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Ammonoids of the Middle Devonian family Maenioceratidae in the Anti-Atlas of Morocco

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Abstract. The ammonoids of the family Maenioceratidae from Givetian sedimentary rocks of the Anti-Atlas (Morocco) are investigated. The study is based on new collections stored in the Museum für Naturkunde, Berlin. The genera *Maenioceras* Schindewolf, 1933 and *Afromaenioceras* Göddertz, 1987 are revised; the genus *Trimaenioceras* is newly described. The species *Maenioceras afroterebratum* sp. nov., *Maenioceras mzerrebense* sp. nov., *Maenioceras oufranense* sp. nov., *Maenioceras beckeri* sp. nov., *Afromaenioceras sulcatostriatum* (Bensaïd, 1974), *Afromaenioceras hiemale* sp. nov., *Afromaenioceras bensaidi* sp. nov., *Afromaenioceras brumale* sp. nov., *Afromaenioceras crassum* (Bensaïd, 1974), *Trimaenioceras klugi* gen. et sp. nov., *Trimaenioceras eculeus* gen. et sp. nov., *Trimaenioceras fuscina* gen. et sp. nov. and *Trimaenioceras paucum* gen. et sp. nov. are described in detail.

Keywords. Ammonoida, Middle Devonian, Givetian, Morocco, Anti-Atlas.

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Introduction

Maenioceras Schindewolf, 1933 is a genus of Middle Devonian ammonoids, which early on acquired the status of an important index fossil; Wedekind (1918) used "*Goniatites terebratus*" to define the "Maenecerasstufe" with "*Goniatites terebratus* Sandberger & Sandberger, 1851", which according to the interpretation of the time was supposed to characterise the youngest period of the Middle Devonian. At that time, specimens of *Maenioceras* and related genera were only known from a few regions, namely the Rhenish Slate Mountains (Sandberger & Sandberger 1850–1856; Kayser 1872; Holzapfel 1895; Foord & Crick 1897; Frech 1897–1902), the Harz Mountains (Roemer 1852), southern England (Phillips 1841; Whidborne 1890; Foord & Crick 1897) and the Montagne Noire (Frech 1902). First reports and descriptions from other regions, such as the Anti-Atlas in Morocco (Termier & Termier

1950; Bensaïd 1974), the Saoura Valley in Algeria (Petter 1959; Göddertz 1987) and British Columbia in Canada (Wissner & Norris 1991), were only added with some time lag.

More recently, assemblages with maenioceratid ammonoids have been studied mainly from the Rhenish Mountains and the Anti-Atlas. House & Ziegler (1977) provided information about the occurrence of *Maenioceras* in the classical Adorf section. Ebbighausen *et al.* (2007) described the new species *M. heinorum* and Korn & Bockwinkel (2021) described the new species *M. ornatum*, both from the Rhenish Mountains. In the latter article it was already questioned whether the reports of *M. terebratum* from the various regions really refer to this species.

Much more detailed information about the stratigraphic distribution of the species of *Maenioceras* and *Afromaenioceras* Göddertz, 1987 have been published for sections in the Anti-Atlas in the last few decades (Belka *et al.* 1999; Aboussalam & Becker 2001, 2004; Korn & Klug 2002; Aboussalam *et al.* 2004; Becker *et al.* 2004). However, these finds were often not illustrated; the specimens were attributed species known from Europe. A monographic study of the Maenioceratidae Bogoslovsky, 1958 has not yet taken place and is presented here.

Material and methods

Our material comes from the following localities in the Anti-Atlas of Morocco (Fig. 1), all from a short interval in the middle part of the Givetian stage, from the "*Maenioceras terebratum* Zone" and the *Afromaenioceras sulcatostriatum* Zone according to Becker & House (2000) (Fig. 2):

Oued Mzerreb

The locality is located 27 km south-east of the town of Tata (Fig. 1B), which itself is located in the south-western part of the Anti-Atlas, about 175 km east-southeast of Agadir. The Oued Mzerreb-W

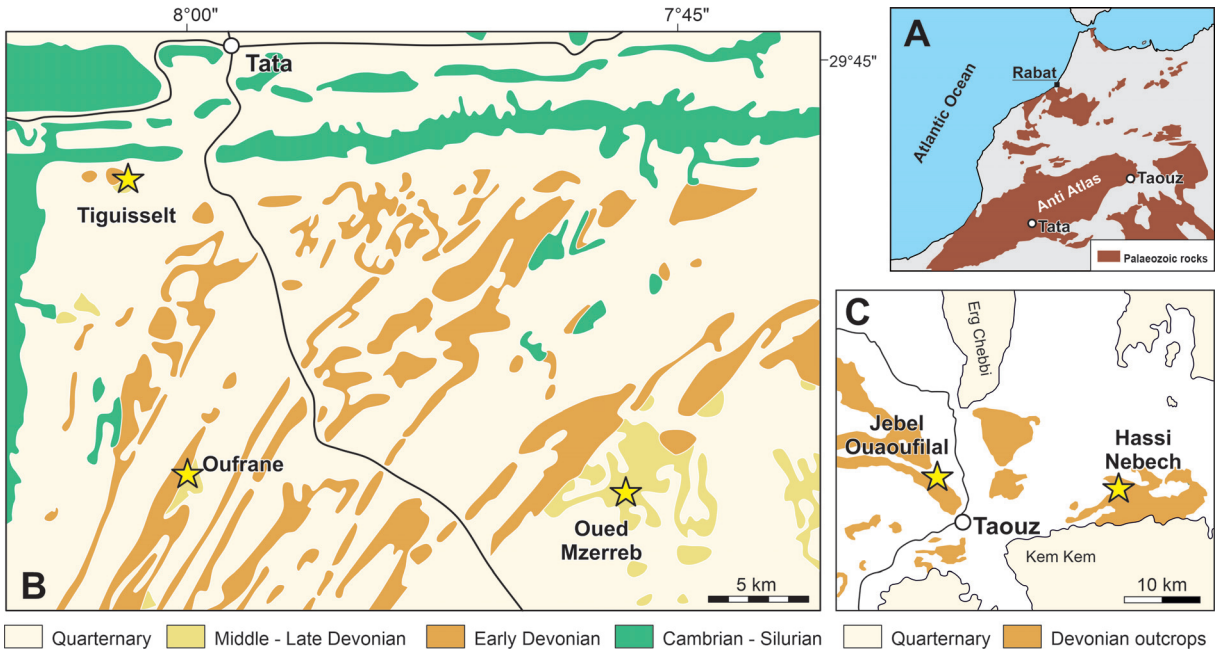

Fig. 1. Geographic position of the fossil sites that yielded the material described here. **A**. Overview on the north-western part of Africa with the locations of Tata and Taouz. **B**. Geological map of the area south of Tata with the fossil localities at Oued Mzerreb, Oufrane and Tiguisselt. **C**. Geological map of the area of Taouz with the fossil localities at Jebel Ouaoufilal and Hassi Nebech.

section is particularly important for the Givetian biostratigraphy; it was first described by Bensaïd (1974) and discussed in detail by Becker *et al.* (2004). According to the latter study, the section consists mainly of shales with thin embedded beds of limestone and marl. The thickness of the layers with maenioceratids exceeds 55 m. According to their study, *Bensaidites* Korn, 2002 occurs only in the lowest 1.15 m (bed -1; "*Bensaidites* Bed"), *Maenioceras* in a 5.00 m thick interval in the middle part (bed 6; "Upper *Maenioceras* Bed") and *Afromaenioceras* in the uppermost 6.70 m of this section (beds 10–11a; "*Afromaenioceras* Beds"). One has to note that the representative specimen of "*Bensaidites* n. sp." of Becker *et al.* (2004: pl. 1 fig. 22) belongs to *Maenioceras*. The following maenioceratid specimens are available:

Bed 6:
Maenioceras afroterebratum sp. nov. – 23 specimens
Maenioceras mzerrebense sp. nov. – 11 specimens

Beds 10/11:
Afromaenioceras hiemale sp. nov. – 1 specimen
Afromaenioceras bensaidi sp. nov. – 11 specimens
Afromaenioceras brumale sp. nov. – 25 specimens
Afromaenioceras crassum (Bensaïd, 1974) – 25 specimens
Trimaenioceras klugi gen. et sp. nov. – 24 specimens

Oufrane

The second significant locality is located 20 km south of Tata in the south-western part of the Anti-Atlas (Fig. 1B). Already known to Bensaïd (1974), two sections (Oufrane-W and Oufrane-E) were described by Aboussalam *et al.* (2004). These authors showed for the Oufrane-W section that the strata containing maenioceratid ammonoids are over 38 m thick in total and consist largely of shales and marls. According to this study, *Maenioceras* occurs first in the 5 m thick bed 3 ("Upper *Maenioceras* Bed") and *Afromaenioceras* occurs in the top 3 m (bed 11; "*Afromaenioceras* Bed").

			"standard zones"	Anti-Atlas, Morocco	
M. DEVONIAN	GIVETIAN	*Pharciceras*	*Petteroceras errans*	*Petteroceras errans*	*Petteroceras errans*
			Pseudoprobeloceras pernai	*Pseudoprobeloceras pernai* "*Pharciceras*" *taouzensis*	*Taouzites taouzensis*
			Synpharciceras clavilobum	*Synpharciceras clavilobum*	*Synpharciceras clavilobum*
			Stenopharciceras lateseptatum	*Stenopharciceras lunulicosta* *Mzerrebites erraticus*	*Lunupharciceras* n. sp.
					Mzerrebites erraticus
			Pharciceras amplexum	*Pharciceras tridens* *Pharciceras* cf. *amplexum*	*Pharciceras* aff. *amplexum*
		Maenioceras	*Afromaenioceras sulcatostriatum*	*Afromaenioceras sulcatostriatum*	*Afromaenioceras* n. sp
					Afromaenioceras sulcatostriatum
			Maenioceras terebratum	*Maenioceras terebratum*	*Sellagoniatites waldschmidti*
			Maenioceras molarium	*Wedekindella* aff. *psittacina* *Maenioceras undulatum*	*Sobolewia* n. sp.
			Maenioceras undulatum	*Maenioceras koeneni*	*Bensaidites koeneni*

Fig. 2. Givetian ammonoid "standard zones" (from Becker & House 2000) and zonations for the Anti-Atlas of Morocco (from Becker & House 2000; Aboussalam & Becker 2011; Becker *et al.* 2018). Interval with the species described here highlighted.

For the Oufrane-E section, Aboussalam *et al.* (2004) designated a 4 m thick succession (beds 10–11) as "*Afromaenioceras* Bed" and the following 4.30 m thick succession of strata (beds 12–14) as "*Juvenocostatus* Beds", in which the three genera *Maenioceras*, *Afromaenioceras* and *Pharciceras* Hyatt, 1884 are supposed to occur together. The following maenioceratid specimens are available:

Oufrane-W, bed 3:
Maenioceras afroterebratum sp. nov. – 25 specimens
Maenioceras oufranense sp. nov. – 48 specimens

Oufrane-W, bed 11:
Afromaenioceras hiemale sp. nov. – 1 specimen

Oufrane-E, bed 10:
Afromaenioceras sulcatostriatum (Bensaïd, 1974) – 19 specimens

Oufrane-E, bed 11:
Afromaenioceras sulcatostriatum (Bensaïd, 1974) – 5 specimens
Afromaenioceras brumale sp. nov. – 6 specimens

Oufrane-E, beds 14–15:
Afromaenioceras sulcatostriatum (Bensaïd, 1974) – 2 specimens

Tiguisselt

The third section in the south-western part of the Anti-Atlas is Tiguisselt, which has a position 4 km south-west of Tata (Fig. 1B). It was mentioned by Bensaïd (1974) and described in detail by Aboussalam & Becker (2004). The following maenioceratid specimens are available:

Bed 3:
Maenioceras afroterebratum sp. nov. – 5 specimens

Bed 10:
Afromaenioceras brumale sp. nov. – 1 specimen

Jebel Ouaoufilal

The locality south-west of Jebel Ouaoufilal has a position about 6 km north-east of Taouz (Fig. 1C) and 55 km south-southeast of Erfoud in the eastern Anti-Atlas. The fossil site, which only yielded

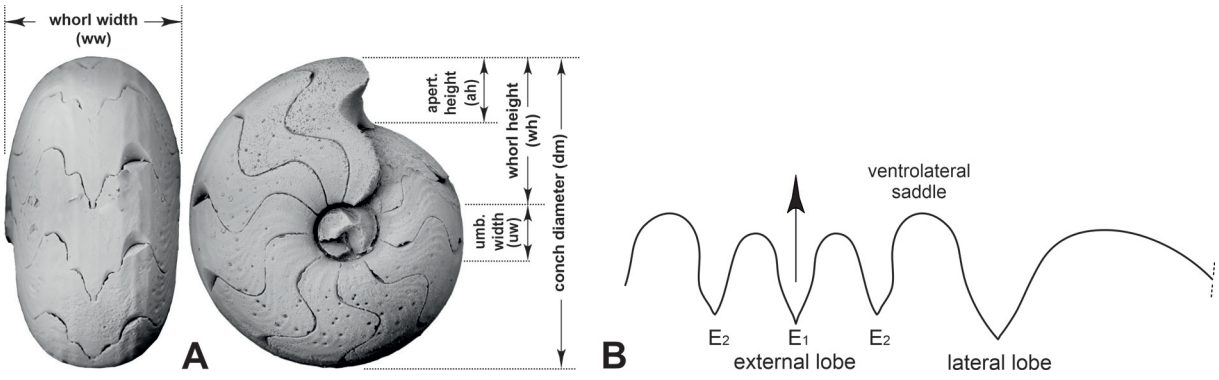

Fig. 3. The morphological terms used in the descriptions of the ammonoid conchs and suture lines.

float material, is located on the southern flank of the Amessoui Syncline, which exposes fossiliferous sedimentary rocks from the Ordovician to the Tournaisian in concordant succession (Klug & Pohle 2018). Haematitic fossils occur in a depression between Eifelian and Frasnian limestone beds. The following maenioceratid specimens are available:

Afromaenioceras hiemale sp. nov. – 26 specimens
Afromaenioceras brumale sp. nov. – 1 specimen
Afromaenioceras crassum (Bensaïd, 1974) – 40 specimens
Trimaenioceras klugi gen. et sp. nov. – 242 specimens
Trimaenioceras paucum gen. et sp. nov. – 2 specimens

Hassi Nebech

The section is located 20 km east-northeast of Taouz (Fig. 1C). Bensaïd (1974) provided a description of the Givetian part of the section and Bockwinkel *et al.* (2013) studied the very diverse ammonoid assemblage of this locality. The following maenioceratid specimens are available:

Maenioceras beckeri sp. nov. – 3 specimens
Trimaenioceras eculeus gen. et sp. nov. – 33 specimens
Trimaenioceras fuscina s gen. et p. nov. – 2 specimens

The description of the material follows, as far as possible, the scheme for Palaeozoic ammonoids outlined by Korn (2010) and Klug *et al.* (2015) (Fig. 3). However, due to the limitation of ontogenetic data, the descriptions must remain incomplete.

Abbreviations

ah	=	apertural height
dm	=	conch diameter
IZR	=	imprint zone rate
uw	=	umbilical width
WER	=	whorl expansion rate
wh	=	whorl height
ww	=	whorl width

Repositories

IGBP	=	collection of the Institut für Geowissenschaften, Abt. Paläontologie, Universität Bonn
MB.C.	=	collection of fossil cephalopods in the Museum für Naturkunde, Berlin

Results

Order Agoniatitida Ruzhencev, 1957
Suborder Pharciceratina Korn, 1998
Superfamily Pharciceratoidea Hyatt, 1900

Family **Maenioceratidae** Bogoslovsky, 1958

Diagnosis

Family of the superfamily Pharciceratoidea without or with ventrolateral grooves; sutural formula (E_2 E_1 E_2) L U_2 U_1 I; wide to extremely wide external lobe.

Included genera

Maenioceras Schindewolf, 1933; *Afromaenioceras* Göddertz, 1987; *Bensaidites* Korn in Korn & Klug, 2002; *Trimaenioceras* gen. nov.

Remarks

The four genera of the family are very easily distinguished on the basis of the suture line, particularly the shape of the external lobe. This shows a small, rounded E_2 lobe in *Maenioceras* and *Afromaenioceras*, but deep and pointed in *Trimaenioceras* gen. nov. *Maenioceras* and *Afromaenioceras* differ in the shape of the E_2 lobe, which in the latter genus has a rectangular form.

The stratigraphic distribution of the four genera is only in part well-known. *Bensaidites* is probably the stratigraphically oldest representative of the family with "*B. koeneni*" defining the earliest Givetian (Aboussalam & Becker 2011; Becker *et al.* 2018) in the Moroccan sections. Becker *et al.* (2004: pl. 1 fig. 22) illustrated a specimen from the basal part of the Oued Mzerreb section (bed -1a), which they named "*Bensaidites* n. sp.". However, due to its suture line with a shallow, rounded E_2 lobe, this specimen belongs to *Maenioceras*.

It is clear that *Maenioceras* precedes *Afromaenioceras* (Fig. 2), but the position of the material assigned here to the new genus *Trimaenioceras* gen. nov. has been conclusively determined. In Oued Mzerreb, *Trimaenioceras klugi* gen. et sp. nov. co-occurs with several *Afromaenioceras* species in the high part of the section ("*Afromaenioceras* Beds").

Genus ***Maenioceras*** Schindewolf, 1933

Type species

Goniatites terebratus Sandberger & Sandberger, 1851; original designation.

Diagnosis

Genus of the family Maenioceratidae with ventrolateral grooves; shell usually without constrictions or internal thickenings. External lobe very wide or extremely wide; E_2 lobe usually very shallow, broadly rounded; ventrolateral saddle narrowly rounded or subangular; lateral lobe V-shaped, angular or blunt.

Included species

Rhenish Mountains (Sandberger & Sandberger 1850–1856; Holzapfel 1895; Ebbighausen *et al.* 2007; Korn & Bockwinkel 2021; this paper): *Goniatites terebratus* Sandberger & Sandberger, 1851; *Maeneceras tenue* Holzapfel, 1895; *Maeneceras Decheni* Holzapfel, 1895; *Maenioceras heinorum* Ebbighausen, Becker & Bockwinkel in Ebbighausen *et al*., 2007; *Maenioceras ornatum* Korn & Bockwinkel, 2021.

Anti-Atlas (this paper): *Maenioceras afroterebratum* sp. nov.; *Maenioceras mzerrebense* sp. nov.; *Maenioceras oufranense* sp. nov.; *Maenioceras beckeri* sp. nov.

Remarks

The North African records of *Maenioceras* needed revision. Increasing knowledge led to the result that the North African species differ from those described from material of the Rhenish Mountains, although there is close resemblance between some of the species. With respect to the morphological differences, new species are described here.

Maenioceras afroterebratum sp. nov.
urn:lsid:zoobank.org:act:A50A8AFC-D773-4DF9-BAF2-3DA91E3E0250
Fig. 4; Table 1

Maenioceras terebratum – Termier & Termier 1950: pl. 143 fig. 28. — Petter 1959: 122, pl. 6 figs 18, 22, text-figs 16, 31a. — Aboussalam & Becker 2001: 89, pl. 1 figs 10–11. — Becker *et al*. 2004: pl. 1 figs 17–18.

Maenioceras terebratum terebratum – Bensaïd 1974: 103, pl. 1 figs 12, 12a (? fig. 11), pl. 2 figs 1, 1a, 4, pl. 3 fig. 5, text-fig. 12$b_{1,}$ (non b_2).

Maenioceras (*Maenioceras*) *terebratum* – Göddertz 1987: 176, pl. 12 figs 3–9, text-figs 27a, 28a–e.

? *Maenioceras terebratum* – Termier & Termier 1950: pl. 143 figs 25–27. — Petter 1959: 122, pl. 6 fig. 10.

Diagnosis

Species of *Maenioceras* with thickly discoidal and subinvolute conch at 10 mm dm (ww/dm ~ 0.50; uw/dm ~ 0.25); conch thinly discoidal and involute at 17 mm dm (ww/dm ~ 0.40; uw/dm ~ 0.13) with weakly depressed whorl profile (ww/wh ~ 0.90) and low coiling rate (WER ~ 1.70). Whorl profile at 17 mm conch diameter trapezoidal with flattened, nearly parallel, weakly convergent flanks, narrowly rounded ventrolateral shoulder and broad, nearly flat venter. Ventrolateral shoulder with a faint spiral groove in juvenile and deeper groove in adult specimens. Growth lines coarse, lamellar. Suture line with very wide external lobe, shallow, asymmetrically rounded E_2 lobe, narrowly rounded ventrolateral saddle and blunt, V-shaped lateral lobe.

Etymology

Named because of the resemblance with *M. terebratum* and the origin from North Africa.

Type material

Holotype

MOROCCO • Anti-Atlas, Oued Mzerreb-W; bed 6, middle Givetian; Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31947.1 (illustrated in Fig. 4A).

Paratypes

MOROCCO • 22 specs; same collection data as for holotype; MB.C.31947.2 to MB.C.31947.23 • 25 specs; Anti-Atlas, Oufrane-W; bed 3, middle Givetian; Bockwinkel and Ebbighausen 2002–2004 Coll.; MB.C.31948.1 to MB.C.31948.25 • 5 specs; Anti-Atlas, Tiguisselt; bed 3, middle Givetian; Bockwinkel and Ebbighausen 2002–2004 Coll.; MB.C.31949.1 to MB.C.31949.5.

Description

Holotype MB.C.31947.1 is a partly corroded limonitic internal mould with 17 mm conch diameter (Fig. 4A). The conch is thinly discoidal and involute (ww/dm = 0.40; uw/dm = 0.13) with a low coiling rate (WER ~ 1.70). The whorl profile is weakly compressed (ww/wh = 0.90); the flanks are slightly flattened and converge towards the pronounced ventrolateral shoulder, which is accompanied by a faint spiral groove, which begins at about 10 mm conch diameter and becomes distinct at 15 mm diameter. The venter is broadly convex and becomes flattened during the last preserved volution. Growth lines are only poorly preserved as imprints on the internal mould, which appears to be smooth. The phragmocone consists of about 18 chambers in the last preserved volution; there is a rather clear trend toward shorter chambers.

Paratype MB.C.31947.2 is a well-preserved specimen with 10.5 mm conch diameter (Fig. 4C). The conch is thickly discoidal and subinvolute (ww/dm = 0.50; uw/dm = 0.24) with moderately high coiling rate (WER ~ 1.82). The whorl profile is weakly depressed (ww/wh = 1.16); it shows very slightly convex flanks that converge towards the subangular ventrolateral shoulder. This is accompanied by a faint spiral groove. Traces of growth lines are visible on the internal mould; they are coarse, lamellar with strongly biconvex course. The suture line has, at approximately 10 mm conch diameter, an extremely wide external lobe with a very shallow, asymmetrically rounded E_2 lobe. On the flank follow a narrowly rounded ventrolateral saddle and a V-shaped, blunt lateral lobe (Fig. 4E). The phragmocone consists of about 14 chambers in the last preserved volution.

Paratypes MB.C.31948.1 (13.5 mm dm; Fig. 4B) and MB.C.31948.2 (10 mm dm; Fig. 4D) agree, in their conch morphology, with the holotype and the above described paratype. However, they possess only very weak longitudinal grooves.

Paratype MB.C.31947.3 was used for a cross section (Fig. 4F). It shows, at 12 mm conch diameter, a thickly discoidal and subinvolute conch (ww/dm = 0.51; uw/dm = 0.24) with low coiling rate (WER ~ 1.62). The whorl profile is weakly depressed (ww/dm = 1.11); it is remarkable for its flattened flanks, which are even weakly concave near the umbilicus. The flanks are weakly convergent and the venter is slightly flattened.

Remarks

Maenioceras afroterebratum sp. nov. is similar to *M. terebratum* and *M. ornatum* from the Rhenish Mountains. However, the lateral lobe is broadly rounded and the ventrolateral saddle is narrowly rounded in the new species, while both are subacute in *M. terebratum* (Korn & Bockwinkel 2021: text-fig. 4b) and even acute in *M. ornatum* (Holzapfel 1895: pl. 6 fig. 6c). *Maenioceras afroterebratum* differs by the much stouter conch and the more widely rounded venter from *M. oufranense* sp. nov. (ww/

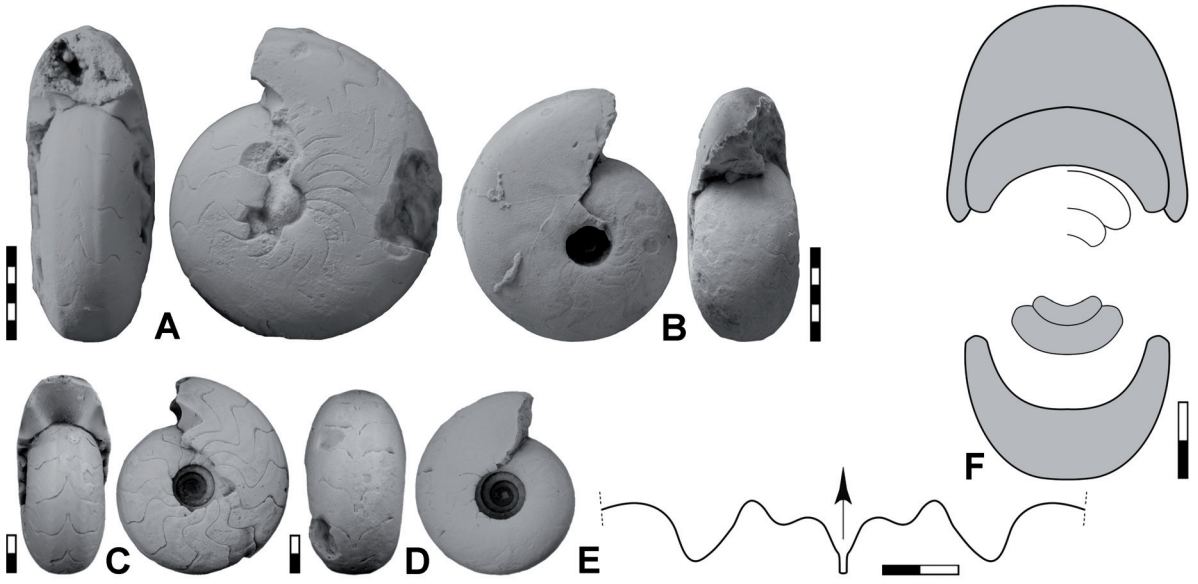

Fig. 4. *Maenioceras afroterebratum* sp. nov. **A**. Holotype MB.C.31947.1 from Oued Mzerreb-W, bed 6. **B**. Paratype MB.C.31948.1 from Oufrane-W, bed 3. **C**. Paratype MB.C.31947.2 from Oued Mzerreb-W, bed 6. **D**. Paratype MB.C.31948.2 from Oufrane-W, bed 3. **E**. Paratype MB.C.31947.2 from Oued Mzerreb-W, bed 6; suture line at dm = 10.0 mm. **F**. Paratype MB.C.31947.3 from Oued Mzerreb-W, bed 6; cross section. Scale bar units = 1 mm.

Table 1. Conch dimensions (in mm) and ratios of *Maenioceras afroterebratum* sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31947.1	16.9	6.8	7.4	2.2	3.9	0.40	0.91	0.13	1.69	0.47
MB.C.31948.1	13.6	5.8	6.7	2.5	3.6	0.43	0.90	0.18	–	–
MB.C.31947.4	13.1	5.8	6.4	2.0	3.1	0.44	0.91	0.15	1.72	0.51
MB.C.31947.3	12.1	6.1	5.5	2.9	2.6	0.51	1.11	0.24	1.62	0.53
MB.C.31947.2	10.4	5.2	4.5	2.5	2.7	0.50	1.16	0.24	1.82	0.40
MB.C.31948.2	9.9	5.4	4.3	2.6	2.3	0.55	1.25	0.26	1.67	0.48

dm ~ 0.35). Finally, *M. afroterebratum* is more slender and more involute (ww/dm ~ 0. 50; uw/dm ~ 0.25) than *M. mzerrebense* sp. nov. (ww/dm ~ 0.65; uw/dm ~ 0.30) at a comparable size.

Maenioceras mzerrebense sp. nov.
urn:lsid:zoobank.org:act:99A40866-EEC7-4B6C-90DC-E6F00D6C3E8F
Fig. 5; Table 2

? *Maenioceras* aff. *terebratum* – Aboussalam & Becker 2001: 89, pl. 1 figs 8–9.

Diagnosis

Species of *Maenioceras* with thinly pachyconic and subinvolute conch at 8 mm dm (ww/dm ~ 0.65; uw/dm ~ 0.30); conch thickly discoidal and subinvolute at 13 mm dm (ww/dm ~ 0.55; uw/dm ~ 0.25) with weakly depressed whorl profile (ww/wh ~ 1.15) and moderately high coiling rate (WER ~ 1.80). Whorl profile at 13 mm conch diameter horseshoe-shaped with convex, weakly convergent flanks, rounded ventrolateral shoulder and convex venter. Ventrolateral shoulder with a very faint spiral groove. Growth lines coarse, lamellar. Suture line with very wide external lobe, very shallow, asymmetrically rounded E_2 lobe, narrowly rounded ventrolateral saddle and blunt, V-shaped lateral lobe.

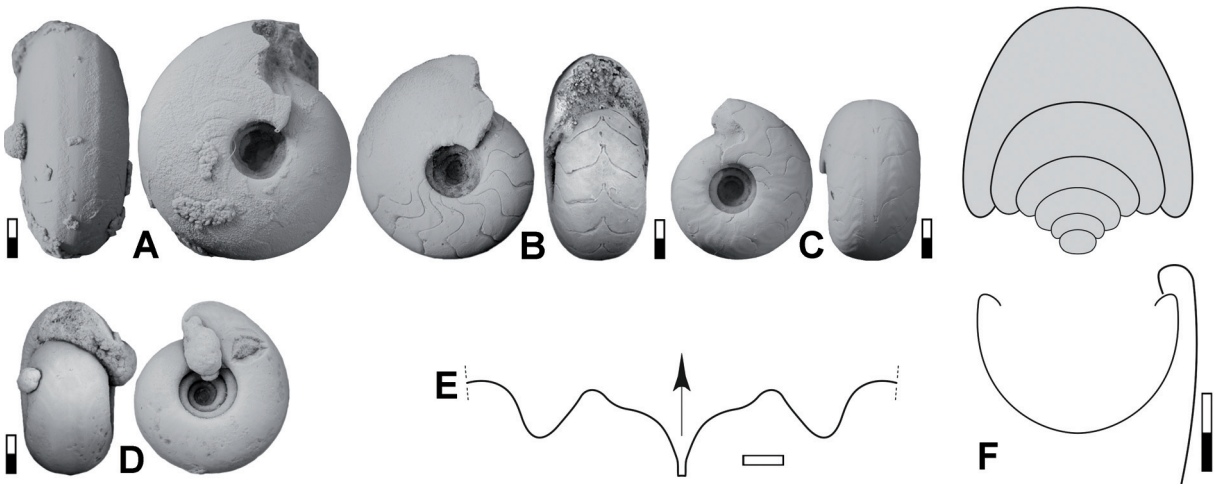

Fig. 5. *Maenioceras mzerrebense* sp. nov. from Oued Mzerreb-W, bed 6. **A**. Paratype MB.C.31950.2. **B**. Holotype MB.C.31950.1. **C**. Paratype MB.C.31950.3. **D**. Paratype MB.C.31950.4. **E**. Holotype MB.C.31950.1; suture line at wh = 3.8 mm. **F**. Paratype MB.C.31950.5; cross section. Scale bar units = 1 mm.

Table 2. Conch dimensions (in mm) and ratios of *Maenioceras mzerrebense* sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31950.2	12.6	6.9	5.9	2.8	3.2	0.55	1.17	0.25	1.80	0.46
MB.C.31950.6	12.0	6.2	5.6	2.5	3.0	0.52	1.11	0.21	1.78	0.46
MB.C.31950.1	10.6	5.6	4.8	2.8	2.4	0.53	1.17	0.26	1.67	0.50
MB.C.31950.4	9.2	5.2	4.1	3.2	2.2	0.68	1.44	0.31	1.73	0.46
MB.C.31950.3	8.4	5.2	3.8	2.5	2.0	0.62	1.36	0.29	1.72	0.47

Etymology

Named after the type locality Oued Mzerreb.

Type material

Holotype

MOROCCO • Anti-Atlas, Oued Mzerreb-W; bed 6, middle Givetian; Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31950.1 (illustrated in Fig. 5B).

Paratypes

MOROCCO • 10 specs; same collection as for holotype; MB.C.31950.2 to MB.C.31950.11.

Description

Holotype MB.C.31950.1 is a well-preserved limonitic internal mould with parts of the body chamber preserved (Fig. 5B). It has, at 10.6 mm conch diameter, a thickly discoidal and subinvolute conch (ww/dm = 0.53; uw/dm = 0.26) with low coiling rate (WER = 1.67). The whorl profile is weakly depressed (ww/wh = 1.17) with slightly arched flanks that converge towards the narrowly rounded ventrolateral shoulder, which forms a very inconspicuous margin of the rounded venter. The growth lines are impressed as lamellar, strongly biconvex remains on the surface of the internal mould. The last suture line shows, at 3.8 mm whorl height, a very wide external lobe, a very shallow E_2 lobe at the upper flank of the E lobe, a small and low, rounded ventrolateral saddle and a V-shaped lateral lobe with narrowly rounded base. (Fig. 5E). The last half volution of the phragmocone has eight septa, of which the last are more closely spaced.

Paratype MB.C.31950.3 is a well-preserved limonitic internal mould of a fully chambered specimen (Fig. 5C). It has at 8.4 mm diameter a thinly pachyconic and subinvolute conch (ww/dm = 0.62; uw/dm = 0.29) with low coiling rate (WER = 1.72). The whorl profile is weakly depressed (ww/wh ~ 1.36); the flanks are slightly convex and converge towards the rounded ventrolateral shoulder and the rounded venter. The growth lines appear to be coarse, lamellar and strongly biconvex in their course. The last volution of the phragmocone has 12 chambers.

Paratype MB.C.31950.2 is a well-preserved limonitic internal mould (Fig. 5A). It has, at 12.6 mm diameter, a thickly discoidal and subinvolute conch (ww/dm = 0.55; uw/dm ~ 0.25) and shows that the umbilicus starts closing at about 10 mm conch diameter. The flanks are convex and converge towards the ventrolateral shoulder, which appears to be subangular with a weak ventrolateral groove; the venter is nearly flat.

Remarks

Maenioceras mzerrebense sp. nov. is stouter and more evolute (ww/dm ~ 0.55; uw/dm ~ 0.25) than *M. afroterebratum* sp. nov. (ww/dm ~ 0.45; uw/dm ~ 0.15) at a conch diameter of 13 mm. It is also much stouter and more widely umbilicate than *M. oufranense* sp. nov. (ww/dm ~ 0.45; uw/dm ~ 0.12).

Maenioceras oufranense sp. nov.
urn:lsid:zoobank.org:act:C6A0EE25-33C2-48E1-97BD-3C45967DC002
Fig. 6; Table 3

Maenioceras terebratum var. *tenue* – Petter 1959: 124, pl. 6 fig. 15, text-fig. 31b.
Maenioceras terebratum tenue – Bensaïd 1974: 104, text-fig. 12a.

? *Maenioceras terebratum* – Belka *et al*. 1999: pl. 4 figs 7–8. — Aboussalam & Becker 2011: text-fig. 8.1–2.
? *Bensaidites* n. sp. Becker *et al*. 2004: pl. 1 fig. 22.

Diagnosis

Species of *Maenioceras* with thickly discoidal and subinvolute conch at 8 mm dm (ww/dm ~ 0.55; uw/dm ~ 0.25); conch thinly discoidal and involute at 15 mm dm (ww/dm ~ 0.40; uw/dm ~ 0.10) with weakly compressed whorl profile (ww/wh ~ 0.75) and low coiling rate (WER ~ 1.60). Whorl profile at 15 mm conch diameter narrow horseshoe-shaped with convex, weakly convergent flanks, rounded ventrolateral shoulder and narrowly rounded venter. Ventrolateral shoulder with a faint spiral groove in juvenile and deeper groove in adult specimens. Growth lines coarse, strongly biconvex. Suture line with very wide external lobe, shallow, asymmetrically rounded E_2 lobe, narrowly rounded ventrolateral saddle and blunt, tongue-shaped lateral lobe.

Etymology

Named after the type locality Oufrane.

Type material

Holotype
MOROCCO • Anti-Atlas, Oufrane-W; bed 3, middle Givetian; Bockwinkel and Ebbighausen 2002–2004 Coll.; MB.C.31951.1 (illustrated in Fig. 6A).

Paratypes
MOROCCO • 47 specs; same collection data as for holotype; MB.C.31951.2 to MB.C.31951.48.

Description

Holotype MB.C.31951.1 is a limonitic, dessert-polished internal mould; it is fully septate and, with 20 mm conch diameter, the largest available specimen (Fig. 6A). It is an extremely discoidal and involute conch (ww/dm = 0.33; uw/dm = 0.04) with an apparently low coiling rate. The whorl profile is compressed (ww/wh = 0.58); the flanks stand almost parallel in the umbilical area, but becoming convergent towards the rather narrowly rounded venter. The ventrolateral shoulder shows a pronounced spiral groove. The growth lines, which are visible as impressions, were probably coarse and clustered. They extend with strongly biconvex course. The suture lines are difficult to trace, but it is clear that the last chambers of the phragmocone are very closely spaced.

Paratype MB.C.31951.2 is a well-preserved limonitic internal mould of a phragmocone (Fig. 6B) with 12.5 mm diameter. It is a thinly discoidal and involute conch (ww/dm = 0.41; uw/dm = 0.13) with low coiling rate (WER = 1.61). The whorl profile is weakly compressed (ww/wh = 0.80); the flanks are flatly

convex and converge towards the narrowly rounded venter. The ventrolateral shoulder possesses a faint spiral groove. The growth lines are apparently coarse and strongly biconvex.

Paratypes MB.C.31951.4 (7.5 mm conch diameter; Fig. 6D) and MB.C.31951.3 (13 mm conch diameter; Fig. 6C) demonstrate the transition from the juvenile stage with slow but constant opening of the umbilicus to the intermediate growth stage, in which the umbilicus becomes narrower by increased overlap of the inner flank area upon the umbilicus.

The cross section of paratype MB.C.31951.6 demonstrates the transformation from the juvenile to the preadult conch morphology (Fig. 6F). This ontogenetic transformation shows that the C-shaped whorl profile of the juvenile stage with a ww/wh ratio of about 2.00 is, beginning at a conch diameter of 5 mm, rapidly reduced to a value of 0.77 at 14 mm conch diameter. Parallel to this development, the uw/dm ratio is reduced markedly caused by overlap upon the umbilicus. The conch is thinly discoidal and involute at 14.2 mm dm (ww/dm = 0.40; uw/dm = 0.11); the flanks are almost parallel near the umbilicus and converge towards the narrowly rounded venter.

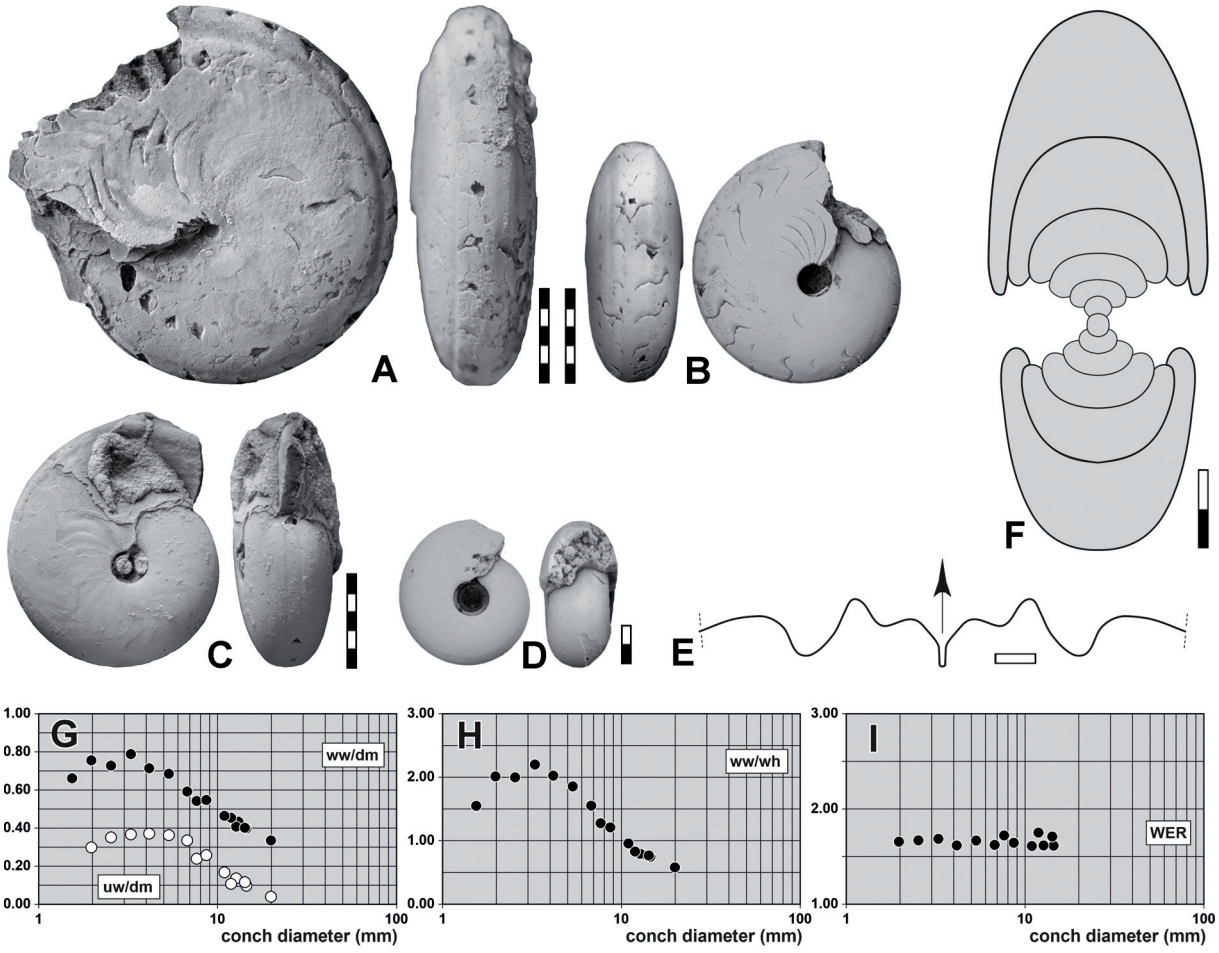

Fig. 6. *Maenioceras oufranense* sp. nov. from Oufrane-W, bed 3. **A**. Holotype MB.C.31951.1. **B**. Paratype MB.C.31951.2. **C**. Paratype MB.C.31951.3. **D**. Paratype MB.C.31951.4. **E**. Paratype MB.C.31951.5; suture line at dm = 12.0 mm. **F**. Paratype MB.C.31951.6; cross section. **G–I**. Ontogenetic trajectories of the cardinal conch parameters. Scale bar units = 1 mm.

Table 3. Conch dimensions (in mm) and ratios of *Maenioceras oufranense* sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31951.1	20.0	6.7	11.4	0.8	–	0.33	0.58	0.04	–	–
MB.C.31951.7	14.5	5.7	7.6	1.4	3.1	0.39	0.75	0.09	1.61	0.60
MB.C.31951.3	13.1	5.7	7.2	1.6	–	0.43	0.79	0.12	–	–
MB.C.31951.2	12.7	5.2	6.5	1.7	2.7	0.41	0.80	0.13	1.61	0.58
MB.C.31951.8	11.9	5.4	6.5	1.3	2.9	0.45	0.83	0.11	1.75	0.55
MB.C.31951.4	7.6	4.1	3.2	1.8	1.8	0.54	1.28	0.24	1.72	0.44
MB.C.31951.6	14.24	5.69	7.38	1.62	3.33	0.40	0.77	0.11	1.70	0.55
MB.C.31951.6	10.91	5.04	5.24	1.81	2.30	0.46	0.96	0.17	1.61	0.56
MB.C.31951.6	8.61	4.69	3.86	2.20	1.89	0.55	1.22	0.26	1.64	0.51
MB.C.31951.6	6.72	3.96	2.55	2.24	1.44	0.59	1.56	0.33	1.62	0.43
MB.C.31951.6	5.28	3.61	1.94	1.91	1.19	0.68	1.86	0.36	1.66	0.39
MB.C.31951.6	4.09	2.91	1.44	1.51	0.87	0.71	2.03	0.37	1.61	0.39
MB.C.31951.6	3.22	2.53	1.15	1.17	0.74	0.79	2.21	0.36	1.68	0.36
MB.C.31951.6	2.49	1.80	0.90	0.87	0.56	0.73	2.00	0.35	1.67	0.38
MB.C.31951.6	1.93	1.45	0.72	0.57	0.43	0.75	2.02	0.30	1.65	0.40

The suture line of paratype MB.C.31951.5 shows a very wide external lobe, a very shallow, asymmetrically rounded E_2 lobe and a narrowly rounded, small ventrolateral saddle; the asymmetric lateral lobe has a convex ventral flank and a steeper dorsal flank (Fig. 6E).

Remarks

Maenioceras oufranense sp. nov. is characterised by the extremely discoidal and involute conch in specimens with about 20 mm conch diameter (ww/dm ~ 0.35; uw/dm ~ 0.05) and the narrowly rounded venter, which is broadly rounded in *M. afroterebratum* sp. nov. and nearly flat in *M. mzerrebense* sp. nov.

Maenioceras oufranense sp. nov. shows close similarity to *M. tenue* in the conch proportions, but differs in the narrowly rounded venter from *Maenioceras tenue*, which has an almost completely flat venter.

Maenioceras beckeri sp. nov.
urn:lsid:zoobank.org:act:48EAD7CA-D85E-40E0-B32C-7A6C5A078A7C
Fig. 7; Table 4

Maenioceras excavatum – Petter 1959: 124, pl. 6 fig. 11.

? *Maenioceras* cf. *excavatum* – Petter 1959: 125, pl. 6 fig. 13. — Bensaïd 1974: pl. 2 fig. 5.
? *Maenioceras* n. sp. III – Becker *et al*. 2004: pl. 1 figs 11–12.

Diagnosis

Species of *Maenioceras* with thickly discoidal and subinvolute conch at 17 mm dm (ww/dm ~ 0.50; uw/dm ~ 0.30) with weakly depressed whorl profile (ww/wh ~ 1.20) and low coiling rate (WER ~ 1.55). Whorl profile at 17 mm conch diameter horseshoe-shaped with flattened, nearly parallel, weakly convergent flanks, subangular ventrolateral shoulder and broad, nearly flat venter. Ventrolateral

shoulder with a faint groove in adult specimens. Growth lines coarse, strongly biconvex. Suture line with extremely wide external lobe, deep, U-shaped E_2 lobe, inverted U-shaped ventrolateral saddle and blunt, tongue-shaped lateral lobe.

Etymology

Named after R. Thomas Becker, who possibly already recognised this species as new.

Type material

Holotype

MOROCCO • Anti-Atlas, Hassi Nebech, section 2; middle Givetian; Bockwinkel and Ebbighausen Coll.; MB.C.31952.1 (illustrated in Fig. 7A).

Paratypes

MOROCCO • 2 specs; same collection data as for holotype; MB.C.31952.2, MB.C.31952.3.

Description

Holotype MB.C.31952.1 is a limonitic internal mould of a fully chambered specimen (Fig, 7A) with 17 mm conch diameter; it is rather well-preserved only on the right side. The conch is thickly discoidal and subinvolute (ww/dm = 0.49; uw/dm = 0.24) with low coiling rate (WER = 1.57). The whorl profile is weakly depressed (ww/wh = 1.18) with slightly convex flanks. The ventrolateral shoulder forms a rather distinct margin separating the flanks and the almost flat, but slightly convex venter. The growth lines are bundled with a strongly biconvex course. The suture line is somewhat unusual for *Maenioceras* with an extremely wide external lobe and a symmetrically rounded E_2 lobe that is half as deep as the E_1 lobe. On the flank follow a narrowly rounded asymmetrical ventrolateral saddle and a deep, tongue-shaped lateral lobe (Fig, 7C).

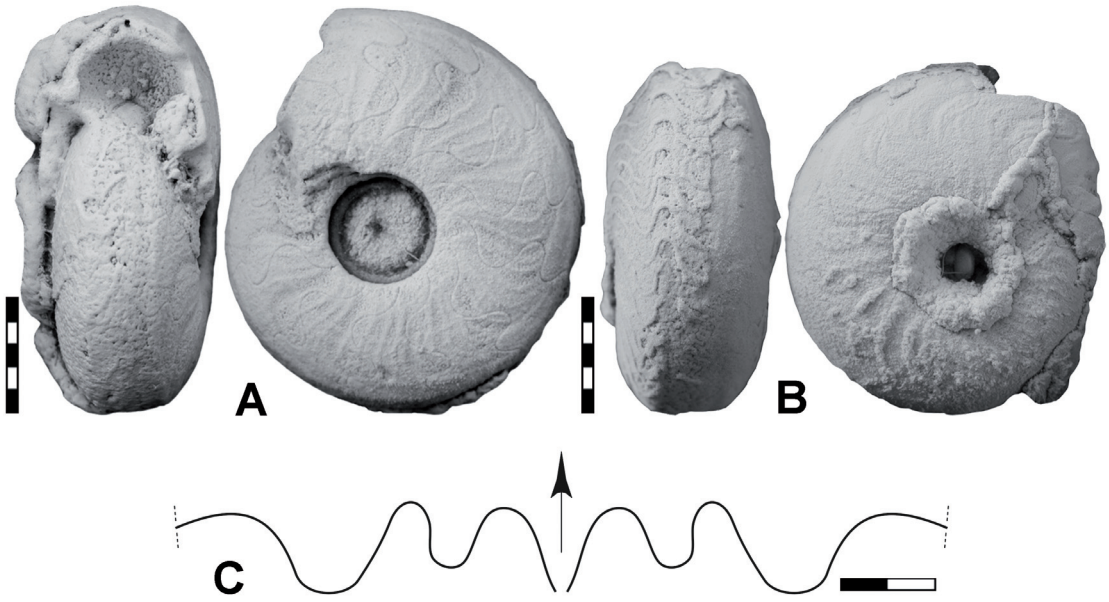

Fig. 7. *Maenioceras beckeri* sp. nov. from Hassi Nebech.**A**. Holotype MB.C.31952.1. **B**. Paratype MB.C.31952.2. **C**. Holotype MB.C.31952.1; suture line at wh = 6.4 mm. Scale bar units = 1 mm.

Table 4. Conch dimensions (in mm) and ratios of *Maenioceras beckeri* sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31952.1	17.3	8.5	7.2	4.2	3.5	0.49	1.18	0.24	1.57	0.51
MB.C.31952.2	15.2	7.5	7.4	–	–	0.49	1.01	–	–	–
MB.C.31952.3	14.6	6.5	4.7	5.3	3.3	0.45	1.38	0.36	1.67	0.30

Paratype MB.C.31952.2 shows the same conch proportions as the holotype with a ww/dm ratio of 0.49 and an estimated uw/dm ratio of 0.30 at 15 mm dm. Numerous dense growth lines are visible in this specimen (Fig, 7B).

Paratype MB.C.31952.3 is, with a ww/dm ratio of 0.45 and a uw/dm ratio of 0.36 at 14.5 mm conch diameter, slightly more slender and more evolute than the other two type specimens.

Remarks

The deep E_2 lobe in *Maenioceras beckeri* sp. nov. is the cardinal character to separate the new species from the other species of the genus, which possess a shallow E_2 lobe.

Genus ***Afromaenioceras*** Göddertz, 1987

Type species

Maenioceras sulcatostriatum Bensaïd, 1974; original designation.

Diagnosis

Genus of the family Maenioceratidae with or without ventrolateral grooves; shell with constrictions or internal thickenings. External lobe wide; E_2 lobe usually rectangular stair-shaped, narrowly rounded; ventrolateral saddle inverted U-shaped; lateral lobe U-shaped or tongue-shaped.

Included species

Anti-Atlas (Bensaïd 1974; this paper): *Maenioceras sulcatostriatum* Bensaïd, 1974; *Maenioceras crassum* Bensaïd, 1974; *Afromaenioceras hiemale* sp. nov.; *Afromaenioceras bensaidi* sp. nov.; *Afromaenioceras brumale* sp. nov.

Afromaenioceras sulcatostriatum (Bensaïd, 1974)

Fig. 8; Table 5

Maenioceras sulcatostriatum Bensaïd, 1974: 105, pl. 2 figs 2–3, 6, 8–9, text-fig. 13.

Maenioceras (*Afromaenioceras*) *sulcatostriatum* – Göddertz 1987: 179, pl. 12 figs 10–12, pl. 13 fig 2, fig 1?, text-figs 27b, 28f–k.

Afromaenioceras sulcatostriatum – Korn & Klug 2002: 140, text-fig. 133b.

Diagnosis

Species of *Afromaenioceras* with thinly pachyconic and subevolute conch at 7 mm dm (ww/dm ~ 0.60; uw/dm ~ 0.40); conch thickly discoidal and subinvolute at 12 mm dm (ww/dm ~ 0.50; uw/dm ~ 0.30) with weakly depressed whorl profile (ww/wh ~ 1.15) and low coiling rate (WER ~ 1.65). Whorl profile at 12 mm conch diameter C-shaped with convex, weakly convergent flanks, broadly rounded ventrolateral

shoulder and broadly rounded venter. Ventrolateral shoulder with more or less deep spiral groove. Growth lines pronounced, bundled, forming nodes at the ventrolateral shoulder. Suture line with wide external lobe, incipient, subangular E_2 lobe, inverted U-shaped ventrolateral saddle and semicircular lateral lobe.

Type material

Holotype

MOROCCO • Anti-Atlas, Oufrane; middle Givetian; IGPB-Bensaid-15 (illustrated by Bensaïd 1974: pl. 2 fig. 3).

Additional material

MOROCCO • 19 specs; Anti-Atlas, Oufrane-E; bed 10 (middle Givetian); Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31953.1 to MB.C.31953.19 • 5 spec; Anti-Atlas, Oufrane-E; bed 11 (middle Givetian); Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31954.1 to MB.C.31954.5 • 2 specs; Anti-Atlas, Oufrane-E; beds 14/15 (middle Givetian); Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31955.1, MB.C.31955.2.

Description

Specimen MB.C.31953.1 is a partially corroded but otherwise rather well-preserved limonitic internal mould with 12.2 mm conch diameter (Fig. 8A). The conch is thickly discoidal and subinvolute (ww/dm = 0.52; uw/dm = 0.30) with a low coiling rate (WER = 1.65); the whorl profile is weakly depressed (ww/wh = 1.15). The internal mould shows traces of pronounced, partly bundled growth lines, which produce faint tubercles at the ventrolateral shoulder. On the last volution, there are 13 constrictions of the internal mould; these extend with a low dorsolateral projection, a shallow lateral sinus, an extremely high, subacute ventrolateral projection and a very deep and narrow ventral sinus. These constrictions are deepest in the outer flank area. The specimen possesses a long body chamber and therefore, the suture line not visible.

Specimen MB.C.31953.2 is a well-preserved limonitic internal mould with 8 mm conch diameter, of which half of the last volution belong to the body chamber (Fig. 8C). The conch is thickly discoidal and subevolute (ww/dm = 0.54; uw/dm = 0.36) with a low coiling rate (WER = 1.71); the whorl profile

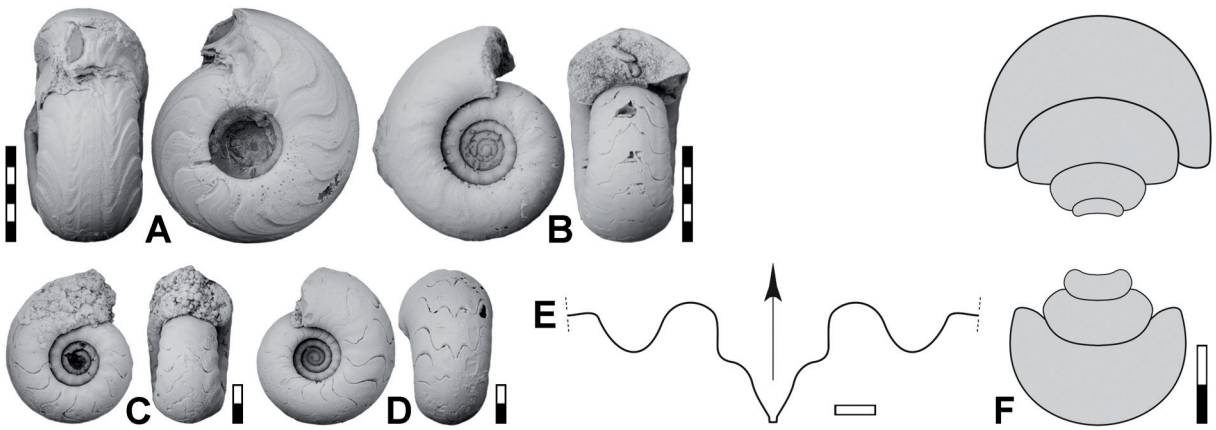

Fig. 8. *Afromaenioceras sulcatostriatum* (Bensaïd, 1974) from Oufrane-E. **A**. Specimen MB.C.31953.1, bed 10. **B**. Specimen MB.C.31955.1, bed 14/15. **C**. Specimen MB.C.31953.2, bed 10. **D**. Specimen MB.C.31955.2, bed 14/15. **E**. Specimen MB.C.31954.1, bed 11; suture line at wh = 3.0 mm. **F**. Specimen MB.C.31953.3, bed 10; cross section. Scale bar units = 1 mm.

Table 5. Conch dimensions (in mm) and ratios of *Afromaenioceras sulcatostriatum* (Bensaïd, 1974).

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31953.1	12.2	6.3	5.5	3.6	2.7	0.52	1.15	0.30	1.65	0.51
MB.C.31955.1	11.3	6.4	3.8	4.6	2.7	0.57	1.68	0.41	1.73	0.29
MB.C.31955.2	8.3	4.8	3.2	2.7	2.2	0.58	1.50	0.33	1.85	0.31
MB.C.31953.2	8.1	4.4	3.2	2.9	1.9	0.54	1.38	0.36	1.71	0.41
MB.C.31953.3	10.90	6.00	4.05	3.72	2.18	0.55	1.48	0.34	1.56	0.46
MB.C.31953.3	8.72	4.68	3.13	3.28	2.12	0.54	1.49	0.38	1.75	0.32
MB.C.31953.3	6.60	4.08	2.31	2.79	1.74	0.62	1.77	0.42	1.84	0.25
MB.C.31953.3	4.86	2.91	1.50	2.08	1.20	0.60	1.94	0.43	1.77	0.20
MB.C.31953.3	3.66	2.51	1.28	1.56	0.95	0.68	1.96	0.43	1.82	0.26

is weakly depressed (ww/wh = 1.38). Traces of the growth lines shows that these are bundled at the umbilical margin and that they extend with a strongly biconvex course.

Specimens MB.C.31955.2 (8 mm conch diameter; Fig, 8D) and MB.C.31955.1 (11 mm conch diameter; Fig. 8B) show somewhat weaker indications of growth lines and weaker constrictions of the internal mould when compared with the specimens MB.C.31953.1 and MB.C.31953.2, but agree in the general conch ratios.

Specimen MB.C.31953.3 was used for the production of a cross section (Fig. 8F), in which three volutions up to a conch diameter of nearly 11 mm can be studied. The cross section shows that the ontogenetic changes in the shape of the whorl profiles do not significantly change between 3.5 and 11 mm conch diameter; there is a trend toward a more slender conch with a narrower umbilicus. During this growth interval, the whorl profile changes from crescent-shaped to C-shaped.

The suture line of the specimen MB.C.31954.1 shows, at 3 mm whorl height, a wide external lobe with parallel flanks in its upper half (Fig. 8E); the stair-shaped E_2 lobe has a position on the flanks of the external lobe. The ventrolateral saddle is asymmetrically rounded and the lateral lobe is U-shaped and slightly asymmetric. The lateral lobe has only one third of the depth of the external lobe.

Remarks

Afromaenioceras sulcatostriatum is more involute and more slender than *A. hiemale* sp. nov.

Afromaenioceras hiemale sp. nov.
urn:lsid:zoobank.org:act:6D5CA601-FB40-471A-9A07-34526CBE4CD6
Fig. 9; Table 6

Diagnosis

Species of *Afromaenioceras* with thickly pachyconic and subevolute conch at 6 mm dm (ww/dm ~ 0.75; uw/dm ~ 0.45); conch thinly pachyconic and subevolute at 16 mm dm (ww/dm ~ 0.65; uw/dm ~ 0.40) with moderately depressed whorl profile (ww/wh ~ 1.90) and low coiling rate (WER ~ 1.55). Whorl profile at 16 mm conch diameter C-shaped with convex, weakly convergent flanks, broadly rounded

ventrolateral shoulder and flattened venter. Ventrolateral shoulder without spiral groove. Growth lines coarse, bundled, strongly biconvex. Suture line with wide external lobe, small, subangular E_2 lobe, inverted U-shaped ventrolateral saddle and U-shaped lateral lobe.

Etymology

After the Latin adjective '*hiemalis*, *-e*' = 'winterly'; the conch resembles a winter tire.

Type material

Holotype

MOROCCO • Anti-Atlas, Tafilalt, Jebel Ouaoufilal; middle Givetian; Bockwinkel and Ebbighausen 2002–2004 Coll.; MB.C.31956.1 (illustrated in Fig. 9A).

Paratypes

MOROCCO • 25 specs; same collection data as for holotype; MB.C.31956.2 to MB.C.31956.26 • 1 spec.; Anti-Atlas, Oufrane-W; bed 11 (middle Givetian); Bockwinkel and Ebbighausen 2002–2004 Coll.; MB.C.31957 • 1 spec.; Anti-Atlas, Oued Mzerreb-W; bed 11 (middle Givetian); Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31958.

Description

Holotype MB.C.31956.1 is a limonitic internal mould with 16 mm conch diameter, of which the left side well-preserved and the right side is somewhat corroded (Fig. 9A). The conch is thinly pachyconic and subevolute (ww/dm = 0.64; uw/dm = 0.39) with a low coiling rate (WER = 1.57); the umbilicus starts closing at 14 mm diameter. The whorl profile is moderately depressed (ww/wh = 1.88) with broadly rounded flanks and a nearly flat venter. The internal mould shows riblet-like traces of bundled growth lines, which extend with a strongly biconvex course; they form small tubercles at the umbilical margin. The suture line has a Y-shaped external lobe with stair-shaped flanks, a rectangular and blunt E_2 lobe, a slightly asymmetric, inverted U-shaped ventrolateral saddle and a deep, broadly rounded U-shaped

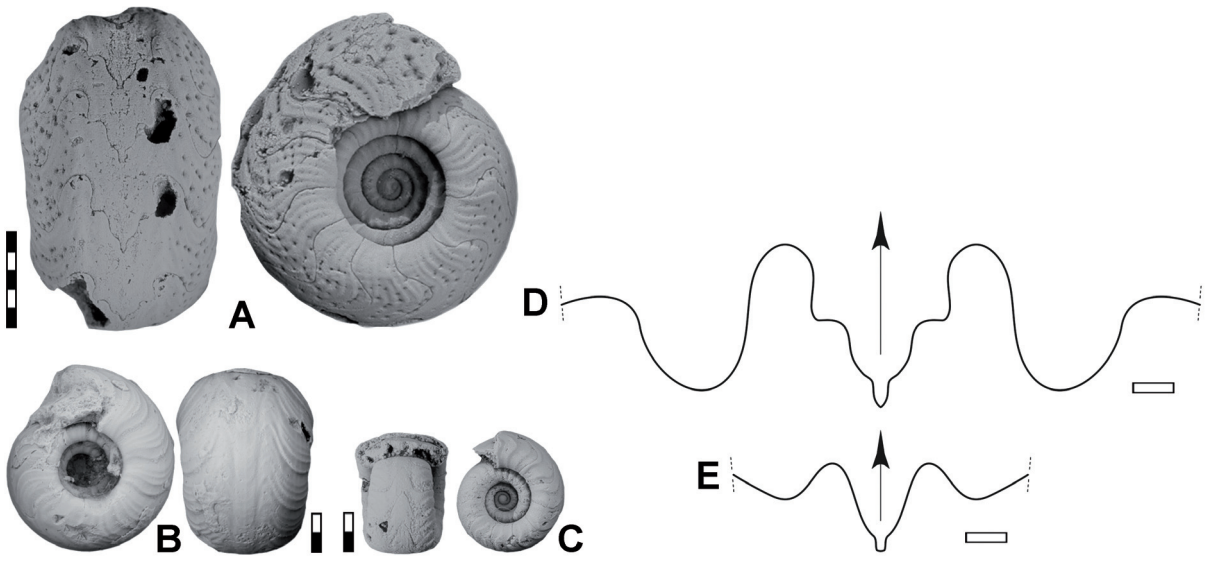

Fig. 9. *Afromaenioceras hiemale* sp. nov. **A**. Holotype MB.C.31956.1 from Jebel Ouaoufilal. **B**. Paratype MB.C.31957 from Oufrane. **C**. Paratype MB.C.31956.2 from Jebel Ouaoufilal. **D**. Holotype MB.C.31956.1 from Jebel Ouaoufilal; suture line at wh = 4.5. **E**. Paratype MB.C.31956.2 from Jebel Ouaoufilal; suture line at wh =1.6 mm. Scale bar units = 1 mm.

Table 6. Conch dimensions (in mm) and ratios of *Afromaenioceras hiemale* sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31956.1	16.4	10.5	5.6	6.4	3.3	0.64	1.88	0.39	1.57	0.41
MB.C.31956.3	14.5	9.4	5.6	3.9	3.8	0.65	1.68	0.27	1.84	0.32
MB.C.31957	9.7	7.1	3.2	3.9	2.3	0.73	2.22	0.40	1.72	0.28
MB.C.31956.4	8.6	6.0	2.6	3.3	1.9	0.69	2.29	0.38	1.65	0.27
MB.C.31956.2	6.3	4.8	2.0	2.9	1.4	0.76	2.46	0.45	1.65	0.28

lateral lobe (Fig. 9D). On the outer flank and the ventrolateral region occurs, on both sides of the conch, a sequence of densely arranged Housean pits (compare De Baets *et al.* 2011). The last phragmocone volution has only eleven chambers.

Paratype MB.C.31957 is a well-preserved internal mould with nearly 10 mm conch diameter (Fig. 9B). The conch is thickly pachyconic and subevolute (ww/dm = 0.73; uw/dm = 0.40); the whorl profile is strongly depressed (ww/wh = 2.22) and the coiling rate is moderate (WER = 1.72). The internal mould shows traces of riblets and weak constrictions with strongly biconvex course.

Paratype MB.C.31956.2 is a well-preserved small internal mould with 6 mm conch diameter (Fig. 9C). It is thickly pachyconic and evolute (ww/dm = 0.76; uw/dm = 0.45) with a strongly depressed whorl profile (ww/wh = 2.46) and a low coiling rate (WER = 1.65). The internal mould shows traces of riblets with strongly biconvex course. The suture line has a V-shaped, unsubdivided external lobe with slightly curved flanks and a shallow, broadly rounded lateral lobe (Fig. 9E).

Remarks

The conch of *Afromaenioceras hiemale* sp. nov. is, with a ww/dm ratio of about 0.65 and a uw/dm ratio of about 0.40 at 16 mm conch diameter, significantly stouter and more evolute than the conch of *A. sulcatostriatum* with the ratios ww/dm ~ 0.50 and uw/dm ~ 0.30 at 12 mm conch diameter.

Afromaenioceras bensaidi sp. nov.
urn:lsid:zoobank.org:act:5066DF05-35BC-424A-A3C1-AD7598BD3405
Fig. 10; Table 7

Afromaenioceras n. sp. – Aboussalam & Becker 2011: text-fig. 8.5–6.

Diagnosis

Species of *Afromaenioceras* with thinly pachyconic and subinvolute conch at 10 mm dm (ww/dm ~ 0.60; uw/dm ~ 0.20); conch thickly discoidal and involute at 22 mm dm (ww/dm ~ 0.45; uw/dm ~ 0.05) with moderately compressed whorl profile (ww/wh ~ 0.85) and moderately high coiling rate (WER ~ 1.85). Whorl profile at 22 mm conch diameter horseshoe-shaped with convex, weakly convergent flanks, broadly rounded ventrolateral shoulder and flattened venter. Ventrolateral shoulder with faint or pronounced spiral groove. Growth lines coarse, bundled, strongly biconvex. Suture line with wide external lobe, small, subangular E_2 lobe, inverted U-shaped ventrolateral saddle and asymmetric, tongue-shaped lateral lobe.

Etymology

Named after Mohamed Bensaïd, to honour his contribution to Moroccan palaeontology.

Type material

Holotype

MOROCCO • Anti-Atlas, Oued Mzerreb-W; beds 10/11 (middle Givetian); Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31959.1 (illustrated in Fig. 10A).

Paratypes

MOROCCO • 10 specs; same collection data as for holotype; MB.C.31959.2 to MB.C.31959.11.

Description

Holotype MB.C.31959.1 is a moderately well-preserved, somewhat corroded specimen with 22 mm conch diameter (Fig. 10A). The conch is thinly discoidal and involute (ww/dm = 0.46; uw/dm = 0.06); the whorl profile is weakly compressed (ww/wh = 0.86) and the coiling rate moderately high (WER = 1.83). The flanks are slightly convex and terminated by a striking spiral groove on the ventrolateral shoulder; the venter is flattened. The internal mould shows traces of coarse, lamellar growth lines with strongly biconvex course. The suture line is not well-preserved, but possesses a wide external lobe with stair-shaped flanks, a high asymmetrically rounded ventrolateral saddle and a deep, asymmetrically rounded lateral lobe.

Paratypes MB.C.31959.4 (Fig. 10B) and MB.C.31959.2 (Fig. 10C) are thinly pachyconic, involute conchs with 10 mm dm (ww/dm ~ 0.60; uw/dm ~ 0.20) with a weakly depressed whorl profile (ww/wh ~ 1.25) and a moderate coiling rate. Paratype MB.C.31959.2 shows the typical *Afromaenioceras* suture line with a Y-shaped external lobe with stair-shaped flanks, an asymmetrically rounded, inverted U-shaped ventrolateral saddle and a deep, asymmetrically rounded lateral lobe (Fig. 10E).

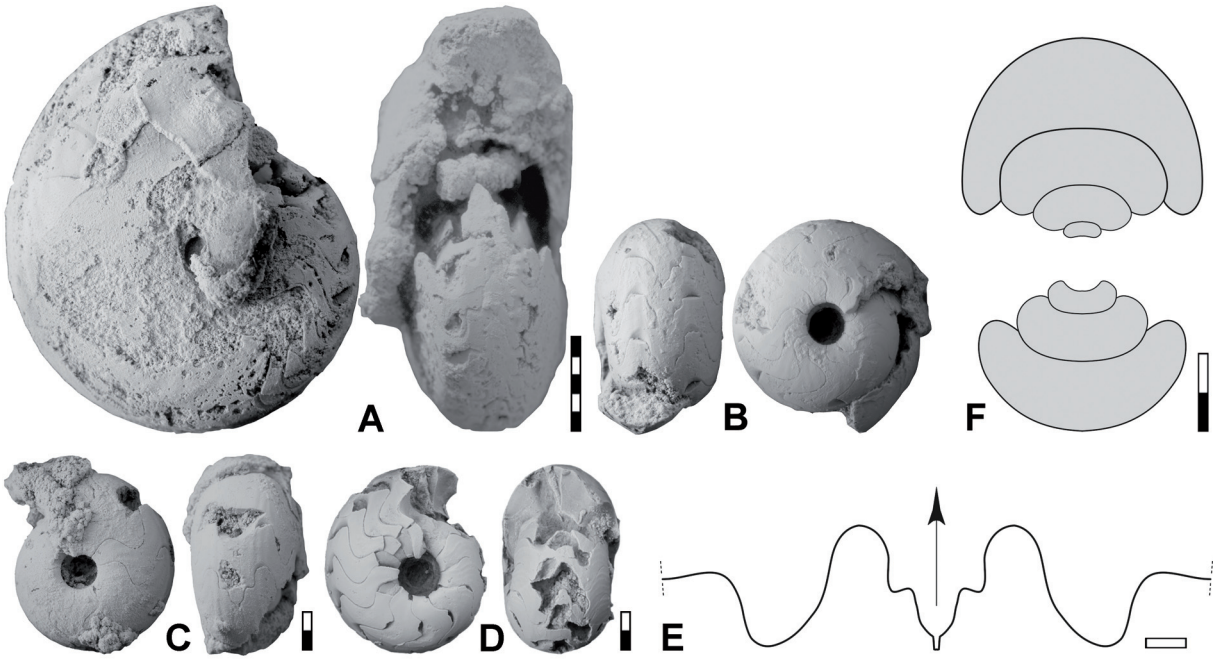

Fig. 10. *Afromaenioceras bensaidi* sp. nov. from Oued Mzerreb-W, beds 10/11. **A**. Holotype MB.C.31959.1. **B**. Paratype MB.C.31959.4. **C**. Paratype MB.C.31959.2. **D**. Paratype MB.C.31959.3. **E**. Paratype MB.C.31959.2; suture line at wh = 5.2 mm. **F**. Paratype MB.C.31959.5; cross section. Scale bar units = 1 mm.

Table 7. Conch dimensions (in mm) and ratios of *Afromaenioceras bensaidi* sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31959.1	22.3	10.3	12.0	1.4	5.8	0.46	0.86	0.06	1.83	0.52
MB.C.31959.2	10.0	6.1	4.9	1.9	2.5	0.61	1.24	0.19	1.78	0.49
MB.C.31959.3	9.4	5.8	4.5	1.6	2.2	0.62	1.29	0.17	1.70	0.51
MB.C.31959.5	10.38	6.34	4.67	2.8	2.4	0.61	1.36	0.27	1.69	0.49
MB.C.31959.5	7.99	5.27	2.91	2.8	1.9	0.66	1.81	0.35	1.69	0.36
MB.C.31959.5	6.14	4.49	2.29	2.1	1.5	0.73	1.96	0.35	1.74	0.35
MB.C.31959.5	4.65	3.45	1.72	1.7	1.2	0.74	2.01	0.37	1.86	0.28
MB.C.31959.5	3.41	2.59	1.20	1.3	1.0	0.76	2.16	0.39	1.95	0.19

Paratype MB.C.31959.3 is an internal mould with a conch diameter of 9.5 mm (Fig. 10D). The conch is thinly pachyconic and subinvolute (ww/dm = 0.62; uw/dm = 0.17) with a weakly depressed whorl profile (ww/wh = 1.29) and a low coiling rate (WER = 1.70). The flanks are convex and the venter broadly rounded.

Paratype MB.C.31959.5 was sectioned and shows the ontogenetic development of the conch geometry between diameters of 4.5 and 10 mm (Fig. 10F). Three volutions can be studied; they show only minor ontogenetic changes in the shape of the whorl profiles. A trend toward a more slender conch with a narrower umbilicus can be observed. During this growth interval, the whorl profile changes from crescent-shaped to C-shaped.

Remarks

Afromaenioceras bensaidi sp. nov. is characterised by the involute conch in the adult stage and is thus clearly separate from the other species of the genus.

Afromaenioceras brumale sp. nov.
urn:lsid:zoobank.org:act:A55F968F-58F4-48D2-9D54-B3CD46403010
Fig. 11; Table 8

? *Maenioceras* cf. *crassum* – Bensaïd 1974: 105, pl. 1 fig. 10, 10a.
? *Afromaenioceras* n. sp. – Becker *et al*. 2004: pl. 1 figs 7–8.

Diagnosis

Species of *Afromaenioceras* with thinly pachyconic and subevolute conch at 6 mm dm (ww/dm ~ 0.70; uw/dm ~ 0.38); conch thickly discoidal and subinvolute at 16 mm dm (ww/dm ~ 0.55; uw/dm ~ 0.18) with weakly depressed whorl profile (ww/wh ~ 1.15) and low coiling rate (WER ~ 1.55). Whorl profile at 16 mm conch diameter C-shaped with convex, weakly convergent flanks, broadly rounded ventrolateral shoulder and rounded venter. Ventrolateral shoulder with faint spiral groove. Growth lines coarse, strongly biconvex. Suture line with wide external lobe, small, subangular E_2 lobe, inverted U-shaped ventrolateral saddle and symmetric, blunt V-shaped lateral lobe.

Etymology

After the Latin adjective '*brumalis*, *-e*' = 'summery'; the conch resembles a summer tire.

Type material

Holotype

MOROCCO • Anti-Atlas, Oufrane-E; bed 12, middle Givetian; Bockwinkel and Ebbighausen 2002–2004 Coll.; MB.C.31960 (illustrated in Fig. 11A).

Paratypes

MOROCCO • 25 specs; Anti-Atlas, Oued Mzerreb-W; beds 10/11, middle Givetian; Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31962.1 to MB.C.31962.25 • 1 spec.; Anti-Atlas, Tafilalt, Jebel Ouaoufilal; middle Givetian; Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31961 • 6 specs; Anti-Atlas, Oufrane-E; bed 11, middle Givetian; Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31963.1 to MB.C.31963.6 • 1 spec.; Anti-Atlas, Tiguisselt; bed 10, middle Givetian; Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31964.

Description

Holotype MB.C.31960 is a very well-preserved limonitic internal mould with 16 mm conch diameter (Fig. 11A). It is a thickly discoidal, subinvolute conch (ww/dm = 0.55; uw/dm = 0.18) with a weakly depressed whorl profile (ww/wh = 1.16) and a low coiling rate (WER = 1.53); flanks and venter are broadly rounded. The ventrolateral shoulder has a faint spiral groove. Traces of coarse growth lines are visible on the flanks. The last volution of the phragmocone has only ten chambers.

Paratype MB.C.31961 is a thickly discoidal, subinvolute conch with 16 mm conch diameter and shows, like the two specimens described above, rows of Housean Pits in the outer flank region (Fig. 11B).

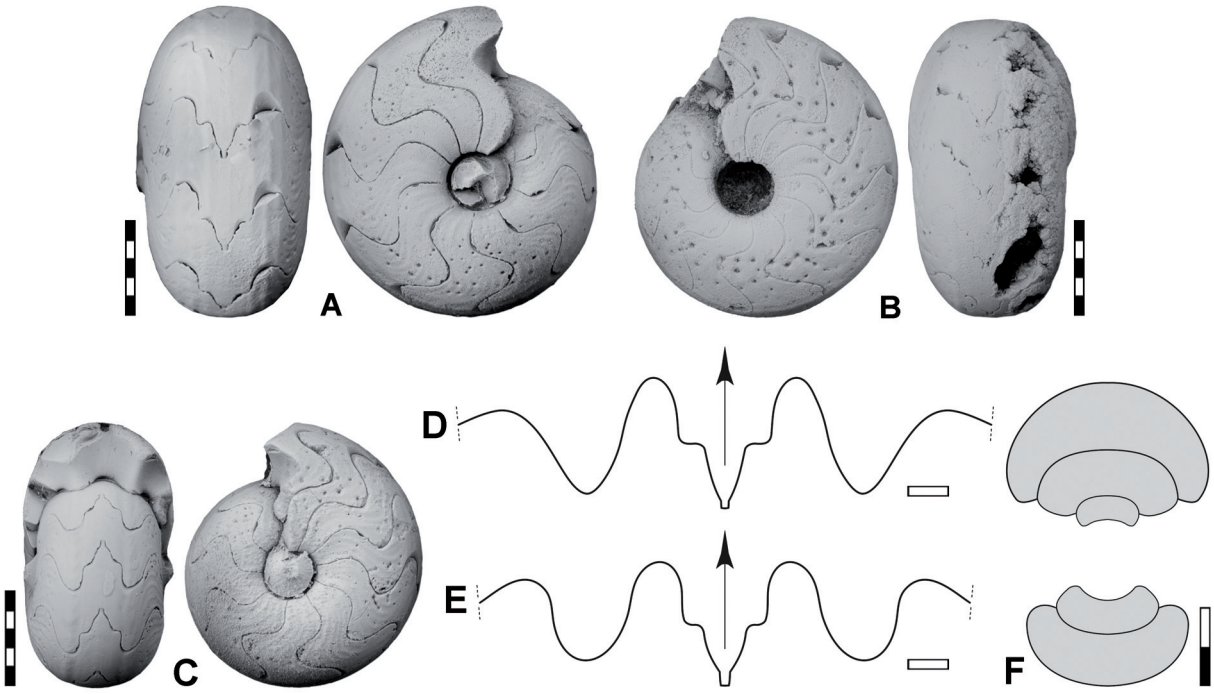

Fig. 11. *Afromaenioceras brumale* sp. nov. **A**. Holotype MB.C.31960 from Oufrane-E, bed 12. **B**. Paratype MB.C.31961 from, Jebel Ouaoufilal. **C**. Paratype MB.C.31962.1 from Oued Mzerreb-W, beds 10/11. **D**. Paratype MB.C.31962.2 from Oued Mzerreb-W, bed 10/11; suture line at wh = 4.5 mm. **E**. Paratype MB.C.31962.3 from Oued Mzerreb-W, beds 10/11; suture line at wh = 3.8 mm. **F**. Paratype MB.C.31962.4 from Oued Mzerreb-W, bed 10/11; cross section. Scale bar units = 1 mm.

Table 8. Conch dimensions (in mm) and ratios of *Afromaenioceras brumale* sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31960	16.2	9.0	7.7	2.9	3.1	0.55	1.16	0.18	1.53	0.60
MB.C.31961	15.8	8.9	7.7	3.1	–	0.57	1.16	0.20	–	–
MB.C.31962.1	13.9	7.9	6.7	2.5	3.0	0.57	1.17	0.18	1.63	0.55
MB.C.31962.4	8.22	5.45	3.24	2.80	1.82	0.66	1.68	0.34	1.65	0.44
MB.C.31962.4	6.40	4.38	2.19	2.43	1.40	0.69	2.00	0.38	1.64	0.36
MB.C.31962.4	5.00	3.81	1.78	1.91	1.24	0.76	2.14	0.38	1.77	0.30

Paratype MB.C.31962.4 was sectioned (Fig. 11F) and shows two volutions up to a conch diameter of 8.2 mm. Between 5 and 8 mm conch diameter, the whorl profile changes from crescent-shaped to C-shaped and the conch becomes more slender and narrowly umbilicate.

Paratypes MB.C.31962.2 (Fig. 11D) and MB.C.31962.3 (Fig. 11E)

Suture lines were drawn from those at wh = 4.5 and wh = 3.8 mm, respectively. Both show the Y-shaped external lobe with stair-shape flanks. However, they differ in the shape of the ventrolateral saddle, which is narrower in paratype MB.C.31962.2, and in the shape of the lateral lobe, which is blunt V-shaped in paratype MB.C.31962.2, but nearly U-shaped in paratype MB.C.31962.3.

Remarks

Afromaenioceras crassum is a similar species but differs in the stouter conch (ww/dm ~ 0.65; ww/wh ~ 1.45; uw/dm 0.24) from *A. brumale* sp. nov. (ww/dm ~ 0.55; ww/wh ~ 1.15; uw/dm 0.25) at ~ 15 mm dm.

Afromaenioceras crassum (Bensaïd, 1974)
Fig. 12; Table 9

Maenioceras crassum Bensaïd, 1974: 105, text-fig. 12c$_1$, c$_2$, pl. 2 fig. 11, 11a.

Afromaenioceras crassum – Becker *et al*. 2004: pl. 1 figs 5–6.

non *Bensaidites crassus* – Korn & Klug 2002: 141, text-fig. 133e, i.

Diagnosis

Species of *Afromaenioceras* with thickly pachyconic and subinvolute conch at 5 mm dm (ww/dm ~ 0.80; uw/dm ~ 0.35); conch thinly pachyconic and subinvolute at 16 mm dm (ww/dm ~ 0.65; uw/dm ~ 0.25) with weakly depressed whorl profile (ww/wh ~ 1.45) and low coiling rate (WER ~ 1.60). Whorl profile at 16 mm conch diameter C-shaped with convex, weakly convergent flanks, broadly rounded ventrolateral shoulder and rounded venter. Ventrolateral shoulder with faint spiral groove. Growth lines coarse, strongly biconvex. Suture line with wide external lobe, small, subangular E$_2$ lobe, inverted U-shaped ventrolateral saddle and U-shaped lateral lobe.

Material examined

Holotype

MOROCCO • Anti-Atlas, Oued Mzerreb; middle Givetian; IGPB-Bensaid-22 (illustrated by Bensaïd 1974: pl. 2 fig. 11).

Additional material

MOROCCO • 25 specs; Anti-Atlas, Oued Mzerreb-W; beds 10/11 (middle Givetian); Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31965.1 to MB.C.31965.25 • 46 specs; Anti-Atlas, Jebel Ouaoufilal; middle Givetian; Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31966.1 to MB.C.31966.46.

Description

Specimen MB.C.31965.1 is a limonitic internal mould with 15.5 mm conch diameter, which is well preserved on the left side (Fig. 12A). The conch is thinly pachyconic and subinvolute (ww/dm = 0.64; uw/dm = 0.26); the umbilicus starts closing at 12 mm conch diameter. The whorl profile is weakly depressed (ww/wh = 1.46) and the coiling rate is low (WER = 1.62). The flanks are broadly convex and the venter is slightly flattened. A faint spiral groove marks the ventrolateral shoulder. Traces of coarse growth lines on the internal mould show a strongly biconvex course. The suture line has a Y-shaped external lobe with stair-shaped flank, and inverted U-shaped ventrolateral saddle and a deep, U-shaped lateral lobe (Fig. 12D). Housean pits are present on the outer flank. The last phragmocone volution has only eleven chambers.

Specimen MB.C.31965.2 is a limonitic internal mould with 10 mm conch diameter, which is well-preserved on the left side (Fig. 12B). It is a thinly pachyconic, subevolute conch (ww/dm = 0.67; uw/dm = 0.33) with a moderately depressed whorl profile (ww/wh 1.79) and a low coiling rate (WER = 1.65). The ventrolateral shoulder shows a poorly developed spiral groove. The suture line has an external lobe with strongly pouched, divergent flanks and a broad and deep lateral lobe (Fig. 12E). The last phragmocone volution has only ten chambers.

Specimen MB.C.31965.3 ss a well-preserved small limonitic internal mould with 5 mm conch diameter (Fig. 12C). It is thickly pachyconic and subevolute (ww/dm = 0.81; uw/dm = 0.34) with a strongly depressed whorl profile (ww/wh = 2.11) and a moderately high coiling rate (WER = 1.78). The umbilical wall is steep, flanks and venter are broadly convex. The suture line of the juvenile specimen shows a V-shaped external lobe with gently convex flanks and a wide, broadly rounded lateral lobe (Fig. 12F).

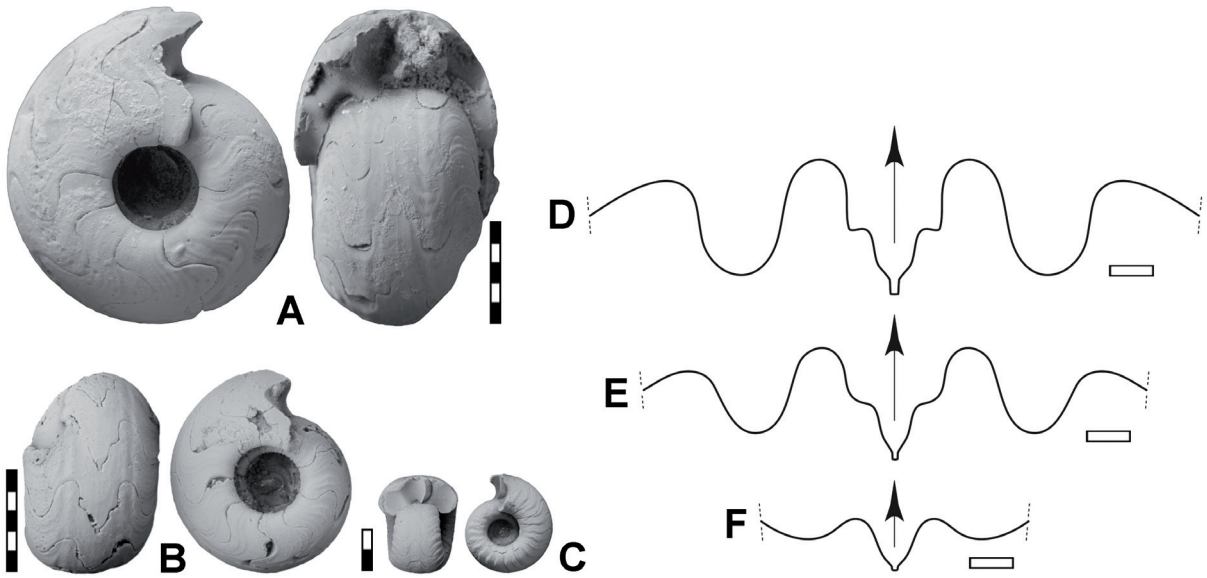

Fig. 12. *Afromaenioceras crassum* (Bensaïd, 1974) from Oued Mzerreb-W, bed 10/11. **A**. Specimen MB.C.31965.1. **B**. Specimen MB.C.31965.2. **C**. Specimen MB.C.31965.3. **D**. Specimen MB.C.31965.1; suture line at wh = 6.6 mm. **E**. Specimen MB.C.31965.2; suture line at wh = 4.5 mm. **F**. Specimen MB.C.31965.3; suture line at wh = 1.5 mm. Scale bar units = 1 mm.

Table 9. Conch dimensions (in mm) and ratios of *Afromaenioceras crassum* (Bensaïd, 1974).

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31965.1	15.5	9.9	6.8	4.0	3.3	0.64	1.46	0.26	1.62	0.51
MB.C.31966.1	12.8	8.6	5.0	4.0	2.9	0.67	1.72	0.31	1.67	0.42
MB.C.31965.2	9.9	6.7	3.7	3.2	2.2	0.67	1.79	0.33	1.65	0.41
MB.C.31966.2	7.7	5.8	2.5	2.5	1.7	0.75	2.32	0.32	1.62	0.34
MB.C.31965.3	4.8	3.9	1.9	1.6	1.2	0.81	2.11	0.34	1.78	0.35

Remarks

Afromaenioceras crassum has a stouter and wider umbilicate conch (ww/dm ~ 0.65; ww/wh ~ 1.50; uw/dm ~ 0.25) at 15 mm dm than *A. brumale* sp. nov. (ww/dm ~ 0.55; ww/wh ~ 1.15; uw/dm ~ 0.20).

Genus ***Trimaenioceras*** gen. nov.
urn:lsid:zoobank.org:act:943E3B40-EF29-4FAF-AD9C-F231591517B8

Type species

Trimaenioceras klugi gen. et sp. nov.

Diagnosis

Genus of the family Maenioceratidae with or without ventrolateral grooves; shell without constrictions or internal thickenings. External lobe very wide or extremely wide; E_2 lobe deep, cuneiform; ventrolateral saddle symmetrically rounded; lateral lobe V-shaped, angular.

Etymology

Named after the trident shape of the external lobe and the close relationship to *Maenioceras*.

Included species

Anti-Atlas (this paper): *Trimaenioceras klugi* gen. et sp. nov.; *Trimaenioceras eculeus* gen. et sp. nov.; *Trimaenioceras fuscina* gen. et sp. nov.; *Trimaenioceras paucum* gen. et sp. nov.

Trimaenioceras klugi gen. et sp. nov.
urn:lsid:zoobank.org:act:D659BF7F-C9C9-4150-9CF5-73B94B957BCE
Fig. 13; Table 10

Bensaidites n. sp. – Korn & Klug 2002: 141, text-fig. 133h, k.
Maenioceras n. sp. II – Aboussalam & Becker 2011: text-figs 8.3–4.

Diagnosis

Species of *Trimaenioceras* gen. nov. with thickly discoidal and involute conch at 20 mm dm (ww/dm ~ 0.50; uw/dm ~ 0.05) with weakly compressed whorl profile (ww/wh ~ 0.95) and low coiling rate (WER ~ 1.55). Whorl profile at 20 mm conch diameter horseshoe-shaped with convex, weakly convergent flanks, rounded ventrolateral shoulder and rounded venter. Ventrolateral shoulder without spiral groove. Growth lines fine. Suture line with very wide external lobe, deep, cuneiform, weakly asymmetric E_2 lobe, symmetrically rounded ventrolateral saddle and V-shaped, slightly asymmetric, acute lateral lobe.

Etymology

Named after Christian Klug, who discovered the ammonoid assemblage.

Type material

Holotype

MOROCCO • Anti-Atlas, Tafilalt, Jebel Ouaoufilal; middle Givetian; Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31967.1 (illustrated in Fig. 13A).

Paratypes

MOROCCO • 241 specs; same collection data as for holotype; MB.C.31967.2 to MB.C.31967.242 • 24 specs; Oued Mzerreb-W; beds 10/11 (middle Givetian); Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31968.1 to MB.C.31968.24.

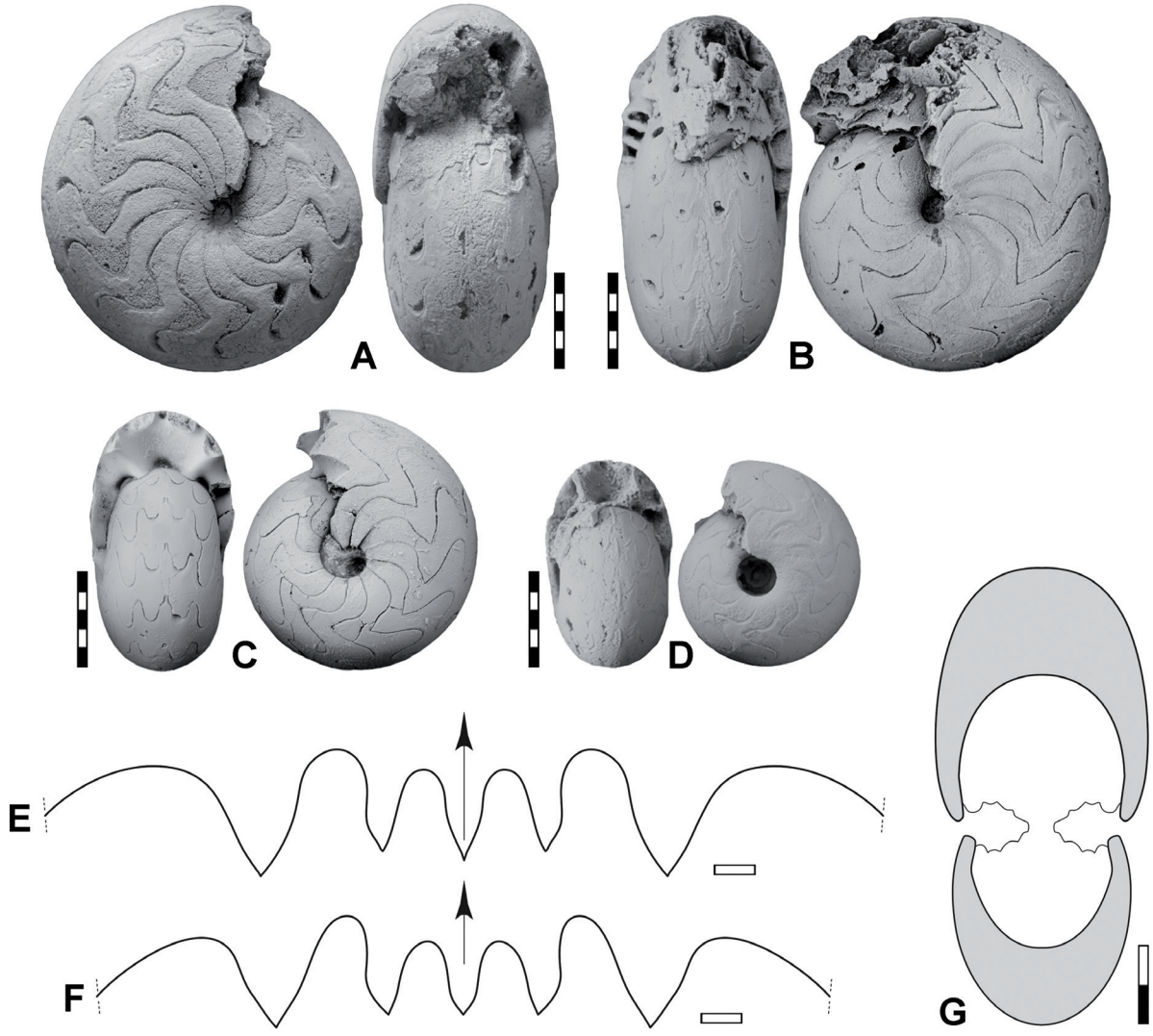

Fig. 13. *Trimaenioceras klugi* gen. et sp. nov. **A**. Holotype MB.C.31967.1 from Jebel Ouaoufilal. **B**. Paratype MB.C.31967.2 from Jebel Ouaoufilal. **C**. Paratype MB.C.31968.1 from Oued Mzerreb-W, beds 10/11. **D**. Paratype MB.C.31967.3 from Jebel Ouaoufilal. **E**. Paratype MB.C.31967.2 from Jebel Ouaoufilal; suture line at wh = 6.4 mm. **F**. Paratype MB.C.31968.1 from Oued Mzerreb-W, beds 10/11; suture line at wh = 6.4 mm. **G**. Paratype MB.C.31967.4 from Jebel Ouaoufilal; cross section. Scale bar units = 1 mm.

Table 10. Conch dimensions (in mm) and ratios of *Trimaenioceras klugi* gen. et sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31967.1	19.2	9.6	10.3	1.1	3.7	0.50	0.93	0.06	1.52	0.65
MB.C.31967.2	18.5	9.0	9.1	1.4	–	0.49	0.99	0.08	–	–
MB.C.31968.1	13.9	7.7	7.5	1.5	3.0	0.55	1.03	0.11	1.63	0.60
MB.C.31967.3	10.7	6.6	5.1	2.0	2.4	0.62	1.29	0.19	1.66	0.53

Description

Holotype MB.C.31967.1 is a well-preserved limonitic internal mould with 19 mm conch diameter (Fig. 13A). The conch is thickly discoidal and involute (ww/dm = 0.50; uw/dm = 0.06) with a weakly compressed whorl profile (ww/wh = 0.93) and a low coiling rate (WER = 1.52). The flanks are nearly parallel; the ventrolateral shoulder and the venter are continuously rounded. The last phragmocone volution has 14 chambers.

Paratype MB.C.31967.2 has, at 18.5 mm diameter, a conch with very similar proportions like the holotype (Fig. 13B). The suture line has an extremely wide external lobe, which is subdivided in three almost identical prongs. The E_1 lobe is lanceolate and separated from the asymmetric, cuneiform E_2 lobe by a nearly symmetric median saddle that reaches three quarters of the depth of the external lobe. The ventrolateral saddle is inverted U-shaped and nearly symmetric; the lateral lobe is slightly asymmetric V-shaped with convex ventral flank and nearly straight dorsal flank (Fig. 13E). The last phragmocone volution has 14 chambers.

Paratypes MB.C.31968.1 (14 mm conch diameter; Fig. 13C) and MB.C.31967.3 (11 mm conch diameter; Fig. 13D) show the morphology of the intermediate growth stage, in which the umbilicus is being closed by increasing overlap of the inner flank upon the umbilicus. The suture line of paratype MB.C.31968.1 is similar to that of paratype MB.C.31967.2, but possesses less deep lobes (Fig. 13F). The ventrolateral saddle is narrowly rounded. The last phragmocone volution of paratype MB.C.31968.1 has 12 chambers.

Paratype MB.C.31967.4 was sectioned, but shows that the inner whorls are not preserved (Fig. 13G). However, it shows clearly that the whorl profile is, at 12 mm conch diameter, horseshoe-shaped. It is widest in the midflank area, from where the flanks converge towards the umbilicus and the continuously rounded venter. The umbilical wall is very low and strongly convex.

Remarks

Trimaenioceras klugi gen. et sp. nov. is similar to *T. eculeus* gen. et sp. nov., but differs in the more slender and narrowly umbilicate conch in comparative growth stages. At around 15 mm conch diameter, ~0. 50 and ~0.05 in *T. klugi*, but ww/dm ~0.60 and uw/dm ~0.25 in *T. eculeus*.

Trimaenioceras eculeus gen. et sp. nov.
urn:lsid:zoobank.org:act:9EBD0D9B-BFCE-4218-B3DA-A78113DF0399
Fig. 14; Table 11

Diagnosis

Species of *Trimaenioceras* gen. nov. with thickly discoidal and subinvolute conch at 15 mm dm (ww/dm ~0.60; uw/dm ~0.25); conch thinly discoidal and subinvolute at 28 mm dm (ww/dm ~0.40; uw/dm ~0.10) with weakly compressed whorl profile (ww/wh ~0.85) and low coiling rate (WER ~1.65). Whorl profile at 28 mm conch diameter horseshoe-shaped with convex, weakly convergent flanks, rounded ventrolateral shoulder and rounded venter. Ventrolateral shoulder without spiral groove.

Growth lines very fine. Suture line with wide external lobe, moderately deep, cuneiform, strongly asymmetric E_2 lobe, rounded ventrolateral saddle and V-shaped, symmetric, acute lateral lobe.

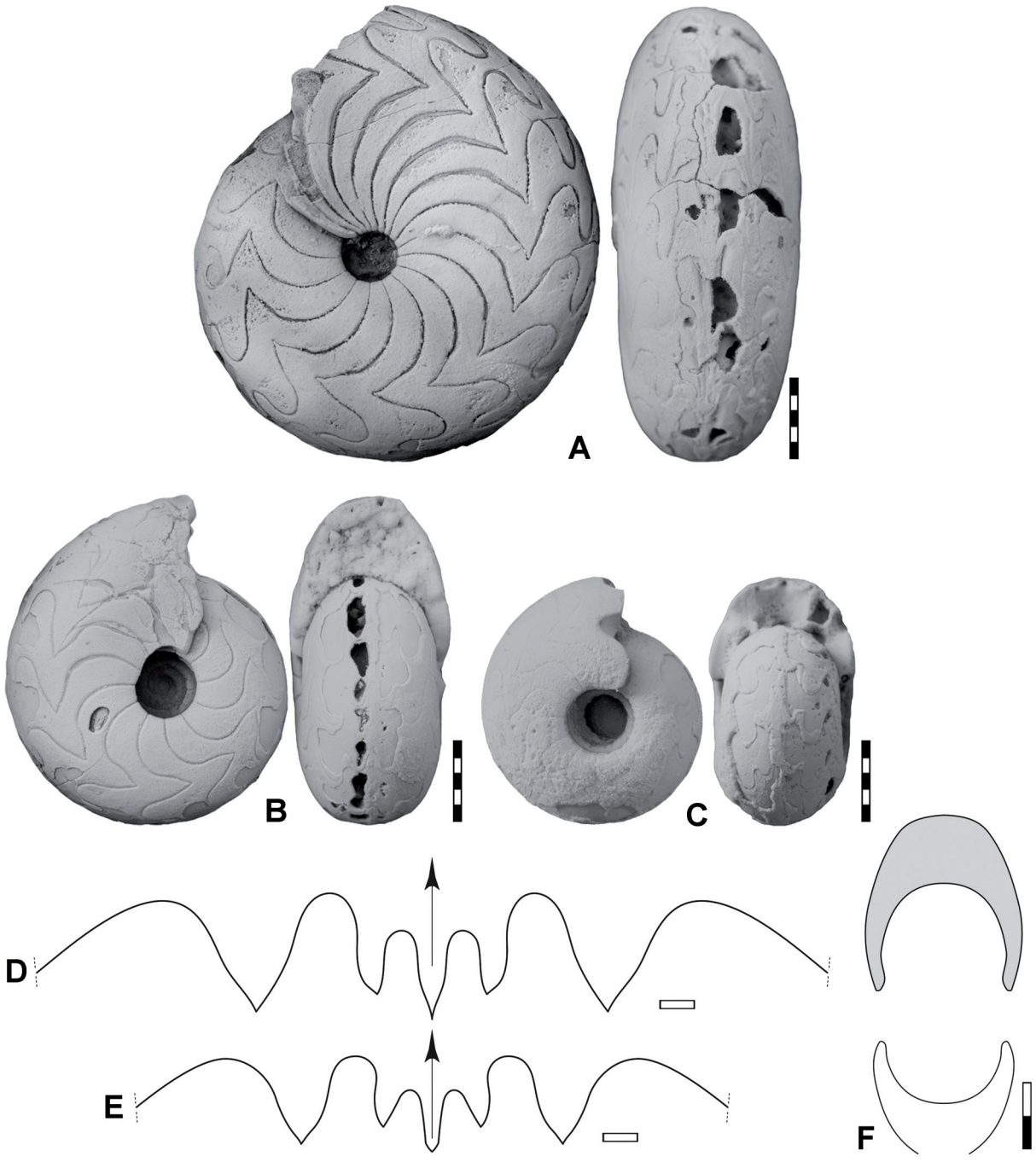

Fig. 14. *Trimaenioceras eculeus* gen. et sp. nov., from Hassi Nebech. **A**. Holotype MB.C.31969.1. **B**. Paratype MB.C.31969.2. **C**. Paratype MB.C.31969.3. **D**. Holotype MB.C.31969.1; suture line at wh = 13.5 mm. **E**. Paratype MB.C.31969.4; suture line at wh = 9.5 mm. **F**. Paratype JB HN 1; cross section. Scale bar units = 1 mm.

Table 11. Conch dimensions (in mm) and ratios of *Trimaenioceras eculeus* gen. et sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31969.1	28.2	11.7	13.9	3.0	6.2	0.41	0.84	0.11	1.64	0.55
MB.C.31969.2	20.5	9.8	9.4	4.1	4.6	0.48	1.04	0.20	1.66	0.51
MB.C.31969.6	17.4	9.2	7.7	3.8	3.8	0.53	1.19	0.22	1.64	0.51
MB.C.31969.3	15.2	9.0	6.6	3.8	3.2	0.59	1.36	0.25	1.60	0.52
MB.C.31969.7	13.4	8.6	5.4	3.9	3.0	0.64	1.59	0.29	1.66	0.44
MB.C.31969.8	10.7	6.6	3.2	3.8	2.2	0.62	2.06	0.36	1.58	0.31

Etymology

From the Latin nomen '*eculeus*' = 'a little horse', because of the horseshoe-shaped whorl profile.

Type material

Holotype

MOROCCO • Anti-Atlas, south-eastern Tafilalt, Hassi Nebech, section 2; middle Givetian; Bockwinkel and Ebbighausen 2002–2004 Coll.; MB.C.31969.1 (illustrated in Fig. 14A).

Paratypes

MOROCCO • 27 specs; same collection data as for holotype; MB.C.31969.2 to MB.C.31969.28 • 5 specs; same collection data as for holotype except collected by locals; MB.C.31970.1 to MB.C.31970.5.

Description

Holotype MB.C.31969.1 is a well-preserved limonitic, fully chambered specimen with 28 mm conch diameter (Fig. 14A). It is thinly discoidal and involute (ww/dm = 0.41; uw/dm = 0.11) and shows that the umbilicus starts closing at about 25 mm conch diameter by overlap of the flanks. The whorl profile is weakly compressed (ww/wh = 0.84) and the coiling rate is low (WER = 1.64). The suture line shows a very wide external lobe that is subdivided into three parts, of which the E_1 lobe is wider and deeper than the asymmetric, cuneiform E_2 lobes. The median saddle reaches about two thirds of the depth of the external lobe. The ventrolateral saddle is nearly symmetric and rounded; the lateral lobe is V-shaped with gently convex flanks (Fig. 14D). The last phragmocone volution has 16 chambers.

Paratypes MB.C.31969.2 (20.5 mm conch diameter; Fig. 14B) and MB.C.31969.3 (15 mm conch diameter; Fig. 14C) demonstrate the ontogenetic transformation of the conch shape. Together with the holotype, they show that the conch width decreases, between 15 and 28 mm conch diameter, from a ww/dm ratio of about 0.60 to about 0.40; parallel to this, the uw/dm ratio decreases from 0.25 to about 0.10. The last phragmocone volution of paratype MB.C.31969.2 has 13 chambers.

The suture line of paratype MB.C.31969.4 shows, at a whorl height of 9.5 mm, a very wide external lobe; the E_2 lobe is nearly V-shaped and blunt. The ventrolateral saddle is inverted U-shaped and the lateral lobe is V-shaped with a convex ventral flank (Fig. 14E).

Remarks

Trimaenioceras eculeus gen. et sp. nov. is similar to *T. klugi* gen. et sp. nov., but differs in the stouter and more widely umbilicate conch in comparative growth stages. At around 15 mm conch diameter, ww/dm ~ 0.60 and uw/dm ~ 0.25 in *T. eculeus*, but ~ 0. 50 and ~ 0.05 in *T. klugi*.

Trimaenioceras fuscina gen. et sp. nov.
urn:lsid:zoobank.org:act:C5B0E733-6BD9-48EB-A89A-009451C83B6F
Fig. 15; Table 12

Diagnosis

Species of *Trimaenioceras* gen. nov. with thinly discoidal and subinvolute conch at 20 mm dm (ww/dm ~ 0.40; uw/dm ~ 0.15) with weakly compressed whorl profile (ww/wh ~ 0.85) and low coiling rate (WER ~ 1.70). Whorl profile at 20 mm conch diameter horseshoe-shaped with flattened subparallel flanks, rounded ventrolateral shoulder and rounded venter. Ventrolateral shoulder without spiral groove. Growth lines very fine. Suture line with wide external lobe, moderately deep, cuneiform E_2 lobe, rounded ventrolateral saddle and V-shaped, acute lateral lobe.

Etymology

After the Latin nomen '*fuscina*' = 'trident', because of the shape of the external lobe.

Type material

Holotype

MOROCCO • Anti-Atlas, south-eastern Tafilalt, Hassi Nebech, section 2; middle Givetian; Bockwinkel and Ebbighausen 2002–2004 Coll.; MB.C.31970.1 (illustrated in Fig. 14B).

Paratype

MOROCCO • 1 spec.; same collection data as for holotype; MB.C.31970.2 (illustrated in Fig. 14A).

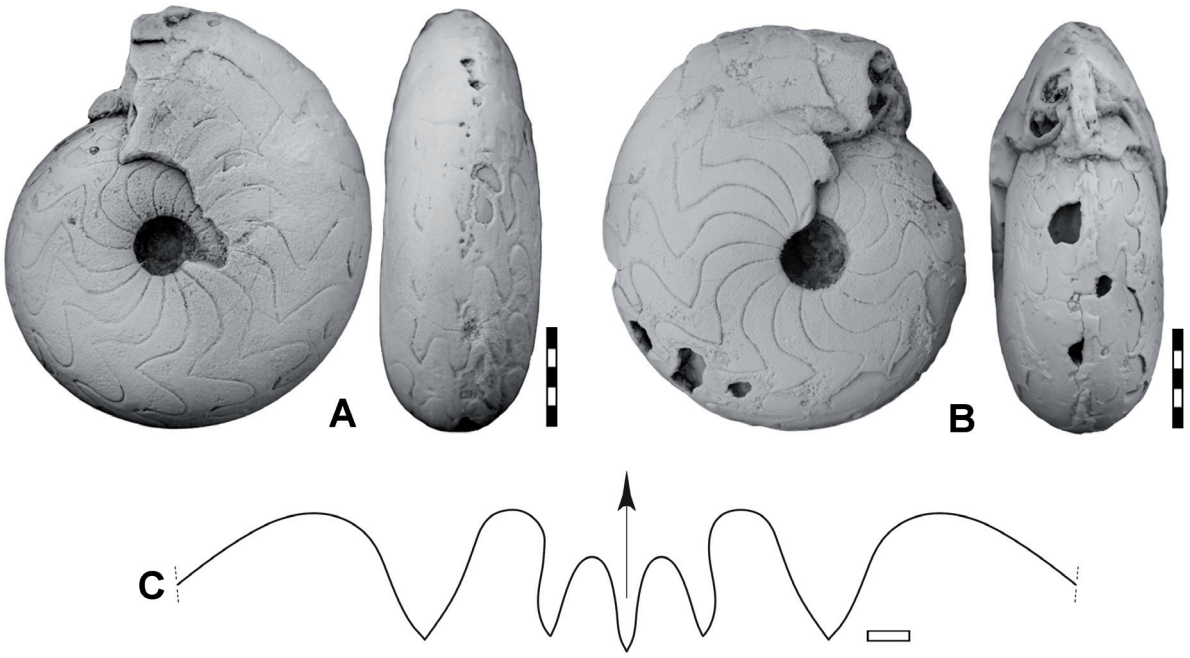

Fig. 15. *Trimaenioceras fuscina* gen. et sp. nov. from Jebel Ouaoufilal. **A**. Paratype MB.C.31970.2. **B**. Holotype MB.C.31970.1. **C**. Paratype MB.C.31970.2; suture line at wh = 9.5 mm. Scale bar units = 1 mm.

Table 12. Conch dimensions (in mm) and ratios of *Trimaenioceras fuscina* gen. et sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31970.2	21.3	8.5	10.2	2.9	5.1	0.40	0.83	0.14	1.73	0.50
MB.C.31970.1	20.8	8.8	9.9	3.2	4.9	0.42	0.89	0.15	1.71	0.51

Description

Holotype MB.C.31970.1 is a fully septate internal mould of a specimen with 21 mm conch diameter (Fig. 15B). The conch is thinly discoidal with a rather small umbilicus (ww/dm = 0.42; uw/dm = 0.15); a weakly compressed whorl profile (ww/wh = 0.89) and a low coiling rate (WER = 1.71). The specimen shows that the umbilicus is being narrowed, caused by increased overlap of the flanks upon the umbilicus, during the last preserved volution.

Paratype MB.C.31970.2 is a specimen with 21.5 mm conch diameter (Fig. 15A), which in size and proportions of the conch closely resembles the holotype (ww/dm = 0.40; uw/dm = 0.14). The suture line shows a very wide external lobe that is subdivided into three almost equally wide and deep prongs, of which the E_2 lobes are asymmetric and cuneiform. The median saddle reaches about two thirds of the depth of the external lobe. The ventrolateral saddle is nearly symmetric and inclined towards the venter; the lateral lobe is V-shaped with gently convex flanks (Fig. 15C). The last phragmocone volution has about 16 chambers.

Remarks

Trimaenioceras fuscina gen. et sp. nov. is the species of the genus with the most slender conch. At about 20 mm conch diameter, its ww/dm ratio is ~ 0.40, while it is ~ 0.50 in *T. klugi* gen. et sp. nov. and *T. eculeus* gen. et sp. nov. *Trimaenioceras fuscina* differs from *T. klugi* in the less deep sutural elements of the external lobe. A suture line very similar to *T. fuscina* can be seen in *T. eculeus*, but this species differs in the wider umbilicus (uw/dm ~ 0.20) at 20 mm conch diameter (uw/dm is only ~ 0.15 in *T. fuscina*).

Trimaenioceras paucum gen. et sp. nov.
urn:lsid:zoobank.org:act:90C42810-1EF6-4CCC-A8AF-DC841BC9539A
Fig. 16; Table 13

Diagnosis

Species of *Trimaenioceras* gen. nov. with thickly discoidal and involute conch at 14 mm dm (ww/dm ~ 0.60; uw/dm ~ 0.15) with weakly depressed whorl profile (ww/wh ~ 1.25) and low coiling rate (WER ~ 1.60). Whorl profile at 14 mm conch diameter C-shaped with convex, convergent flanks, rounded ventrolateral shoulder and rounded venter. Ventrolateral shoulder with faint spiral groove. Growth lines very fine. Suture line with wide external lobe, moderately deep, cuneiform E_2 lobe, rounded ventrolateral saddle and V-shaped, acute lateral lobe.

Etymology

From the Latin adjective '*paucus*, *-um*' = 'poor', because of the rarity of specimens.

Type material

Holotype

MOROCCO • Anti-Atlas, Tafilalt, Jebel Ouaoufilal; middle Givetian; Bockwinkel and Ebbighausen 2004 Coll.; MB.C.31971.1 (illustrated in Fig. 16A).

Table 13. Conch dimensions (in mm) and ratios of *Trimaenioceras paucum* gen. et sp. nov.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31971.1	13.9	8.1	6.5	1.9	2.9	0.58	1.25	0.14	1.60	0.55
MB.C.31971.2	12.3	7.5	5.9	1.8	2.6	0.61	1.27	0.15	1.61	0.56

Paratype

MOROCCO • 1 spec.; same collection data as for holotype; MB.C.31971.2 (illustrated in Fig. 16B).

Description

Holotype MB.C.31971.1 is an incomplete internal mould with a conch diameter of 14 mm (Fig. 16A). It is thickly discoidal and involute (ww/dm = 0.58; uw/dm = 0.14) with a weakly depressed whorl profile (ww/wh = 1.25) and a low coiling rate (WER = 1.60). The flanks are weakly rounded and converge toward the broadly rounded venter; the ventrolateral shoulder shows a shallow spiral groove. The suture line has a wide external lobe, a moderately deep, asymmetric E_2 lobe, a slightly asymmetric rounded ventrolateral saddle and a wide, pointed L lobe (Fig. 16C).

Paratype MB.C.31971.2 (Fig. 16B) largely agrees, in its conch morphology, with the holotype.

Remarks

Trimaenioceras paucum gen. et sp. nov. is the only one *Trimaenioceras* gen. nov. with ventrolateral grooves and thus easily distinguishable from the other species.

Discussion

Ammonoids of the Givetian family Maenioceratidae are important index fossils in the Devonian sedimentary rocks of the Anti-Atlas (Morocco). Our study shows that the diversity of the family is

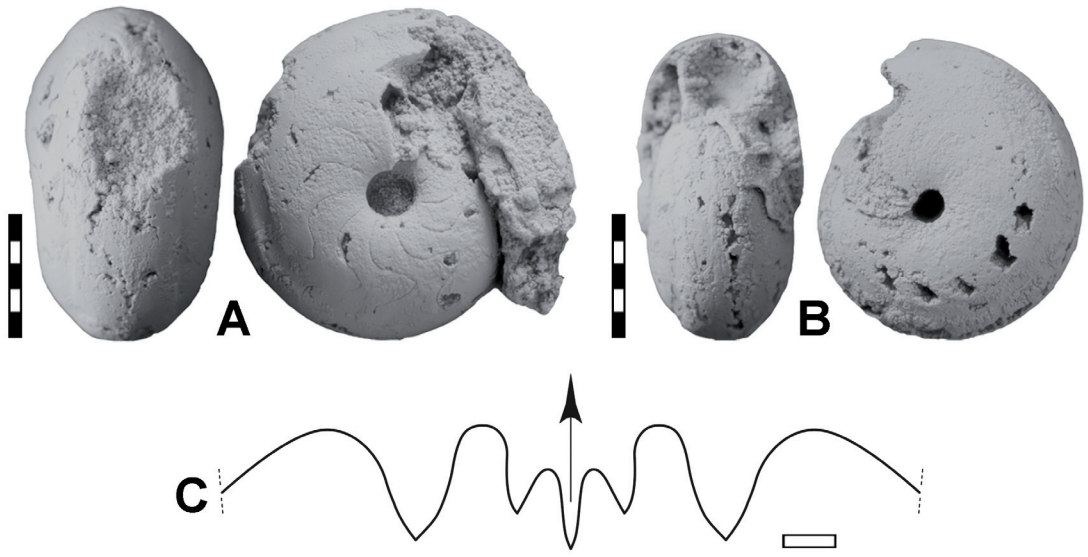

Fig. 16. *Trimaenioceras paucum* gen. et sp. nov. from Hassi Nebech. **A**. Holotype MB.C.31971.1. **B**. Paratype MB.C.31971.2. **C**. Holotype MB.C.31971.1; suture line at wh = 5.0 mm. Scale bar units = 1 mm.

rather high in this region with three genera and thirteen species occurring in at least two successive stratigraphic units.

The genera *Maenioceras* Schindewolf, 1933 and *Afromaenioceras* Göddertz, 1987 are revised; the genus *Trimaenioceras* gen. nov. is newly described. The species *Maenioceras afroterebratum* sp. nov., *Maenioceras mzerrebense* sp. nov., *Maenioceras oufranense* sp. nov., *Maenioceras beckeri* sp. nov., *Afromaenioceras sulcatostriatum* (Bensaïd, 1974), *Afromaenioceras hiemale* sp. nov., *Afromaenioceras bensaidi* sp. nov., *Afromaenioceras brumale* sp. nov., *Afromaenioceras crassum* (Bensaïd, 1974), *Trimaenioceras klugi* gen. et sp. nov., *Trimaenioceras eculeus* gen. et sp. nov., *Trimaenioceras fuscina* gen. et sp. nov. and *Trimaenioceras paucum* gen. et sp. nov. are described in detail.

The stratigraphic occurrence of the genera in the family Maenioceratidae is cleared. *Bensaidites* is the stratigraphically oldest representative of the family, followed by *Maenioceras*, which precedes *Afromaenioceras*. The new genus *Trimaenioceras* co-occurs with *Afromaenioceras*.

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