

Thrincoceras devolvere sp. nov. differs from the two North American species T. kentuckiense and T. depressum first in the size of the conch, which in the two latter species reaches well over 100 mm (Hyatt 1893). T. kentuckiense, however, has a very similar whorl profile to T. devolvere sp. nov., but shows no detachment of the whorls from the preceding one.

The species known from Ireland, *T. hyatti* and *T. hibernicum*, have more subangular ventrolateral shoulders and flattened flanks (Foord 1891, 1900) and therefore differ in whorl profile from *T. devolvere* sp. nov.

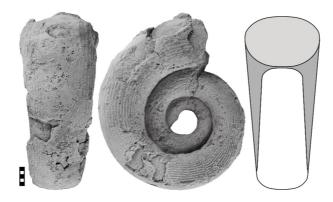


Fig. 7. *Thrincoceras devolvere* sp. nov., holotype MB.C.30380. Scale bar units = 1 mm.

Table 3. Conch dimensions (in mm) and ratios of *Thrincoceras devolvere* sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30380	43.2	18.8	13.7	20.9	13.7	0.44	1.37	0.48	2.14	0.00

Genus *Rineceras* Hyatt, 1893

Type species

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

Diagnosis

Genus of the family Trigonoceratidae with evolute conch; whorls detached or slightly in contact; whorl profile elliptical or rounded triangular with broad venter. Ornament with coarse growth lines and coarse spiral ridges; coarse granulation at the crossing points of growth lines and spiral ridges. Suture line with shallow external and lateral lobes. Siphuncle small with subcentral position (after Kummel 1964; emended).

Included Early Carboniferous species

Rhineceras alapaevskensis Kruglov, 1934, Urals; Pararineceras balladoolense Turner, 1954, Isle of Man; Nautilus canaliculatus von Eichwald, 1857, south Urals; Rineceras carinatiforme Shimansky, 1967, Kazakhstan; Nautilus carinatus von Eichwald, 1857, western Russia; Nautilus (Discus) digonus Meek & Worthen, 1860, Indiana; Nautilus Luidii Fleming, 1828, Derbyshire; Nautilus (Trematodiscus) Meekianus Winchell, 1862, Michigan; Gyroceras Meyerianum de Koninck, 1844, Belgium; Rineceras multituberculatum sp. nov., Algeria; Rineceras ohioense Miller & Garner, 1953, Ohio; Triboloceras patteiskyi Schmidt, 1951, Rhenish Mountains; Gyroceras propinquum de Koninck, 1880, Belgium; Rineceras rectangulatum sp. nov., Algeria; Nautilus rhenanus Holzapfel, 1889, Rhenish Mountains; Nautilus (Trematodiscus) strigatus Winchell, 1862, Michigan.

Remarks

Turner (1954) introduced the genus *Pararineceras* on the basis of the species originally described by Martin (1793, 1809) as "Conchyliolithus N. Ammonites (*Luidii*)", but as Martin did not follow the Linnaean binomial procedure, Fleming (1828) is regarded as the author of the species (Turner 1953). This species differs from most of the species assigned to the genus *Rineceras* only by the more densely coiled conch, a character that might be gradual and not useful for a separation of genera. While Kummel (1964) accepted both of the two genera, Shimansky (1967) and Dzik (1984) regarded *Pararineceras* as a synonym of *Rineceras*. In the following, we treat *Pararineceras* a junior synonym of *Rineceras* until a clear separation can be demonstrated.

Stratigraphic range

Middle Tournaisian to Serpukhovian.

Rineceras multituberculatum sp. nov. urn:lsid:zoobank.org:act:B0489DAA-C8AB-4809-92D3-6F3120899BBD Fig. 8; Table 4

Etymology

After the Latin 'multi', meaning 'many', and 'tuberculum', meaning 'tubercle' and referring to the shell ornament.

Table 4. Conch dimensions (in mm) and ratios of *Rineceras multituberculatum* sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30381	21.3	9.9	6.9	9.7	6.2	0.47	1.45	0.45	1.99	0.09

Type material

Holotype

ALGERIA • Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); illustrated in Fig. 8; MB.C.30381.

Diagnosis

Species of *Rineceras* with weakly depressed, rounded-trapezoidal whorl profile (ww/wh \sim 1.45), venter slightly flattened, ventrolateral shoulder broadly rounded. Whorls slightly embracing. Ornament with about 25 spiral lines on the flank and the venter.

Description

Holotype MB.C.30381 has a conch diameter of 21 mm (Fig. 8), with a depressed, rounded-trapezoidal whorl profile (ww/wh = 1.44) with a flattened venter and a broadly rounded ventrolateral shoulder. The whorl embraces the preceding only a very little. The well-preserved ornament consists of about 20 (from umbilicus to midventer) coarse spiral lines with a coarse granulation at the points of intersection with the growth lines. The spiral lines are equally coarse on the flanks and the venter.

Remarks

With its rounded trapezoidal whorl profile, *Rineceras multituberculatum* sp. nov. differs from species such as *R. propinquum* (de Koninck, 1880), *R. carinatum* (von Eichwald, 1857), *R. alapaevskense* and *R. ohioense*, which are loosely coiled and have either a rounded triangular, or an oval whorl profile (Koninck 1880; Miller & Garner 1953; Shimansky 1967). In this respect, *R. multituberculatum* sp. nov. and *R. meekianum* (Winchell, 1862) are similar (Winchell 1862), but have only weak spiral lines on the venter. *Rineceras canaliculatum* (von Eichwald, 1857) has a whorl profile similar to *R. multituberculatum* sp. nov., but much coarser spiral lines on the flank (Shimansky 1967).

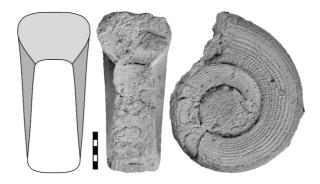


Fig. 8. Rineceras multituberculatum sp. nov., holotype MB.C.30381. Scale bar units = 1 mm.

Rineceras rectangulatum sp. nov.

urn:lsid:zoobank.org:act:B6626858-751D-4EA3-B80C-76D5D11CAAC7 Fig. 9; Table 5

Etymology

Referring to the rectangular ventrolateral shoulder.

Type material

Holotype

ALGERIA • Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); illustrated in Fig. 9, MB.C.30382.

Diagnosis

Species of *Rineceras* with weakly depressed, rounded-trapezoidal whorl profile (ww/wh ~ 1.45), venter flattened, umbilical shoulder broadly rounded without clean boundary between the flank and the umbilical wall. Whorls slightly embracing. Ornament in the juvenile stage with weak spiral lines on the flank.

Description

Holotype MB.C.30382 is an incomplete specimen with 50 mm diameter (Fig. 9). A little more than a quarter whorl belongs to the body chamber. The conch is thickly discoidal and subevolute (ww/dm = 0.57; uw/dm = 0.42) with a flat venter and an angular ventrolateral shoulder. The flanks are very slightly concave and diverge slowly towards the venter; the umbilical margin and the umbilical wall are broadly rounded. The penultimate volution differs in its oval whorl profile and the wider umbilicus (uw/dm = 0.50 at 24 mm dm). The umbilical window has a width of approximately 6 mm.

Most of the specimen is exfoliated and corroded, but the penultimate whorl shows about five spiral ridges on the flanks. Traces of these ridges are still visible on the last preserved volution. The suture line has a broadly V-shaped external lobe with rounded base on the venter, a shallow lobe on the flank and an incipient lobe on the umbilical wall.

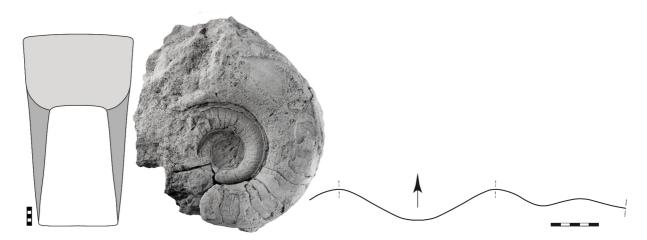


Fig. 9. Rineceras rectangulatum sp. nov., dorsal view reconstruction, lateral view and suture line (at 36 mm dm, 21 mm ww, 14 mm wh) of holotype MB.C.30382. Scale bar units = 1 mm.

Table 5. Conch dimensions (in mm) and ratios of *Rineceras rectangulatum* sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30382	50.7	29.0	20.1	21.2	18.9	0.57	1.44	0.42	2.54	0.06

Remarks

Rineceras rectangulatum sp. nov. differs from most species of the genus by the trapezoidal whorl profile with angular ventrolateral shoulder. *Rineceras carinatiforme* has a similar shape, but in this species the venter is broadly rounded here and not perfectly flat as in *R. rectangulatum* sp. nov. *Rineceras strigatum* (Winchell, 1862) is also similar, but shows a sharp ventrolateral shoulder (Shimansky 1967).

Genus Vestinautilus Ryckholt, 1852

Type species

Nautilus Koninckii d'Orbigny, 1850; subsequent designation by Hyatt (1883–1884).

Diagnosis

Genus of the family Trigonoceratidae with evolute conch; whorls slightly impressed; whorl profile rounded triangular or trapezoidal with flattened or weakly concave venter and pronounced ventrolateral shoulder. Ornament with fine lines and very coarse spiral ridges around the ventrolateral shoulder, sometimes also on the venter. Suture line slightly sinuous. Siphuncle small with subcentral position (after Kummel 1964; emended).

Included species

Nautilus (Trematodiscus) altidorsalis Winchell, 1862, Michigan; Nautilus biangulatus Sowerby, 1825, Southwest England; Nautilus cariniferus Sowerby, 1825, Ireland; Vestinautilus concinnus sp. nov. Algeria; Triboloceras formosum Foord, 1900, Ireland; Nautilus Koninckii d'Orbigny, 1850, Belgium; Nautilus multicarinatus Sowerby, 1825, Ireland; Vestinautilus padus sp. nov., Algeria; Coelonautilus paucicarinatus Foord, 1891, Ireland; Nautilus pinguis de Koninck, 1844, Belgium; Vestinautilus semiglaber Foord, 1900, Ireland; Vestinautilus semiplicatus Foord, 1900, Ireland.

Remarks

When Turner (1954) revised the genus *Vestinautilus*, he explicitly 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 profile, and a conch ornamented with spiral ribs, lirae and sulci." At the same time, he introduced the new genus *Subvestinautilus*, which he placed in the family Temnocheilidae Mojsisovics, 1902. 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 Hyatt, 1884, he indirectly regarded the close morphological similarity as a result of convergent evolution. This opinion was followed (albeit with other family names) by Shimansky (1967) and Histon (1999), but rejected by Dzik (1984), who treated *Subvestinautilus* as a synonym of *Vestinautilus*.

Here, we accept the separation of the two genera, but not the restrictive practice of Turner (1954), who considered the ventral shape (concave or convex) as the distinguishing character. The rather variable shape of the venter, which often changes throughout ontogeny in some of the species, can hardly be regarded as a criterion for distinguishing between the two families. We therefore assign those species

with coarse spiral ridges and a broad trapezoidal whorl profile, whether they possess a concave or convex venter, to *Vestinautilus*.

Stratigraphic range

Late Tournaisian to Viséan.

Vestinautilus padus sp. nov. urn:lsid:zoobank.org:act:9743A462-BB55-45D0-9BA6-1C1AB43DE9DC Fig. 10; Table 6

Etymology

After the Latin nomen 'padus', meaning 'twine, yarn' and referring to the conch shape like a yarn reel.

Type material

Holotype

ALGERIA • Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); illustrated in Fig. 10; MB.C.30383.

Diagnosis

Species of *Vestinautilus* with strongly depressed, rounded-trapezoidal whorl profile (ww/wh ~ 2.10), venter broadly arched, ventrolateral shoulder defined by an angular margin produced by a broad ridge. A second, sharper ridge is located on the umbilical wall near the ventrolateral shoulder. Whorls weakly embracing, coiling very high (WER ~ 2.55). Ornament with delicate growth lines.

Description

Holotype MB.C.30383 is a rather well-preserved specimen with a diameter of 34 mm (Fig. 10). It is a subevolute conch (ww/dm = 0.90; uw/dm = 0.33) with a very high coiling rate (WER = 2.57). The diameter of the umbilical window is about 5 mm. The whorl profile is strongly depressed (ww/wh = 2.11) and rounded-trapezoidal in outline with a broadly arched venter. The flanks and the venter are fused together; they are separated from the convex umbilical wall by two longitudinal ridges, which are separated by a shallow longitudinal groove. While the outer of the two ridges is subangular in cross section, the inner one is sharp and probably raised only by shell material. The shell ornament consists of delicate growth lines, which are reinforced on the inner longitudinal ridge.



Fig. 10. *Vestinautilus padus* sp. nov., holotype MB.C.30383. Scale bar units = 1 mm.

Table 6. Conch dimensions (in mm) and ratios of *Vestinautilus padus* sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30383	33.5	30.2	14.3	11.1	12.6	0.90	2.11	0.33	2.57	0.12

Remarks

Vestinautilus padus sp. nov. belongs to the species of the genus that possess a very broad whorl profile (ww/wh > 2.00) and an ornament with only a few spiral ridges. In this respect, *V. cariniformis* (Sowerby, 1825), *V. paucicarinatus* (Foord, 1891), *V. pinguis* (de Koninck, 1844) and *V. semiplicatus* are similar, but these four species have a concave venter at least in some phases in ontogeny (Sowerby 1825; de Koninck 1844; Foord 1891, 1900). Subvestinautilus crassimarginatus (Foord, 1900) and *S. crateriformis* (Foord, 1900) have a convex venter in all stages (Foord 1900), but they do not have the spiral ridges that are characteristic for *V. padus* sp. nov.

Vestinautilus concinnus sp. nov. urn:lsid:zoobank.org:act:B1F94168-8870-4D86-9220-ADC18E85D2AB Fig. 11; Table 7

Etymology

After the Latin 'concinnus', meaning 'harmonic, elegant' and referring to the ornament.

Type material

Holotype

ALGERIA • Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); illustrated in Fig. 11; MB.C.30384.

Diagnosis

Species of *Vestinautilus* with weakly depressed, trapezoidal whorl profile (ww/wh \sim 1.45), venter flattened, ventrolateral shoulder defined by an angular margin produced by a distinct ridge. Another four sharp ridges are located on the outer umbilical wall and two on the outer ventral area. Whorls weakly embracing. Ornament with sharp growth lines on the flank, producing elongate granulation when crossing the spiral ridges; growth lines delicate on the venter forming a deep sinus.

Description

Holotype MB.C.30384 is an incomplete specimen 32 mm in diameter (Fig. 11). It is a thickly discoidal, subevolute conch (ww/dm ~ 0.50 ; uw/dm ~ 0.45) with a weakly depressed whorl profile (ww/wh ~ 1.45). The whorl profile is subtrapezoidal with a broadly rounded umbilical wall, flattened and weakly converging flanks, a narrowly rounded ventrolateral shoulder and an almost flat venter. The flanks and the marginal part of the venter bear seven ridges. The interspace between the 4th and the 5th ridges is deepened to a longitudinal groove. The shell ornament consists of sharp, biconvex growth lines, which are coarsest on the flank; they are even coarser and produce a granulation when crossing the ridges. The suture line is only visible in some parts; broadly rounded ventral and lateral lobes are visible.

Remarks

Vestinautilus concinnus sp. nov. belongs to the species of the genus with a rather slender conch and hence a rather low ratio of whorl width and whorl height; therefore, the new species is easily distinguishable

Table 7. Conch dimensions (partly estimated; in mm) and ratios of *Vestinautilus concinnus* sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30384	32.1	16.0	11.1	14.3	10.7	0.50	1.44	0.45	2.25	0.04



Fig. 11. *Vestinautilus concinnus* sp. nov., holotype MB.C.30384. Scale bar units = 1 mm.

from most species of the genus including *V. padus* sp. nov. A fairly similar species is only *V. semiglaber*, but this species has seven spiral ridges on the flank (*V. concinnus* sp. nov. has only four) and a weakly concave venter (convex in *V. concinnus* sp. nov.) (Foord 1900).

Genus *Planetoceras* Hyatt, 1893

Type species

Planetoceras retardatum Hyatt, 1893; original designation.

Diagnosis

Genus of the family Trigonoceratidae with subevolute conch; whorls slightly impressed; whorl profile rectangular with weakly flattened venter, convex flanks and narrowly rounded umbilical margin. Ornament with fine growth lines, in the preadult stage with fine spiral ridges. Suture line with shallow external and lateral lobes. Siphuncle small with subcentral position (after Kummel 1964; emended).

Included species

Planetoceras bellilineatum Miller, Dunbar & Condra, 1933, Kentucky; Planetoceras destrictum sp. nov., Algeria; Nautilus globatus Sowerby, 1824, Ireland; Planetoceras invenustum Shimansky, 1967, South Urals; Planetoceras janischewskyi Shimansky, 1967, South Urals; Planetoceras retardatum Hyatt, 1893, Belgium; Nautilus schartimiensis Janischewsky, 1900, South Urals; Planetoceras tiltoni Miller, Dunbar & Condra, 1933, Iowa; Planetoceras transforme sp. nov., Algeria.

Remarks

Planetoceras was an insufficiently described and delimited genus; the type species *P. retardatum* was described by Hyatt (1893: 421) but not illustrated. Kummel (1964: K426) then published a photographic illustration of the type species. Miller *et al.* (1933: 138), Shimansky (1967: 130) and Histon (1999: 63) provided a more accurate diagnosis of the genus.

Stratigraphic range

Late Tournaisian to Bashkirian.

Planetoceras destrictum sp. nov. urn:lsid:zoobank.org:act:42BD8B9E-A638-4C4F-9472-0B0EE6AB489E Figs 12–13; Table 8

Diagnosis

Species of *Planetoceras* with moderately depressed, rounded-pentagonal whorl profile (ww/wh \sim 1.65), venter slightly flattened, ventrolateral shoulder broadly rounded. Umbilical margin subangular to narrowly rounded, umbilical wall steep, flattened. Whorls slightly embracing.

Etymology

After the Latin 'destrictum', meaning 'sharp' and referring to the angular umbilical margin.

Type material

Holotype

ALGERIA • Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); illustrated in Fig. 12; MB.C.30385.

Description

Specimen MB.C.30385 is a fully chambered specimen with a diameter of 67 mm (Fig. 12). It is a stout, subinvolute conch (ww/dm = 0.76; uw/dm = 0.29) and has a depressed, subtrapezoidal whorl profile with a broadly rounded venter, a rounded ventrolateral shoulder, weakly flattened, slightly converging flanks,



Fig. 12. Planetoceras destrictum sp. nov., holotype MB.C.30385. Scale bar units = 1 mm.

Table 8. Conch dimensions (in mm) and ratios of *Planetoceras destrictum* sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30385	67.1	50.8	30.8	19.5	25.4	0.76	1.65	0.29	2.59	0.18

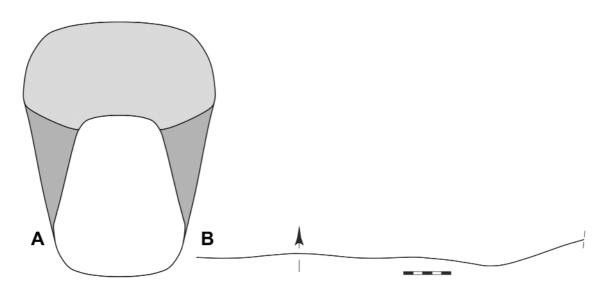


Fig. 13. *Planetoceras destrictum* sp. nov., holotype MB.C.30385. **A.** Dorsal view reconstruction. **B.** Suture line at 52 mm dm, 42 mm ww, 22 mm wh. Scale bar units = 1 mm.

a rounded umbilical margin and a rounded umbilical wall. It has a very high coiling rate (WER = 2.59). The specimen shows a morphological change in the shape of the umbilicus. During the last volution of the phragmocone, the umbilical margin changes from subangular to rounded. At the same time, the umbilical wall changes from flattened to rounded. The suture line extends nearly linearly across the venter and possesses a very shallow lobe on the flank (Fig. 13).

Remarks

Planetoceras destrictum sp. nov. differs from the species described from Belgium, the South Urals and North America in the flattened venter, which is rounded in those species. More similar is *P. globatum* (Sowerby, 1824), a species with a very similar whorl profile (Histon 1999) but a more slender conch (ww/dm ~ 0.55 at 58 mm dm) than *P. destrictum* sp. nov. (ww/dm ~ 0.76 at 67 mm dm). *Planetoceras transforme* sp. nov. (described below) has a much stouter conch (ww/dm ~ 0.85).

Planetoceras transforme sp. nov. urn:lsid:zoobank.org:act:CDD3B745-0819-4EA2-8728-D0CAB8CE609B Fig. 14; Table 9

Diagnosis

Species of *Planetoceras* with moderately depressed, rounded-pentagonal whorl profile (ww/wh > 2.00), venter slightly flattened, ventrolateral shoulder broadly rounded. Umbilical margin changes

Table 9. Conch dimensions (in mm) and ratios of *Planetoceras transforme* sp. nov.

Specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
MB.C.30386	43.8	37.4	18.0	11.8	16.5	0.85	2.08	0.27	2.57	0.08
MB.C.30386	27.8	23.0	11.1	10.2	10.3	0.83	2.07	0.37	2.52	0.07

from subangular to rounded, umbilical wall steep, changing from flattened to rounded. Whorls slightly embracing.

Etymology

After the Latin 'transforme', meaning 'changing', because of the rapid early ontogenetic change in morphology.

Type material

Holotype

ALGERIA • Gourara, Sebkha de Timimoun 14.5 km west-southwest of Timimoun; "Dalle à *Merocanites*" (Tournaisian-Viséan boundary interval); illustrated in Fig. 14; MB.C.30386.

Description

Holotype MB.C.30386 consists of the first whorl with a diameter of about 28 mm (Fig. 14A) and a fragment of the second whorl making a total diameter of 44 mm (Fig. 14B). The conch is stout and has a subtrapezoidal whorl profile at 28 mm in diameter and an angular umbilical edge raised by a sharp keel. A vertical, flattened umbilical wall extends from here on one side and a converging flank on the other. At a short distance from the umbilical margin there is a pronounced but rounded ventrolateral shoulder. On the broad, slightly flattened venter there is a shallow longitudinal furrow next to the ventrolateral shoulder. Half a whorl before, at about 16 mm in diameter, the whorl profile is oval and depressed; at this diameter four longitudinal ridges are present. Of these, the innermost one becomes the ridge on the umbilical margin during the next half whorl, and the second one becomes the ridge at the inside of the ventrolateral shoulder. The third and fourth ridges become weaker and disappear on the next half whorl.

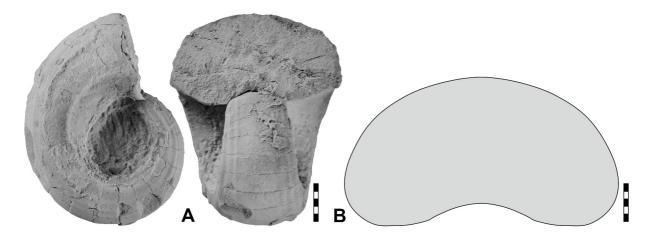


Fig. 14. *Planetoceras transforme* sp. nov., holotype MB.C.30386. **A**. Photograph of the inner whorl. **B**. Whorl profile of a larger phragmocone segment. Scale bar units = 1 mm.

The suture line extends almost straight across flanks and venter. The fragment of the larger whorl shows that the umbilical margin became rounded at 44 mm conch diameter (Fig. 14B).

Remarks

Planetoceras transforme sp. nov. differs from the other species of the genus in the very broad whorl profile (ww/wh > 2.00), which has a value of about 1.60 in other species such *as P. destrictum* sp. nov. and *P. globatum* (Histon 1999).

Discussion

An assemblage of nine species from the Dalle à *Merocanites* (Tournaisian-Viséan boundary interval) of Timimoun in western Algeria is described. The assemblage consists of the species *Maccoyoceras pentagonum* sp. nov., *Lispoceras orbis* sp. nov., *Thrincoceras devolvere* sp. nov., *Rineceras multituberculatum* sp. nov., *Rineceras rectangulatum* sp. nov., *Vestinautilus padus* sp. nov., *Vestinautilus concinnus* sp. nov., *Planetoceras destrictum* sp. nov. and *Planetoceras transforme* sp. nov.

The frequency distribution of the species within the assemblage is very uneven. While *Maccoyoceras pentagonum* sp. nov. is represented with 34 specimens and *Lispoceras orbis* sp. nov. with 15 specimens, the other seven species are present with only one specimen each. It is also significant that all the species discovered belong to a single family, the Trigonoceratidae. This means that the taxonomic diversity is considerably lower than in the time-equivalent assemblages from Belgium (de Koninck 1844, 1878) and Ireland (Foord 1900, 1901; Histon 1999).

A morphometric analysis of the two species represented by several specimens led to the result that the intraspecific variation in these species is within rather narrow limits. Only the coiling rate shows some variation, while the other important conch parameters are rarely variable.

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