Palaeobiogeographic and evolutionary meaning of an early Late Tournaisian ammonoid fauna from the Tafilalt of Morocco

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Korn, D., Bockwinkel, J., Ebbighausen, V., and Klug, C. 2003. Palaeobiogeographic and evolutionary meaning of an early Late Tournaisian ammonoid fauna from the Tafilalt of Morocco. *Acta Palaeontologica Polonica* 48 (1): 71–92.

An early Late Tournaisian (Early Carboniferous/Mississippian) ammonoid fauna is described from the Tafilalt of south-eastern Morocco. Twelve genera, four of which are new, and eleven new species are represented: *Becanites africanus* sp. nov., *Triimitoceras epiwocklumeriforme* gen. et sp. nov., *Irinoceras minutum* sp. nov., *Muensteroceras quadriconstrictum* sp. nov., *Eurites bouhamedensis* sp. nov., *Ouaoufilalites ouaoufilalensis* gen. et sp. nov., *Helicocyclus fuscus* sp. nov., *Pericyclus mercatorius* sp. nov., *Orthocyclus*(?) sp., *Bouhamedites enigmaticus* gen. et sp. nov., *Winchelloceras antiatlanteum* sp. nov., and *Progoniatites maghribensis* gen. et sp. nov. Palaeogeographic analysis of Late Tournaisian ammonoid assemblages shows strong endemism at the species-level, but genera and families had a nearly global distribution in the equatorial seas. The new fauna contains the stratigraphically oldest known representatives of the important Carboniferous goniatite families Girtyoceratidae and Goniatitidae.

Key words: Ammonoide, palaeobiogeographya, Carboniferous, Tournaisian, Morocco.

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Introduction

Early Carboniferous ammonoids display an interesting pattern in their palaeogeographic distribution. Before the Variscan (Hercynian) Orogeny, the genera and evolutionary lineages were largely cosmopolitan, but during the orogenic phase, significant provincialism emerged (Korn 1997; Korn et al. 1999). Little is known, however, about the driving force and the timing of the process. Such is the case with Tournaisian ammonoid faunas, which are less well known than those from the younger Late Viséan and Serpukhovian. For biogeographical analyses, the investigation of diverse faunas is essential, and herein, the richest known early Late Tournaisian (i.e., *Pericyclus–Progoniatites* genus zone) ammonoid fauna so far is described from localities in the eastern Anti-Atlas of Morocco.

Monographic descriptions of the classical Late Tournaisian ammonoid faunas date back to the 19th century or the first half of the 20th century. The rich assemblages from southern Ireland were described by Crick (1899) and Foord (1901, 1903), those from Belgium by de Koninck (1844, 1880) and Delépine (1940), from the Rhenish Massif, Thuringia and the Harz Mountains of Germany by Holzapfel (1889) and Schindewolf (1926, 1939, 1951), from the Montagne Noire of southern France by Böhm (1935), and those from the Tafilalt of Morocco by Delépine (1941). More recently investigated were North American occurrences from Arkansas, Missouri, Indiana, and Michigan (e.g., Miller and Collinson 1951; Miller and Garner 1955; Gordon 1965), faunas from the Holy Cross Mountains of Poland (Czarniecki 1973; Dzik 1997), from the Tian Shan of Kirgizstan (Librovitch 1927, 1940; Popov 1968), and from the South Urals, North Urals, and Pay Khoy of Russia (Kusina 1980, 2000; Popov and Kusina 1997).

Most of these occurrences are latest Tournaisian in age (i.e., *Ammonellipsites–Fascipericyclus* genus zone). Early Late Tournaisian (*Pericyclus–Progoniatites* genus zone) assemblages are rare, and only the Rußschiefer of Thuringia, the Rockford Limestone of Indiana, as well as the Calcaire de Vaulx and Calcaire de Calonne of Belgium represent this timespan with rather diverse faunas. The fauna here described from Ksar Bouhamed in the Tafilalt is the richest of all and hence of special importance in the context of the Early Carboniferous ammonoids. With the description of this early Late Tournaisian assemblage, eleven new species are added to the approximately twenty species already known from this interval.

Late Tournaisian ammonoid occurrences in Africa

Ammonoid faunas of Tournaisian age are known from several places in North Africa (Delépine 1941; Termier and Termier 1950; Pareyn 1961), but the original descriptions were never updated. The only recent investigation of Tournaisian ammonoids in the region is the work by Conrad (1984), who figured specimens from southern Algeria.

The fossil lists from two horizons at the locality Bordj d'Erfoud, provided by Delépine (1941), consist of sixteen species, including one prolecanitid, three pericyclids, as well as species belonging to *Muensteroceras* and *Eurites.* A Late Tournaisian age is thus probable (Fig. 1). However the horizons apparently were never collected again, although the locality is less than one kilometre from the town of Erfoud, one of the centres of Moroccan fossil merchandising. Attempts to study the outcrop in recent years were not successful.

EARLY CARBONIFEROUS	Serp.	*Eumorphoceras – Cravenoceratoides*
		Tumulites – Cravenoceras
	Visean	*Lusitanoceras – Lyrogoniatites*
		Arnsbergites – Neoglyphioceras
		Goniatites – Maxigoniatites
		Beyrichoceras – Entogonites
		Bollandoceras – Bollandites
	Tournaisian	*Ammonellipsites – Fascipericyclus*
		Pericyclus – Progoniatites
		Goniocyclus – Protocanites
		Gattendorfia – Eocanites

Fig. 1. Ammonoid genus zones (right column) of the Early Carboniferous (Mississippian) with indication (bold characters) of the fauna described in this publication. Serp., Serpukhovian.

Pareyn (1961) provided a list of 25 species from the "Série d'Hassi Sguilma", mostly from the locality of Hassi Sguilma in the Saoura Valley of western Algeria. The fauna is composed of species of *Merocanites*, *Imitoceras*, *Irinoceras*, *Muensteroceras*, *Eurites*, *Dzhaprakoceras*, *Ammonellipsites*, *Fascipericyclus*, *Neopericyclus*, and probably *Winchelloceras*. The fossils are not particularly well preserved, but the assemblage may be coeval to the Erdbach Limestone of the Rhenish Massif, which is also latest Tournaisian (*Ammonellipsites–Fascipericyclus* genus zone) in age.

Termier and Termier (1950) contributed the first records of Early Carboniferous ammonoids from southern Algeria. From Hassi Habadra in the Mouydir, northern central Sahara, they mentioned *Pericyclus* and *Rotopericyclus*. Most probably, this is also a Late Tournaisian occurrence. Tournaisian ammonoids from various Central Saharan localities were figured by Conrad (1984). Among them were early Late Tournaisian assemblages with *Becanites*, *Acrocanites*, *Imitoceras*, *Muensteroceras*, *Pericyclus*, and *Winchelloceras* from Timimoun (south-western Algeria) and from Oued Temertasset (Mouydir, southern Algeria). The latter is the fauna mentioned by Follot (1953) without description and illustration. Conrad and Pareyn (1968) figured "*Goniatites* cf. *crenistria*" from Oued Temertasset. Of all the known Tournaisian ammonoid assemblages, these Central Saharan occurrences are the most similar to the assemblage from Ksar Bouhamed.

Material

The ammonoid material described here consists of more than 1250 specimens, all collected from the surface at two localities near Taouz in the vicinity of Jebel Ouaoufilal, east of Ksar Bouhamed (Tafilalt, Morocco) (Fig. 2). All are from the Oued Znaïgui Formation (Middle to Late Tournaisian), This

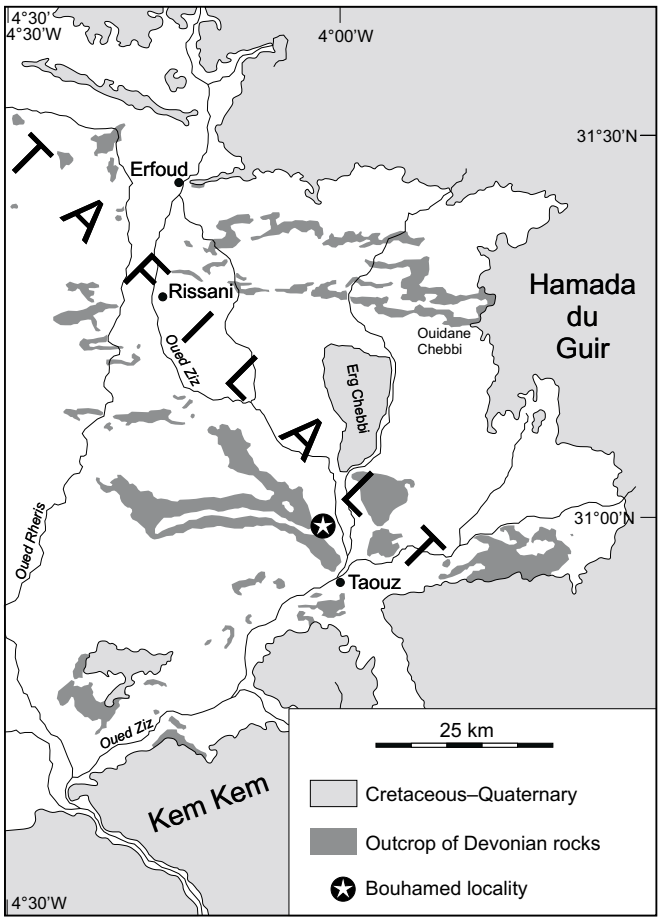

Fig. 2. Map of the Tafilalt (Eastern Anti-Atlas, Morocco) with the Ksar Bouhamed locality (indicated by an asterisk) in the Tafilalt (Eastern Anti-Atlas, Morocco).

formation was first described by Hollard (1958) as "Courte sequence plus argileuse, formée de schistes à nodules alternant avec des bancs gréseux" and later, in the local geological map, named Formation Oued Znaïgui (Fetah et al. 1986). The 500 metres thick unit is composed mostly of pelites. The horizon with the ammonoids is apparently limited to a few metres thickness. Only few other fossils such as gastropods and rugose corals occur.

The ammonoid fauna is remarkable for the small size of the specimens, none exceeding a phragmocone diameter of 27 millimetres. All specimens are preserved as limonitic steinkerns; body chambers and shell remains are only rarely preserved.

Twelve monospecific genera are represented. The number of specimens is as follows:

Locality A (N 30º58.164' W 04º01.378'):

Becanites africanus sp. nov.	39 specimens (13.5%)
Triimitoceras epiwocklumeriforme gen. et sp. nov.	16 specimens (5.6%)
Irinoceras minutum sp. nov.	5 specimens (1.7%)
Muensteroceras quadriconstrictum sp. nov.	185 specimens (64.2%)
Eurites bouhamedensis sp. nov.	3 specimens (1.0%)
Ouaoufilalites ouaoufilalensis gen. et sp. nov.	25 specimens (8.7%)
Winchelloceras antiatlanteum sp. nov.	4 specimens (1.4%)
Progoniatites maghribensis gen. et sp. nov.	11 specimens (3.8%)
total	288 specimens

Locality B (500 metres west of locality A):

Becanites africanus sp. nov.	143 specimens (14.7%)
Triimitoceras epiwocklumeriforme gen. et sp. nov.	43 specimens (4.4%)
Irinoceras minutum sp. nov.	12 specimens (1.2%)
Muensteroceras quadriconstrictum sp. nov.	602 specimens (61.8%)
Eurites bouhamedensis sp. nov.	9 specimens (0.9%)
Ouaoufilalites ouaoufilalensis gen. et sp. nov.	84 specimens (8.6%)
Helicocyclus fuscus sp. nov.	4 specimens (0.4%)
Pericyclus mercatorius sp. nov.	6 specimens (0.6%)
Bouhamedites enigmaticus gen. et sp. nov.	1 specimen (0.1%)
Orthocyclus (?) sp.	1 specimen (0.1%)
Winchelloceras antiatlanteum sp. nov.	48 specimens (4.9%)
Progoniatites maghribensis gen. et sp. nov.	21 specimens (2.2%)
total	974 specimens

Both assemblages are very similar in composition and preservation, and hence it is proposed that they represent the same fossil horizon. It is unclear whether they come from a single fossiliferous bed or rather from a lithological unit of some extent. Time averaging of the fauna may thus be involved. The described and illustrated specimens are housed in the collection of the Museum für Naturkunde der Humboldt-Universität zu Berlin, abbreviated with the catalogue numbers MB.C. 3901 to 3988.

Geological age of the fauna

According to current knowledge, two successive complexes of late Tournaisian ammonoids can be distinguished; the *Pericyclus–Progoniatites* and the *Ammonellipsites–Fascipericyclus* genus zone (Fig. 1). The older is known from the Calcaire de Vaulx and Calcaire de Calonne of Belgium (de Koninck 1844, 1880; Delépine 1940), and is characterised by the genera *Protocanites*, *Imitoceras*, *Muensteroceras*, and *Pericyclus*. A fauna of the same age, but without *Pericyclus*, comes from the Rockford Limestone of Indiana (Hall 1860; Miller and Collinson 1951). The younger complex is known from numerous localities, including the Erdbach limestone of Germany (Rhenish Massif and Harz; Holzapfel 1889; Schindewolf 1951) and time equivalents from Ireland, France, Poland, North Russia, and Central Asia.

Unfortunately, the newly described fauna cannot be precisely dated by other fossils of stratigraphic value; conodonts, for instance, have not been found. The ammonoid assemblage includes elements of Middle Tournaisian (e.g., *Becanites*, *Triimitoceras*) and Late Tournaisian (e.g., *Irinoceras*, *Pericyclus*) aspect.

The genus *Becanites* is the only representative of the prolecanitids, and so far is known mainly from Middle Tournaisian rocks. Advanced Late Tournaisian prolecanitids such as *Michiganites* and *Merocanites* are absent. Prionoceratids are represented by the simple-lobed *Triimitoceras*, which has affinities to Late Devonian and Early Tournaisian forms such as *Mimimitoceras*. As suggested by its suture line, nearest relative of *Triimitoceras* is *Imitoceras*. Another prionoceratid in the fauna is *Irinoceras*, which is known from the latest Tournaisian Erdbach Limestone and its time equivalents as well as younger strata, ranging up into the Serpukhovian (Kullmann 1962; Ruzhencev and Bogoslovskaya 1971). The muensteroceratids of the fauna, *Muensteroceras* and *Eurites*, show suture lines with very low median saddles (less than 20% of the external lobe depth), a characteristic feature of the stratigraphically older species of these genera.

Pericyclids are a minor component of the fauna, and the new species *Pericyclus mercatorius* also possesses a very low median saddle. It shows close similarities to *Pericyclus princeps*, described from the early Late Tournaisian Calcaire de Calonne of Belgium (de Koninck 1880; Delépine 1940).

It can thus be concluded that the Ksar Bouhamed fauna is early Late Tournaisian in age (Fig. 1). This assignment is supported by the absence of advanced pericyclids such as *Ammonellipsites* and *Fascipericyclus*, which are typical for the latest Tournaisian. Supplementary confirmation comes from the stratigraphical position of the similar fauna from Oued Temertasset (Mouydir, Central Sahara; Conrad 1984), which occurs there well below the limestone band with *Merocanites* and *Ammonellipsites*.

Palaeobiogeography of Late Tournaisian ammonoids

All the rich Late Tournaisian ammonoid assemblages come from the tropical and subtropical seas, according to the palaeogeographic maps of Scotese (1997). The localities were distributed between 35º latitude N and S. The North

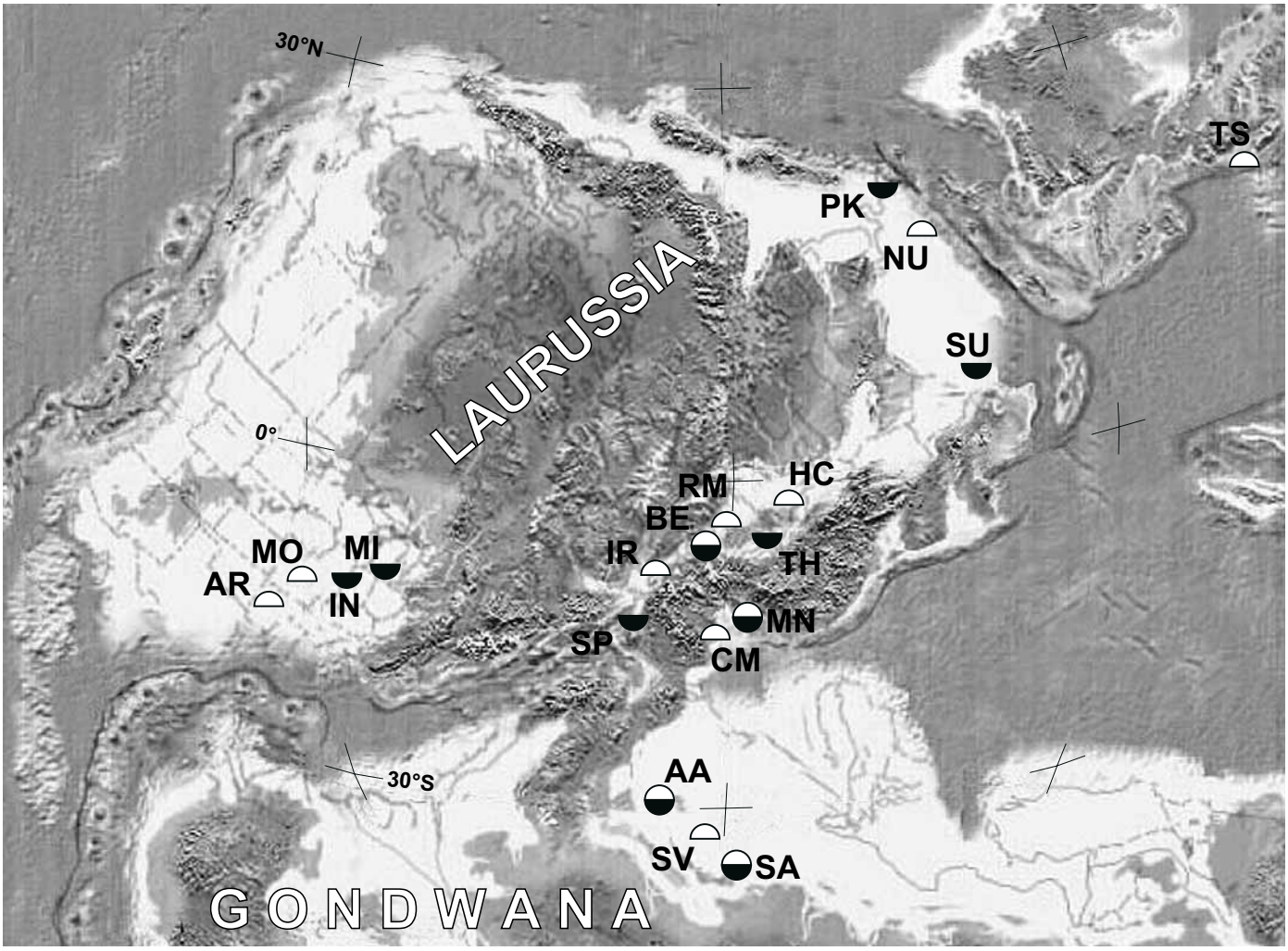

Fig. 3. Palaeogeographical map for the North Atlantic region of the Tournaisian age (after Scotese 1997; image by Ron Blakey, Flagstaff, Arizona), showing ammonoid occurrences of late Tournaisian age. AR, Arkansas; MO, Missouri; IN, Indiana; MI, Michigan; SP, South Portugal; IR, Ireland; BE, Belgium; RM, Rhenish Massif and Harz Mountains; TH, Thuringia; HC, Holy Cross Mountains; SU, South Urals; NU, North Urals; PK, Pay Khoy; TS, Tian Shan; CM, Cantabrian Mountains; MN, Montagne Noire; AA, Anti-Atlas; SV, Saoura Valley; SA, South Algeria.

American faunas were separated from the others by land (the connection between Laurussia and Gondwana) to the east and ocean to the West. The European, North African, and Asian occurrences were located in shelf areas which were probably connected by shallow water seas (Fig. 3).

The early Late Tournaisian ammonoid genera and species are distributed as follows:

- Rußschiefer of Thuringia (Schindewolf 1926, 1939) – six species,
- Rockford Limestone of Indiana (Hall 1860; Miller and Collinson 1951) – five species,
- Silovskaya Svita of the Pay Khoy in North Russia (Kusina 2000) – four species,
- Calcaire de Vaulx and Calcaire de Calonne of Belgium (de Koninck 1844, 1880; Delépine 1940) – eight and nine species respectively,
- Argiles de Teguentour of southern Algeria (Conrad 1984) – seven species.
- Oued Znaïgui Formation of Ksar Bouhamed (described herein) – twelve species.

All the other known occurrences contain four or fewer species (Fig. 4). A quantitative analysis based on such a small data base is not possible. The palaeogeographical distribution of the main evolutionary lineages, represented in the Ksar Bouhamed fauna, is as follows:

Prolecanitids are distributed almost globally. Species of *Becanites* occur in south-western Portugal (Pruvost 1914), the Black Forest (Spiegelhalter 1910) and Upper Franconia (Schindewolf 1926) of Germany, the South Urals of Russia (Librovitch 1940), Chile (House 1996), as well as Missouri and Kentucky (Smith 1903). Prionoceratids are also widely distributed and are represented by *Irinoceras* in the Late

	Germany Rußschiefer	Belgium Calcaire de Vaulx	Belgium Calcaire de Calonne	Morocco Oued Znaïgui Fm.	Algeria Teguentour Fm.	North Urals Silovskaya Svita	Xingjiang Dongguloabatisao Fm.	USA Marshall Sandstone	USA Rockford Lst.	New South Wales Namoi, Luton Fm.
Protocanites	1	2					1	1	1	2
Becanites				1	1					
Acrocanites	1	1			1					
Imitoceras		1	1		1			1	1	
Triimitoceras				1						
Irinoceras				1						?
Zadelsdorfia								?		
Kazakhstania							1	?		
Paraquiannanites						1				
Prodromites									1	
Muensteroceras	1	3	3	1	1			1	2	2
Eurites				1						
Orthocyclus				1		1				
Pericyclus	1	1	3	1	1	1	1			
Rotopericyclus			1							
Stenocyclus	1		1							
Bouhamedites				1						
Ouaoufilalites				1						
Helicocylus				1						
Winchelloceras				1	1					
Progoniatites	1			1	1	1				
Zhifangoceras							1			

Fig. 4. Distribution of early Late Tournaisian ammonoid genera with the numbers of species per genus in various regions.

	Germany Erdbach Limestone	Belgium Calcaire Waulsortien	Poland Radlin Beds	Ireland "Lower Limestone"	Spain Alba Formation	Morocco Niveau d'Erfoud	Algeria Hassi Sguilma Series	USA St. Joe; Marshall Fm.	Kyrgistan Dzhapryk Formation	North Urals Kosvinsky Horizon
Merocanites	1		1	1	1	1	1	1	1	
Imitoceras							1			
Irinoceras	1		1	1			1	1		
Cunitoceras	1									
Muensteroceras	3	2	1	3	2	2	4	2	1	4
Eurites	1	1		4	3	1	1			1
Helicocyclus	1						1		1	1
Hammatocyclus	1	1								1
Ammonellipsites	3	1	1	3	1	1	2		6	1
Neopericyclus	1		1	2	1	1	1		3	
Fascipericyclus	1	1		2		1			2	
Rotopericyclus				2		1	1		1	
Asiacyclus				2						
Riphaeocyclus										1
Dzhaprakoceras	2	2		3	2	3	1	1	7	7
Alekasheceras										1
Bollandoceras									2	1
Bollandites										1
Michiganites				1	1			1	1	1
Intoceras										2
Ouasintoceras										1
Kozhimites										1
Aquilonites										2
Winchelloceras					1	1	1	1	2	1
Eonomismoceras										1
Pseudonomismoceras	1									
Dimorphoceras	1									

Fig. 5. Distribution of latest Tournaisian ammonoid genera with the numbers of species per genus in various regions.

Tournaisian rocks of Belgium (de Koninck 1880; Delépine 1940), Germany (Rhenish Massif, Harz Mountains; Holzapfel 1889, Schindewolf 1951), the Holy Cross Mountains of Poland (Dzik 1997), Ireland (Foord 1901), southern France (Böhm 1935), Algeria (Pareyn 1961), Arkansas, British Columbia (Work, Nassichuk and Richards 2000), and New South Wales in Australia (Campbell, Brown, and Coleman 1983). Most of these faunas with *Irinoceras* are dominated by muensteroceratids, which in the Ksar Bouhamed assemblage comprise more than 60% of the specimens. Such a high value is known from typical occurrences of ammonoid faunas of early Late Tournaisian age. Also distinctive is *Pericyclus* and other pericyclids in the North African, Central European, and North Russian (Kusina 2000) assemblages.

Winchelloceras is a rare genus known from Michigan (Miller and Garner 1955), the North Urals (Kusina 1980), the Tian Shan (Popov 1968), the Cantabrian Mountains (Higgins and Wagner-Gentis 1982), Algeria (Conrad 1984), and Morocco. *Progoniatites* is known from Morocco, Algeria (Follot 1953; Conrad and Pareyn 1968; Conrad 1984), Thuringia (Schindewolf 1926, 1939), and the Pay Khoy (Kusina 2000). This list demonstrates that almost all of the ammonoid groups are distributed worldwide.

Ammonoids from the latest Tournaisian are better known than those from the early Late Tournaisian (Fig. 5). Ten assemblages are included in a cluster analysis with the program STATISTICA. This analysis is based on the distribution of genera. An analysis on the species level was not achieved because of the following reasons: (1) Many of the occurrences have endemic species which are not informative to discover relationships between the regions, and (2) the current knowledge of some of the assemblages is too poor to allow exact considerations about the species composition. Therefore, the distribution of species is only used as a supplementary feature.

The 1-Pearson-r algorithm was used to calculate a distance matrix for the analysed assemblages (Fig. 6A), and the cluster diagram (Fig. 6B) was done in the single linkage mode. As can be seen from both figures, four palaeobiogeographical units can be separated, three of them consisting only of one region.

The western Palaeotethyan unit embraces the Central and Western European as well as the North African occurrences. Distance values within these are moderately high, approximately 0.70 on average, and all are assembled in one cluster. The occurrences of the American Midcontinent (Arkansas, Missouri) are regarded as one assemblage (USA); this is separated from the European/African samples by higher distance values of 0.85 on average. Even more distant from the west-

A

	Germany	Belgium	Poland	Ireland	Spain	Morocco	Algeria	USA	Kirgizstan	Russia
Germany		0.45	0.53	0.70	0.91	0.81	0.70	1.09	1.33	1.14
Belgium	0.45		1.04	0.77	0.83	0.66	1.09	1.17	1.25	0.66
Poland	0.53	1.04		0.53	0.66	0.76	0.53	0.74	0.97	1.38
Ireland	0.70	0.77	0.53		0.59	0.48	0.70	0.77	0.94	1.47
Spain	0.91	0.83	0.66	0.59		0.44	0.59	0.54	0.75	0.74
Morocco	0.81	0.66	0.76	0.48	0.44		0.48	0.96	0.66	1.24
Algeria	0.70	1.09	0.53	0.70	0.59	0.48		0.77	0.94	1.14
USA	1.09	1.17	0.74	0.77	0.54	0.96	0.77		0.90	0.96
Kirgizstan	1.33	1.25	0.97	0.94	0.75	0.66	0.94	0.90		1.03
Russia	1.14	0.66	1.38	1.47	0.74	1.24	1.14	0.96	1.03	

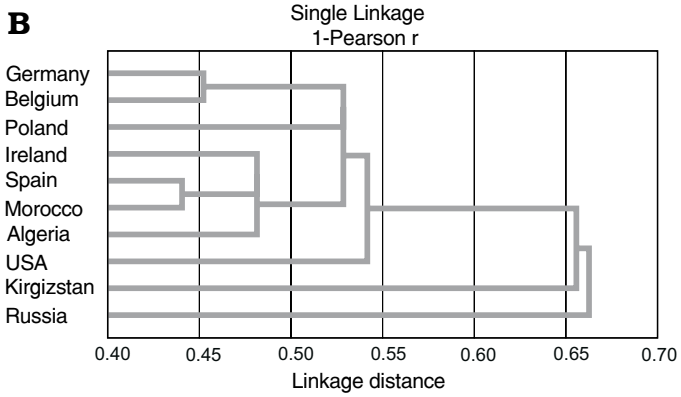

Fig. 6. Distance matrix and cluster diagram for the latest Tournaisian ammonoid-bearing regions.

ern Palaeotethyan are the Tian Shan (Central Asia) and the North Urals.

The geographic distribution of the main evolutionary ammonoid lineages confirms this pattern. Two of them (prolecanitids, muensteroceratids) are present in all the four biogeographical units. The prionoceratids were recorded in North America and Europe/Africa, and the pericyclids are diverse in North Africa, Europe, and Central Asia. Pericyclids are only minor components of the North American and North Russian assemblages.

Evolution of the family Goniatitidae

The presence of *Progoniatites* and *Winchelloceras* means that the Ksar Bouhamed assemblage contains the stratigraphically oldest representatives of the families Goniatitidae and Girtyoceratidae. This is a remarkable fact since the Goniatitidae were thought to appear only in the Late Viséan, with little being known about their ancestry. The morphologically very similar *Progoniatites* and *Goniatites* are separated by a rather large timespan (latest Tournaisian to middle Viséan), from which no representatives of the family are known.

This means that the Goniatitidae, one of the most common and geographically widespread families of the Late Viséan (Korn 1988, 1997), is a Lazarus taxon that suddenly reappeared after a long period of time and then became very diverse (Fig. 7). The cause of the gap in the record may be explained by the relatively poor state of knowledge of the Early and Middle Viséan ammonoids, but also facies differences may play an important role. Late Tournaisian faunas are almost exclusively known from well-oxygenated limestone formations. However, too little is known about the ecology of Carboniferous ammonoids to explain the pattern of distribution within different facies belts. It is interesting that *Progoniatites* is not an endemic genus, known from North Africa, Central Europe, and the North Urals, and that *Goniatites* is also distributed almost globally.

The presence of *Progoniatites* in early Late Tournaisian ammonoid communities does not solve the riddle of the origin of the family Goniatitidae, as the ancestry of *Goniatites* now shifts to *Progoniatites*, of which no morphologically similar form is known from time-equivalents or stratigraphically older sedimentary rocks.

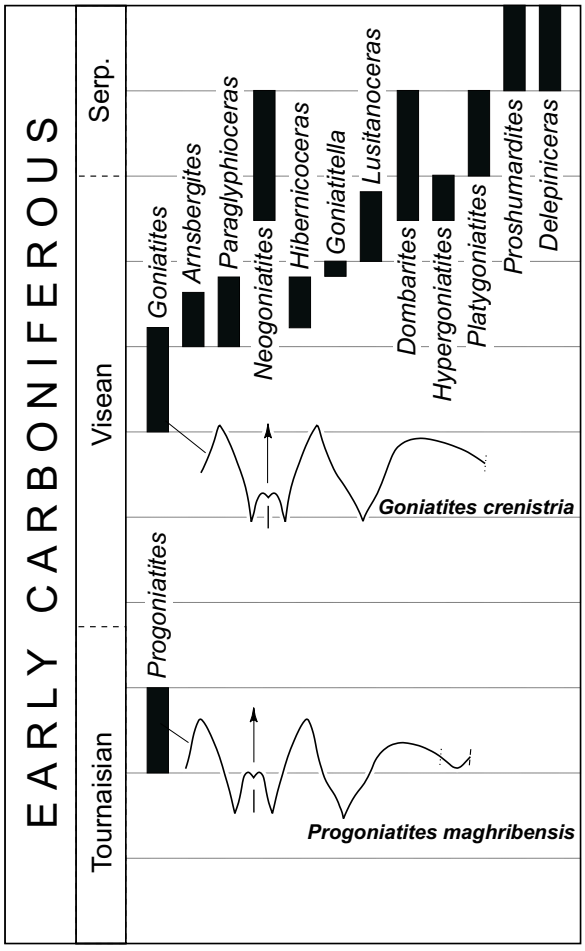

Fig. 7. Stratigraphical distribution of the Early Carboniferous genera of the Goniatitidae, displaying the gap in the record that spans from the latest Tournaisian to the Middle Viséan.

Systematic palaeontology

Abbreviations used in the text are: ah, apertural height; dm, conch diameter; IZR, imprint zone width, calculated (wh-ah)/wh; uw, umbilical width; WER, whorl expansion rate, calculated $[dm/(dm-ah)]^2$; ww, whorl width; wh, whorl height (Fig. 8).

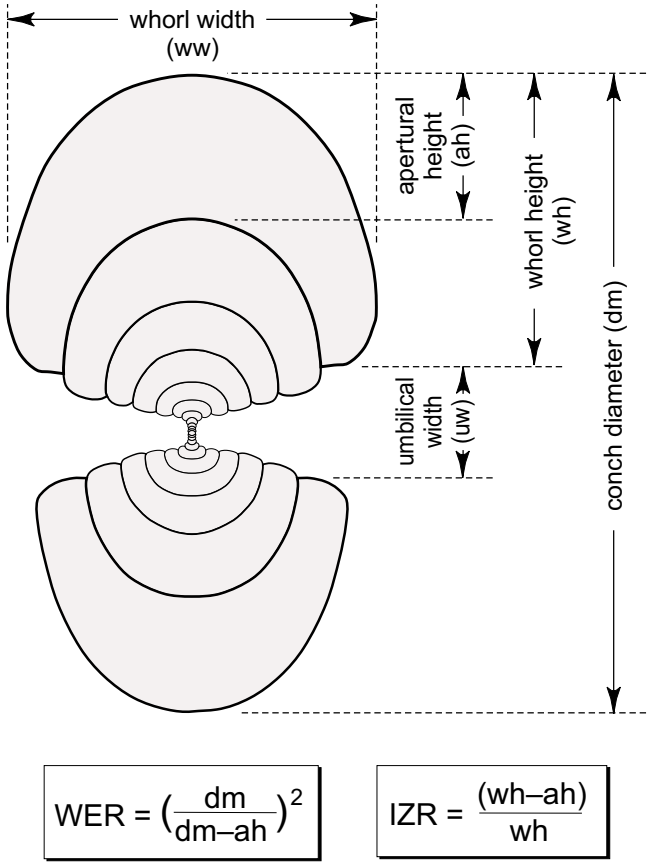

Fig. 8. The conch parameters and ratios as used in the descriptions.

Family Prolecanitidae Hyatt, 1884

Becanites Korn, 1997

Type species: *Protocanites algarbiensis* Pruvost, 1914.

Becanites africanus sp. nov.

Figs. 9, 10, 11A–C.

Derivation of name: After the continent from where the specimens were collected.

Holotype: Specimen MB.C.3901 (coll. Bockwinkel), Fig. 11A.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality A east of Ksar Bouhamed (Tafilalt, Morocco); early Late Tournaisian.

Material.—182 mostly fragmentary specimens, 5 to 20 mm in diameter.

Diagnosis.—*Becanites* with discoidal conch (ww/dm 0.35). Umbilicus wide at 8 mm diameter (uw/dm 0.45 to 0,50) and moderately wide at 15 mm diameter (uw/dm 0.40). Flanks and venter broadly rounded. Suture line with large and deep, pouched external lobe, lanceolate and pouched adventive and lateral lobe on the flank.

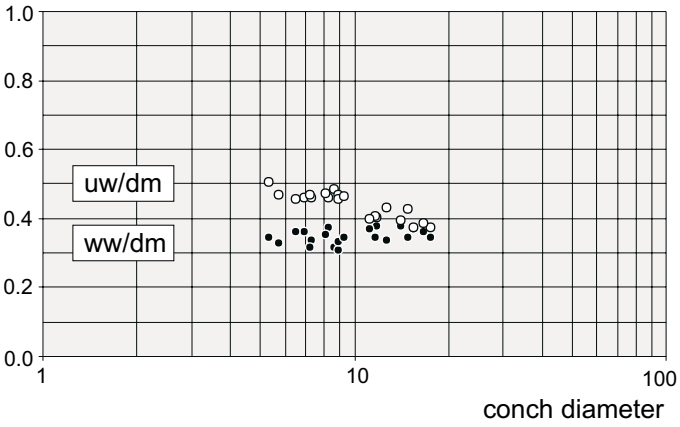

Fig. 9. Whorl width/ conch diameter and umbilical width/ conch diameter ratios of *Becanites africanus* sp. nov.

Description.—All the specimens are similar in their conch geometry and ratios, but juveniles are more evolute than larger specimens (Fig. 9). Juveniles have a circular whorl cross section, and adults display an oval, slightly compressed shape. The relative apertural height increases during ontogeny, resulting in an acceleration of the whorl expansion rate from 1.90 at 5 mm to 2.50 at 18 mm conch diameter. In this respect, *B. africanus* has an ontogeny that is typical for the prolecanitids.

The surface of the steinkern is smooth without any indication of ornament. It can therefore be assumed that the shell is very weakly ornamented.

The suture line is characteristic for *Becanites* (Fig. 10), but the external lobe, as seen in paratype MB.C.3909, is extremely large and bulb-shaped, as known only from stratigraphically younger and more derived genera such as *Michiganites* Ruzhencev, 1962 and *Prolecanites* Mojsisovics, 1882. The adventive lobe and the lateral lobe, which are both located on the flank, are also pouched and pointed at the bottom.

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/dm	ww/wh	uw/dm	IZR
holotype MB.C.3901	17.49	6.14	7.05	6.65	6.39	2.48	0.35	0.87	0.38	0.09
MB.C.3902	16.60	6.05	6.40	6.50	5.70	2.32	0.36	0.95	0.39	0.11
MB.C.3903	14.10	5.40	4.90	5.60	4.60	2.20	0.38	1.10	0.40	0.06
MB.C.3904	11.80	4.50	4.30	4.80	3.80	2.18	0.38	1.05	0.41	0.12
MB.C.3906	8.59	2.77	2.85	4.19	2.28	2.04	0.32	0.97	0.49	0.09
MB.C.3907	6.88	2.53	2.26	3.20	2.05	2.03	0.37	1.12	0.47	0.09
MB.C.3908	6.48	2.38	1.94	3.00	1.87	1.98	0.37	1.23	0.46	0.04
MB.C.3905	5.30	1.85	1.55	2.70	1.45	1.90	0.35	1.19	0.51	0.06

Comparisons.—*B. africanus* sp. nov. is, by its large and strongly pouched external lobe, different from the other species of the genus: *B. algarbiensis* (Pruvost, 1914), *B. abnobensis* (Vöhringer, 1960), *B. geigenensis* (Schmidt,

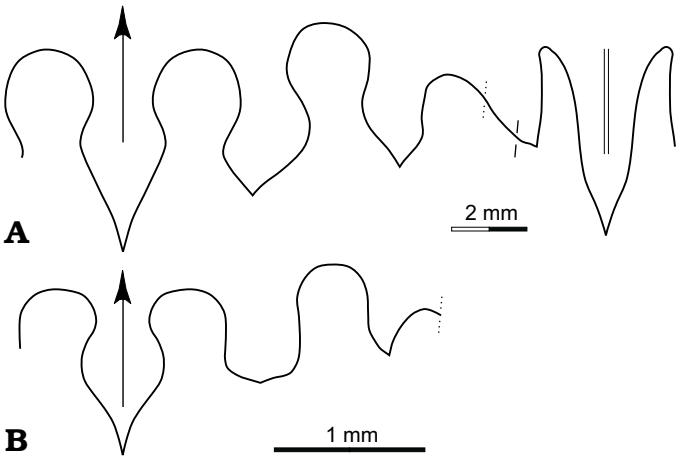

Fig. 10. Suture lines of *Becanites africanus* sp. nov. **A**. MB.C.3909 at ww 6.9 mm, wh 7.9 mm; × 5. **B**. MB.C.3905 at dm 4.8 mm, ww 1.8 mm, wh 1.55 mm; × 20.

1925), *B. gurleyi* (Smith, 1903), *B. sernageominus* (House, 1996), and *B. nuraensis* (Librovitch, 1940). Furthermore, *B. algarbiensis*, *B. sernageominus* and *B. geigenensis* are more widely umbilicate (uw/dm 0.50) than *B. africanus* sp. nov.

Family Prionoceratidae Hyatt, 1884
Subfamily Imitoceratinae Ruzhencev, 1950
Triimitoceras gen. nov.

Derivation of name: After the triangularly coiled inner whorls, and the similarity with *Imitoceras*.

Type species: *Triimitoceras epiwocklumeriforme* sp. nov.

Diagnosis.—Imitoceratidae with discoidal conch that is triangularly coiled in juveniles. Aperture and whorl expansion rate low (WER 1.50 to 1.70). Suture line with slightly pouched external lobe and large, V-shaped adventive lobe.

Comparisons.—*Triimitoceras* has a suture line typical for the family Imitoceratinae. As in *Imitoceras* Schindewolf, 1923, the external lobe is slightly pouched, the ventrolateral saddle is strikingly asymmetrical, and the adventive lobe is much deeper than the external lobe. However, the conch of *Triimitoceras* is thinner with lower aperture, and the conspicuous steinkern constrictions of the type species (see below) are not known from *Imitoceras*. The cardinal difference, of course, is the triangular coiling of the inner whorls of *Triimitoceras*, not known from any other Carboniferous prionoceratid.

Occurrence.—Only known so far from the vicinity of Jebel Ouaoufilal; Oued Znaïgui Formation, early Late Tournaisian.

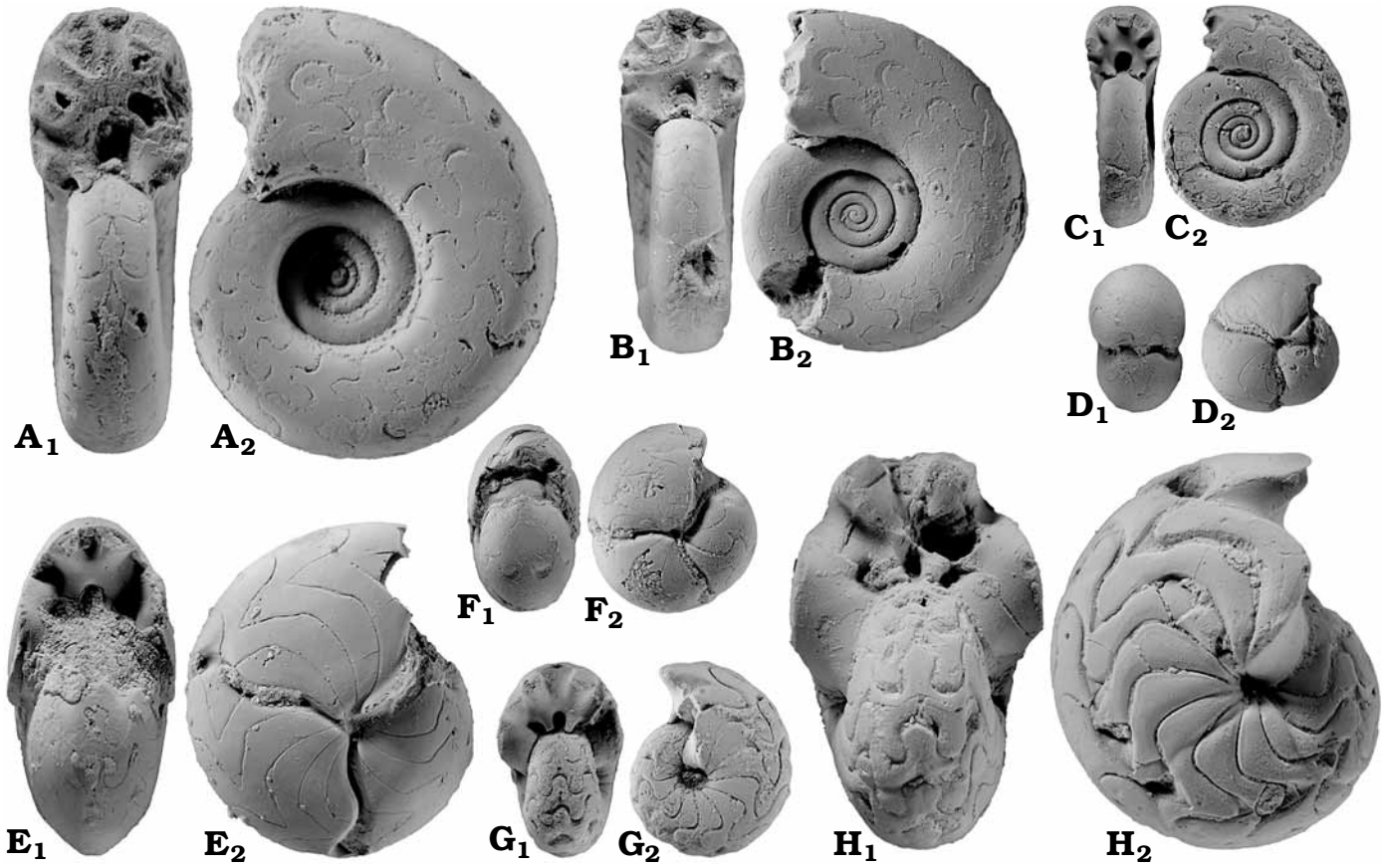

Fig. 11. **A**. *Becanites africanus* sp. nov., holotype MB.C.3901. **B**. *Becanites africanus* sp. nov., MB.C.3904. **C**. *Becanites africanus* sp. nov., MB.C.3906. **D**. *Triimitoceras epiwocklumeriforme* sp. nov., MB.C.3988. **E**. *Triimitoceras epiwocklumeriforme* sp. nov., holotype MB.C.3910. **F**. *Triimitoceras epiwocklumeriforme* sp. nov., MB.C.3914. **G**. *Irinoceras minutum* sp. nov. MB.C.3921. **H**. *Irinoceras minutum* sp. nov. holotype MB.C.3916. All × 3. All specimens figured in apertural (A_1, B_1, etc.; except for D_1 in ventral) and lateral (A_2, B_2, etc.) views.

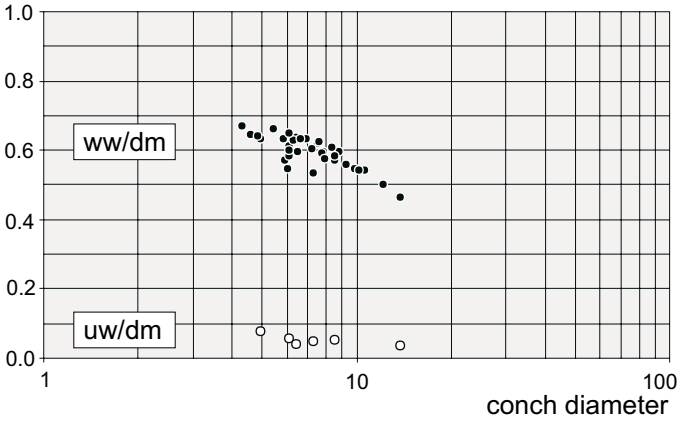

Fig. 12. Whorl width/conch diameter and umbilical width/conch diameter ratios of *Triimitoceras epiwocklumeriforme* sp. nov.

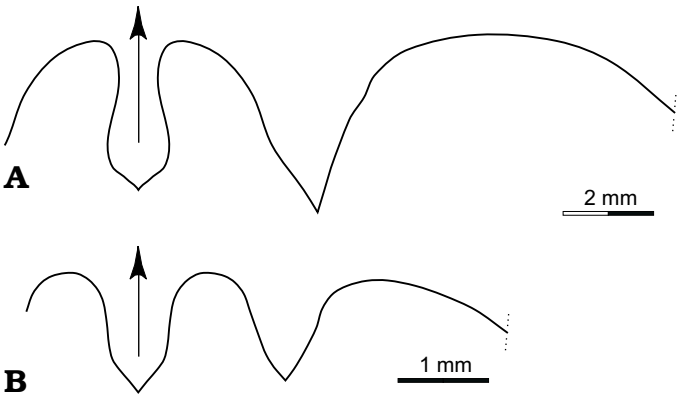

Fig. 13. Suture lines of *Triimitoceras epiwocklumeriforme* sp. nov. **A**. Holotype MB.C.3910 at dm 13.4 mm, ww 6.7 mm, wh 7.7 mm; × 6. **B**. Paratype MB.C.3914 at dm 7.0 mm, ww 4.2 mm; × 12.

Triimitoceras epiwocklumeriforme sp. nov.

Figs. 11D–F, 12, 13.

Derivation of name: After the similarity in the conch to the Devonian *Epiwocklumeria*.

Holotype: Specimen MB.C.3910 (coll. Bockwinkel), Fig. 11E.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality A east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

Material.—59 specimens between 3 and 14 mm in diameter. Most of them are smaller than 10 mm.

Diagnosis.—*Triimitoceras* with pachyconic conch at 6 mm diameter (ww/dm 0.60) and thickly discoidal at 12 mm diameter (ww/dm 0.50). Steinkern with three strongly sinuous constrictions per volution. Suture line with subparallel-sided, slightly pouched external lobe, narrow ventrolateral saddle, and large V-shaped adventive lobe.

Description.—Juveniles are relatively more globose than later stages (Fig. 12). Specimens up to 6 mm conch diameter are, with three prominent constrictions, triangularly coiled. In this respect, the conch resembles that of some Late Devonian wocklumeriid clymeniids.

Three strong constrictions per volution are visible in all specimens (steinkerns). In small individuals (dm 6 mm), such as the paratype MB.C.3915, they form a weak ventrolateral projection, but larger specimens (dm 13 mm), such as the holotype MB.C.3910 display a prominent tongue-shaped extension of the ventrolateral salient and a deep ventral sinus. The conch interior between the constrictions is smooth.

The suture of the holotype MB.C.3910 resembles, in the general outline, that of *Imitoceras*: the external lobe is slightly pouched, it is not as deep as the large adventive lobe, and the ventrolateral saddle is strongly asymmetric (Fig. 13). The lateral saddle is very wide and overspans almost two thirds of the flank.

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/dm	ww/wh	uw/dm	IZR
holotype MB.C.3910	13.80	6.49	7.88	0.58	3.35	1.74	0.47	0.82	0.04	0.57
MB.C.3912	8.50	4.90	4.40	0.50	1.80	1.61	0.58	1.11	0.06	0.59
MB.C.3914	7.25	3.91	3.64	0.38	1.35	1.51	0.54	1.07	0.05	0.63
MB.C.3911	6.40	4.10	3.50	0.30			0.64	1.17	0.05	
MB.C.3915	6.09	3.75	3.01	0.38	1.21	1.56	0.62	1.25	0.06	0.60
MB.C.3913	4.95	3.15	2.20	0.40	1.05	1.61	0.64	1.43	0.08	0.52

Comparisons.—There is no similar Tournaisian ammonoid known. Such combination of features is only known among the Late Devonian prionoceratids. A triangular juvenile conch occurs in some species of *Mimimitoceras* Korn, 1988, but these are always globose. The shape of the steinkern constrictions is similar to that in some species of the genus *Balvia* Lange, 1929, but these show sutures with rounded lobes.

Irinoceras Ruzhencev, 1947

Type species: *Irinoceras arcuatum* Ruzhencev, 1947.

Irinoceras minutum sp. nov.

Figs. 11G, H, 14, 15.

Derivation of name: After the small conch, unlike the type species.

Holotype: Specimen MB.C.3916 (coll. Ebbighausen), Fig. 11H.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality A east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

Material.—17 specimens, mostly fragmentarily preserved, 5 to 24 mm in diameter.

Diagnosis.—Small-sized *Irinoceras* with pachyconic conch between 8 mm and 15 mm diameter (ww/dm 0.60 to 0.65). Umbilicus at 8 mm diameter slightly opened (uw/dm 0.10) and almost closed at 16 mm diameter. Steinkern with weak constrictions but otherwise smooth. Suture line with V-shaped, almost symmetrical adventive lobe.

Description.—All growth stages are very similar (Fig. 14). Only the width of the umbilicus changes, juveniles show a narrow opening, but in adults the umbilicus is punctiform. The steinkern is smooth except for very weak constrictions

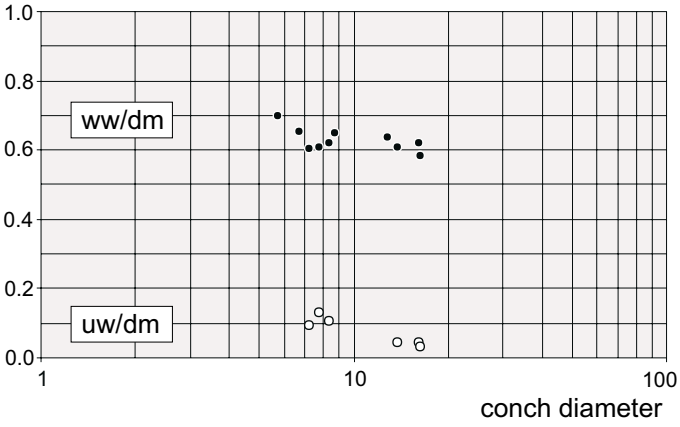

Fig. 14. Whorl width/ conch diameter and umbilical width/ conch diameter ratios of *Irinoceras minutum* sp. nov.

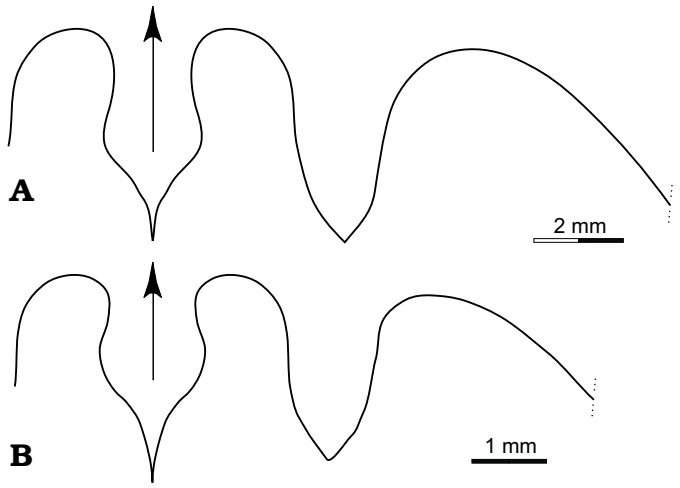

Fig. 15. Suture lines of *Irinoceras minutum* sp. nov. **A**. Holotype MB.C.3916 at dm 14.4 mm, ww 9.6 mm, wh 9.0 mm; × 6. **B**. MB.C.3921 at dm 7.5 mm, ww 4.4 mm, wh 3.7 mm; × 10.

which are irregularly arranged with a low projection over the flank and a rather deep ventral sinus.

As it is characteristic for *Irinoceras*, the external lobe is bulb-shaped with strongly sinuous flanks, followed by an asymmetrical, ventrally inclined ventrolateral saddle and by an almost symmetrical adventive lobe (Fig. 15). As the holotype MB.C.3916 shows, the V-shaped adventive lobe is almost symmetrical with a gently curved ventral flank (Fig. 15A).

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/ dm	ww/ wh	uw/ dm	IZR
MB.C.3918	16.30	9.60	9.40	0.60	5.50	2.28	0.59	1.02	0.04	0.41
holotype MB.C.3916	16.04	10.04	9.22	0.79	5.25	2.21	0.63	1.09	0.05	0.43
MB.C.3917	13.70	8.40	8.30	0.70	4.35	2.15	0.61	1.01	0.05	0.48
MB.C.3920	8.33	5.21	4.25	0.94	2.55	2.08	0.63	1.23	0.11	0.40
MB.C.3921	7.74	4.75	3.93	1.05	2.29	2.02	0.61	1.21	0.14	0.42
MB.C.3919	7.20	4.40	3.70	0.70	2.10	1.99	0.61	1.19	0.10	0.43

Comparisons.—Inadequate knowledge of some *Irinoceras* species makes comparison between the species difficult. The majority of species, such as *I. arcuatum* Ruzhencev, 1947, *I. ornatissimum* (de Koninck, 1881), *I. latecostatum* (Nicolaus, 1963), *I. schulzei* (Kullmann, 1963), and *I. stevanovici* (Kullmann, 1962) possess coarse growth lines or riblets. As far as the sutures are known from these species, the adventive lobe is asymmetrical, with a concave dorsal flank, and thus different from *I. minutum* sp. nov. *I. altayense* Wang, 1983, *I. romingeri* (Winchell, 1862), *I. tuba* Campbell et al., 1983, and *I. weyeri* Work and Nassichuk, 2000 do not have constrictions. *I. bamberi* Work and Nassichuk, 2000 has a similar suture line and also constrictions, but the whorl cross section is almost circular and widest in the midflank area, in contrast to *I. minutum* sp. nov. where the conch is thickest near the umbilicus.

Family Muensteroceratidae Librovitch, 1957

Muensteroceras Hyatt, 1884

Type species: *Goniatites oweni parallela* Hall, 1860.

Muensteroceras quadriconstrictum sp. nov.

Figs. 16, 17, 18A–G.

Derivation of name: After the four constrictions in the steinkerns of the adult stage.

Holotype: Specimen MB.C.3922 (coll. Ebbighausen), Fig. 18A.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality A east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

Material.—787 specimens between 3 and 26 mm conch diameter. Many are almost complete phragmocones. This is the most common species in the Ksar Bouhamed fauna.

Diagnosis.—*Muensteroceras* with pachyconic conch at 5 mm diameter (ww/dm 0.60 to 0.85), thickly discoidal to pachyconic conch at 10 mm diameter (ww/dm 0.50 to 0.75), and thickly discoidal at 20 mm diameter (ww/dm 0.45 to 0.60). Umbilicus in all stages narrow, ranging from 7 to 20 per cent of the conch diameter. Steinkern often with four constrictions, at 90º intervals. Suture line with deep, parallel-sided external lobe, low median saddle, and asymmetrical adventive lobe.

Description.—As can be seen in the list of dimensions and the ratio plot (Fig. 16), there is a wide population variability. The whorl width/ conch diameter ratio decreases during ontogeny; at 5 mm diameter it ranges from 0.62 to 0.84 (arithmetic mean 0.70; median value 0.71), at 10 mm diameter from 0.48 to 0.76 (mean 0.62; median 0.61), and at 20 mm diameter from 0.46 and 0.60 (mean 0.53; median 0.52). The variability in whorls width is greatest in juveniles. In contrast to the whorl section, the width of the umbilicus shows only minor changes throughout ontogeny, with larger specimens slightly more involute than juveniles. Within the sample, however the two morphologies are connected by a complete spectrum of intermediates, and separation is impossible (Fig. 16).

The whorl expansion rate is as variable as the whorl width. Again, a correlation with the whorl width is notable,

more pachyconic forms have a lower aperture (and thus WER of 1.90 to 2.00) than more discoidal specimens (WER 2.00 to 2.30). Also, the whorl overlap rate (imprint zone rate, IZR) is higher in the more globose forms.

The constrictions have a slight forward projection over the flanks and a shallow external sinus. They begin in a short distance from the umbilicus and are deepest on the venter. In specimens over 10 mm diameter, the constrictions are usually arranged 90º apart. These constrictions are already present at 5 mm conch diameter, but at this growth stage they are not as regularly distributed.

The suture line is typical for *Muensteroceras* (Fig. 17) with narrow external lobe and low median saddle (0.20 of external lobe depth). The ventrolateral saddle is asymmetrical and broadly rounded, the adventive lobe is also asymmetric with steep ventral flank and sinuous dorsal flank.

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/ dm	ww/ wh	uw/ dm	IZR
MB.C.3944	26.20	11.92	12.83	3.63	8.80	2.27	0.45	0.93	0.14	0.31
holotype MB.C.3922	18.92	9.23	10.23	1.39	6.46	2.31	0.49	0.90	0.07	0.37
MB.C.3941	18.42	8.78	9.73	1.65	5.90	2.16	0.48	0.90	0.09	0.39
MB.C.3925	15.99	9.50	8.21	1.76	4.64	1.98	0.59	1.16	0.11	0.43
MB.C.3923	15.84	8.64	8.05	1.93	5.00	2.14	0.55	1.07	0.12	0.38
MB.C.3926	13.54	7.65	6.46	1.91	4.05	2.04	0.56	1.18	0.14	0.37
MB.C.3924	13.18	7.88	6.47	1.78	3.87	2.00	0.60	1.22	0.14	0.40
MB.C.3930	11.97	6.69	6.13	1.38	3.70	2.09	0.56	1.09	0.12	0.40
MB.C.3927	11.72	7.79	5.39	2.13	3.19	1.89	0.66	1.45	0.18	0.41
MB.C.3943	11.56	6.61	5.96	1.21	3.68	2.15	0.57	1.11	0.10	0.38
MB.C.3931	9.61	5.95	4.77	1.25	2.74	1.96	0.62	1.25	0.13	0.43
MB.C.3932	9.08	5.53	4.61	1.05	2.60	1.96	0.61	1.20	0.12	0.44
MB.C.3936	9.00	5.85	4.38	1.32	2.57	1.96	0.65	1.34	0.15	0.41
MB.C.3928	8.79	6.10	3.91	1.60	2.44	1.92	0.69	1.56	0.18	0.38
MB.C.3934	8.66	5.21	4.37	1.01	2.60	2.04	0.60	1.19	0.12	0.41
MB.C.3938	8.62	5.24	4.49	1.02	2.47	1.96	0.61	1.17	0.12	0.45
MB.C.3942	8.51	5.12	3.97	1.28	2.42	1.95	0.60	1.29	0.15	0.39
MB.C.3937	8.29	4.75	4.02	1.13	2.48	2.04	0.57	1.18	0.14	0.38
MB.C.3933	8.03	4.64	4.12	1.06	2.48	2.09	0.58	1.13	0.13	0.40
MB.C.3940	7.88	5.35	3.81	1.25	2.38	2.05	0.68	1.40	0.16	0.38
MB.C.3929	5.89	4.16	2.86	0.82	1.69	1.97	0.71	1.45	0.14	0.41
MB.C.3939	5.43	3.42	2.45	1.04	1.49	1.90	0.63	1.40	0.19	0.39
MB.C.3935	5.20	3.37	2.61	0.79	1.57	2.05	0.65	1.29	0.15	0.40

Comparisons.—The new species differs in its conch proportions (whorl width/ conch diameter 0.50 to 0.70; uw/dm around 0.15) from most of the other species of the genus. More discoidal forms include *M. parallelum* (Hall, 1860) (ww/dm 0.35), *M. complanatum* (de Koninck, 1880) (ww/dm 0.35), *M. compressum* Librovitch, 1940 (ww/dm 0.32), *M. multiseptatum* Librovitch, 1940 (ww/dm 0.35), *M. perspectivum* (de Koninck, 1880) (ww/dm 0.35), *M. recticonstrictum* Kusina, 1973 (ww/dm 0.40), *M.*(?) *esbaughti* (Miller et al., 1949) (ww/dm 0.20), and *M.*(?) *pfefferae* (Miller and Werner, 1942) (ww/dm 0.30).

Wider umbilici characterise the species *M. barroisi* (Holzapfel, 1889) (uw/dm 0.20), *M. collinsoni* Gordon, 1965 (uw/dm 0.30), *M. cordatum* (Crick, 1899) (uw/dm 0.20), *M. delepinei* Campbell et al., 1983 (uw/dm 0.24), *M. frequens*

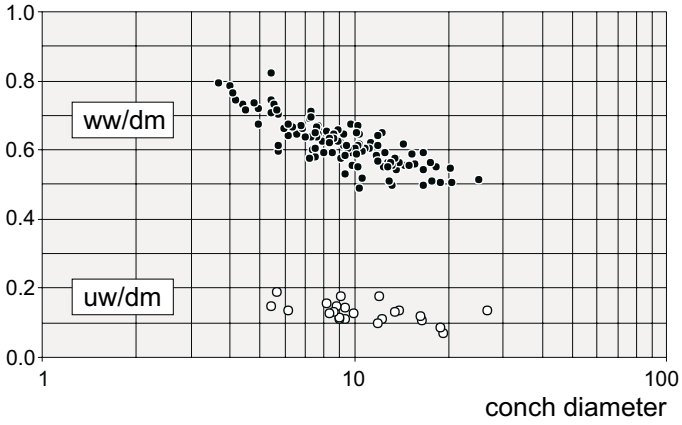

Fig. 16. Whorl width/ conch diameter and umbilical width/ conch diameter ratios of *Muensteroceras quadriconstrictum* sp. nov.

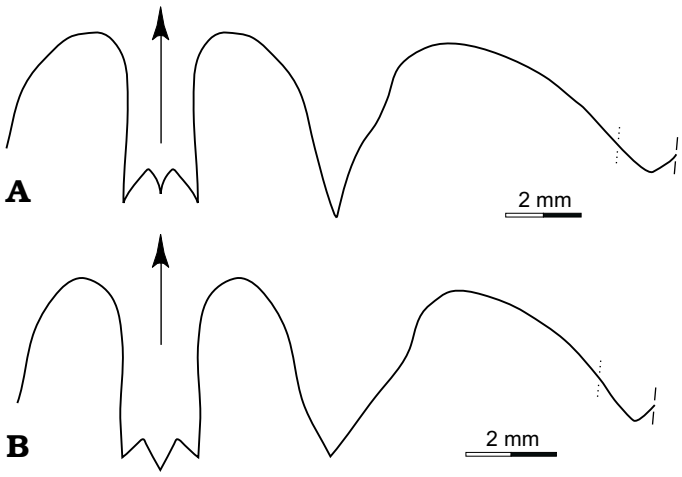

Fig. 17. Suture lines of *Muensteroceras quadriconstrictum* sp. nov. **A**. Holotype MB.C.3922 at dm 16.0 mm, ww 8.4 mm, wh 8.9 mm; × 5. **B**. MB.C.3923 at dm 12.6 mm, ww 7.1 mm, wh 6.7 mm; × 6.

Kusina, 1973 (uw/dm 0.20), *M. jenkinsi* Campbell et al., 1983 (uw/dm 0.35), *M. kazakhstanicum* Librovitch, 1940 (uw/dm 0.20), *M. kozhimense* Kusina, 1980 (uw/dm 0.25), *M. mitchelli* Miller, 1935 (uw/dm 0.24), *M. modestum* Popov and Kusina, 1997 (uw/dm 0.24), *M. oweni* (Hall, 1860) (uw/dm 0.28), *M. pachydiscus* Kusina, 1980 (uw/dm 0.34), *M. parvulum* Kusina, 1983 (uw/dm 0.40), *M. pergibbosum* Miller and Garner, 1955 (uw/dm 0.25), *M. perspectivum* (de Koninck, 1880) (uw/dm 0.25), *M. recticonstrictum* Kusina, 1973 (uw/dm 0.24), *M. rotella* (de Koninck, 1880) (uw/dm 0.20), and *M. rowleyi* Miller and Furnish, 1958 (uw/dm 0.20).

The remaining few species, which have similar conch ratios to *M. quadriconstrictum* sp. nov., differ in the following characters: *M. medium* Miller and Collinson, 1951 has an external lobe in which the flanks stand not as parallel as in *M. quadriconstrictum* sp. nov., and possesses an almost symmetrical ventrolateral saddle.

M. crassum (Foord, 1903) and *M. occidentale* (Foord, 1903) have similar suture lines, but do not possess steinkern

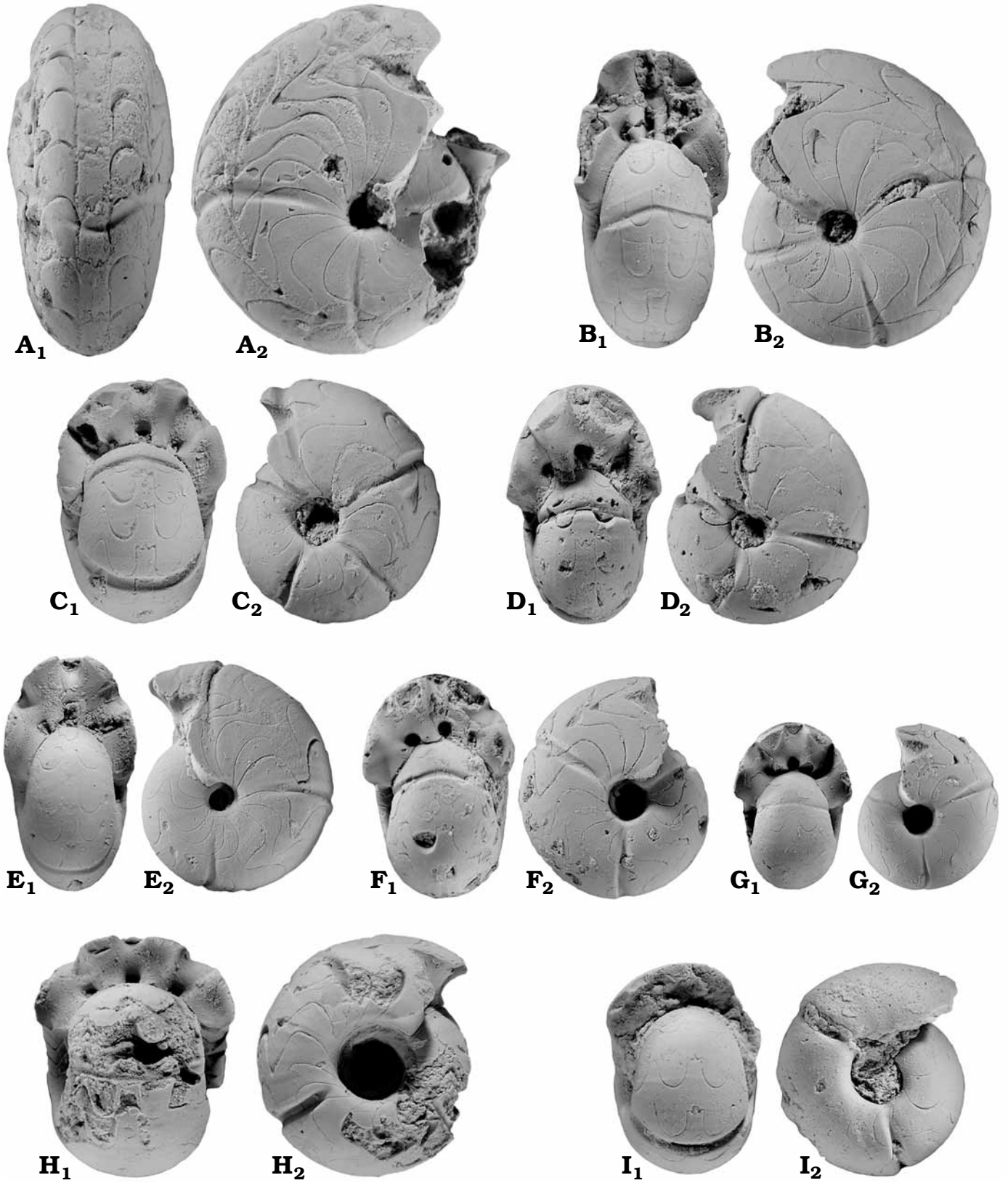

Fig. 18. **A**. *Muensteroceras quadriconstrictum* sp. nov., holotype MB.C.3922. **B**. *Muensteroceras quadriconstrictum* sp. nov., MB.C.3945. **C**. *Muensteroceras quadriconstrictum* sp. nov., MB.C.3946. **D**. *Muensteroceras quadriconstrictum* sp. nov., MB.C.3924. **E**. *Muensteroceras quadriconstrictum* sp. nov., MB.C.3934. **F**. *Muensteroceras quadriconstrictum* sp. nov., MB.C.3927. **G**. *Muensteroceras quadriconstrictum* sp. nov., MB.C.3928. **H**. *Eurites bouhamedensis* sp. nov.; holotype MB.C.3947. **I**. *Eurites bouhamedensis* sp. nov., MB.C.3952. All × 3. All specimens figured in ventral (A_1), apertural (B_1, C_1, etc.), and lateral (A_2, B_2, etc.) views.

constrictions. The latter is also the case for *M. merlewoodense* Campbell et al., 1983 and to *M. stoliczkai* (Miller, 1931).

Thus the combination of the characters: whorl thickness around half of the conch diameter, narrow umbilicus (uw/dm usually less than 0.15), and constrictions distinguish the new species from the others.

Eurites Kusina, 1973

Type species.– *Eurites latus* Kusina, 1973.

Eurites bouhamedensis sp. nov.

Figs. 18H, I, 19, 20.

Derivation of name: After Ksar Bouhamed, where the fauna was collected.

Holotype: Specimen MB.C.3947 (coll. Klug), Fig. 18H.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality B east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

Material.—12 specimens between 5 and 15 mm conch diameter.

Diagnosis.—*Eurites* with pachyconic conch between 8 mm and 15 mm diameter (ww/dm 0.80). Umbilicus narrow to moderately wide (uw/dm 0.25 to 0.35), umbilical margin angular, umbilical wall steep. Steinkern with three or four constrictions. Suture line with moderately deep, V-shaped external lobe, low median saddle, and V-shaped symmetrical adventive lobe.

Description.—Specimens of all growth stages share a similar conch geometry (Fig. 19). The holotype is among the more globose specimens, with a broad venter and a distinct umbilical edge. Smaller specimens show a less pronounced umbilical margin.

Steinkerns possess three or four prominent constrictions per volution, which begin immediately outside of the umbilical margin and are almost linear across flanks and venter.

The suture line of the holotype MB.C.3947 shows a moderately deep external lobe and a much deeper, V-shaped and almost perfectly symmetrical adventive lobe. The ventrolateral saddle is wide, broadly rounded, and nearly symmetrical (Fig. 20).

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/ dm	ww/ wh	uw/ dm	IZR
holotype MB.C.3947	14.30	11.70	5.30	4.30	2.70	1.52	0.82	2.21	0.30	0.49
MB.C.3953	9.45	7.30	3.98	2.83	2.03	1.62	0.77	1.83	0.30	0.49
MB.C.3948	8.70	6.80	3.05	2.50			0.78	2.23	0.29	
MB.C.3949	8.00	6.30	3.15	1.80			0.79	2.00	0.23	
MB.C.3950	6.80	5.60	2.50	2.30	1.55	1.68	0.82	2.24	0.34	0.38
MB.C.3951	5.50	4.20	1.90	1.95			0.76	2.21	0.35	

Comparisons.—Some species belonging to *Eurites* have conchs similar to *E. bouhamedensis* sp. nov.: *E. latus* Kusina, 1973 has a much narrower and deeper external lobe. *E. saginatus* (Gordon, 1957) (whorl width/ conch diameter 0.90) is more globose. *E. ellipsoidalis* (Crick, 1899) and *E. obesus* (Foord, 1903) (ww/dm less than 0.60) are more discoidal and have narrower umbilici (one fifth of the diameter). *E. sphaeroidalis* (McCoy, 1844), *E. corpulentus* (Crick, 1899), *E. latumbilicatus* (Kullmann, 1961), and *E.*? *browni* McCoy, 1844 do not have constrictions. *E. corpulentissimus* (Schindewolf, 1951) is similar in its conch geometry, but has a deeper external lobe and an asymmetrical adventive lobe (in contrast to the moderately deep external lobe and symmetrical adventive lobe in *E. bouhamedensis* sp. nov.). *E. inflatus* (Delépine, 1940) is more narrowly umbilicate (one fifth of the diameter) than the new species.

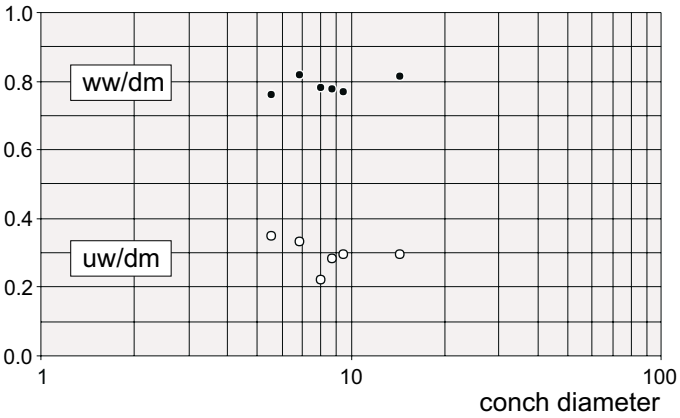

Fig. 19. Whorl width/ conch diameter and umbilical width/ conch diameter ratios of *Eurites bouhamedensis* sp. nov.

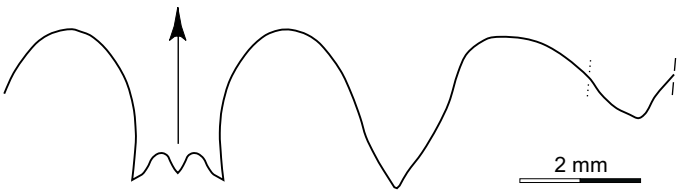

Fig. 20. Suture line of *Eurites bouhamedensis* sp. nov.; holotype MB.C.3947 at dm 11.5 mm, ww 9.0 mm, wh 4.9 mm; × 8.

Family Maxigoniatitidae Korn, Klug, and Mapes, 1999
Ouaoufilalites gen. nov.

Derivation of name: After Jebel Ouaoufilal, where the fauna was found.

Type species: *Ouaoufilalites ouaoufilalensis* sp. nov.

Diagnosis.—Maxigoniatitid with small subglobular adult conch. Umbilical width one third of the conch diameter, umbilical margin broadly rounded. Aperture and whorl expansion rate low (WER 1.60 to 1.70). Suture line with narrow, subparallel external lobe, gently curved flanks and moderately high median saddle. Ventrolateral saddle asymmetrical, subacute. Large, V-shaped adventive lobe.

Comparisons.—Morphology of *Ouaoufilalites* gen. nov. is intermediate between the genera *Dzhaprakoceras* Popov, 1965 and *Bollandites* Bisat, 1930. The flanks of the external lobe are gently curved as in the other two genera, but in *Dzhaprakoceras* they are parallel, and in *Bollandites* the external lobe is V-shaped. Conchs of *Dzhaprakoceras* have a smaller umbilicus (uw/dm less than 0.20), and *Bollandites*

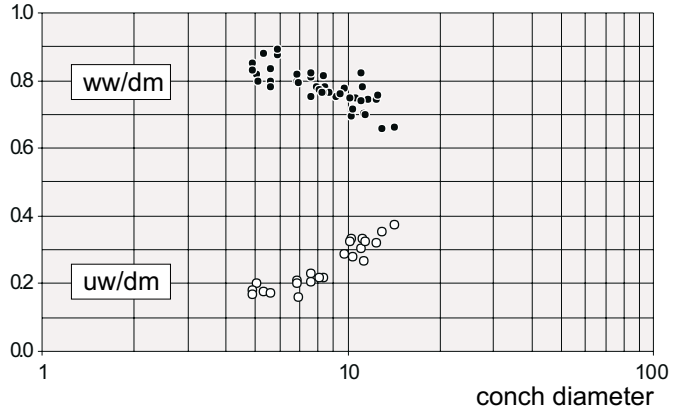

Fig. 21. Whorl width/ conch diameter and umbilical width/ conch diameter ratios of *Ouaoufilalites ouaoufilalensis* sp. nov.

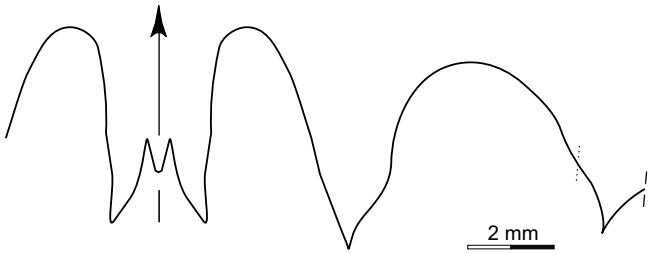

Fig. 22. Suture line of *Ouaoufilalites ouaoufilalensis* sp. nov.; MB.C.3955 at dm 14.0 mm, ww 9.7 mm, wh 4.6 mm; × 6.

possesses a pronounced subangular umbilical margin and steep umbilical wall.

Occurrence.—Only known from the vicinity of Jebel Ouaoufilal; Oued Znaïgui Formation, early Late Tournaisian.

Ouaoufilalites ouaoufilalensis sp. nov.

Figs. 21, 22, 23A, B.

Derivation of name: After Jebel Ouaoufilal, where the specimens came from.

Holotype: Specimen MB.C.3954 (coll. Ebbighausen), Fig. 23A.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality A east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

Material.—109 specimens, 4 to 15 mm in diameter.

Diagnosis.—*Ouaoufilalites* with conch thickly pachyconic at 8 mm diameter (ww/dm 0.75 to 0.85), becoming less pachyconic by 15 mm diameter (ww/dm 0.60 to 0.70). Umbilicus at 8 mm conch diameter narrow (uw/dm 0.20) and moderately wide at 15 mm diameter (uw/dm 0.35). Umbilical margin rounded. Steinkerns with three or four constrictions. Suture line with deep, parallel-sided external lobe, moderate median saddle, and asymmetrical adventive lobe.

Description.—The conch dimensions and ratios show little variability within the population (Fig. 21). Juvenile conchs are wider (ww/dm > 0.80), and specimens over 10 mm diameter show a ratio of less than 0.70. The umbilicus opens remarkably during ontogeny, the uw/dm ratio increases from 0.20 at 6 mm diameter to almost 0.40 at 14 mm. The umbilical margin is rounded in all stages.

The steinkerns are smooth except for three or four constrictions which are linear across flanks and venter.

In specimen MB.C.3955, the external lobe has parallel, slightly sinuous flanks (Fig. 22). The median saddle has a moderate height (0.40 of external lobe depth). The V-shaped adventive lobe is asymmetrical with a linear ventral flank and a sinuous dorsal flank. It is deeper than the external lobe.

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/ dm	ww/ wh	uw/ dm	IZR
MB.C.3955	14.20	9.46	4.80	5.35	3.10	1.64	0.67	1.97	0.38	0.35
holotype MB.C.3954	12.97	8.58	4.59	4.63	3.05	1.71	0.66	1.87	0.36	0.34
MB.C.3958	11.30	8.00	4.40	3.05	2.70	1.73	0.71	1.82	0.27	0.39
MB.C.3957	10.40	7.50	3.80	2.95	2.45	1.71	0.72	1.97	0.28	0.36
MB.C.3961	10.30	7.20	3.65	3.46	2.46	1.73	0.70	1.97	0.34	0.33
MB.C.3959	8.30	6.80	3.40	1.85	2.05	1.76	0.82	2.00	0.22	0.40
MB.C.3956	7.61	5.77	3.02	1.77	1.89	1.77	0.76	1.91	0.23	0.37
MB.C.3960	5.30	4.70	2.05	0.95	1.25	1.71	0.89	2.29	0.18	0.39

Comparisons.—*Ouaoufilalites ouaoufilalensis* sp. nov. resembles some species of *Dzhaprakoceras* Popov, 1965, but is clearly separable because of its rather wide umbilicus. In all species of *Dzhaprakoceras*, the umbilicus is less than one fifth of the conch diameter. The most similar species is *D. djaprakense* (Librovitch, 1927), with a similar whorl width/ conch diameter ratios, but the umbilicus is narrower (one fourth of the conch diameter).

With its pachyconic conch, *O. ouaoufilalensis* sp. nov. resembles species of *Bollandites* Bisat, 1934, but these always show divergent flanks of the external lobe, in contrast to the parallel flanks in *Ouaoufilalites*.

Helicocyclus Schindewolf, 1951

Type species: *Pericyclus* (*Helicocyclus*) *gracillimus* Schindewolf, 1951.

Helicocyclus fuscus sp. nov.

Figs. 23C, D, 24.

Derivation of name: After fuscus (Lat. dark-brown), because of the colour of the material.

Holotype: Specimen MB.C.3985 (coll. Bockwinkel and Ebbighausen), Fig. 23C.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality B east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

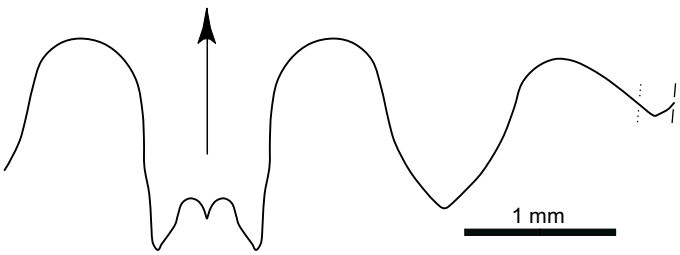

Fig. 24. Suture line of *Helicocyclus fuscus* sp. nov.; holotype MB.C.3985 at dm 6.8 mm, ww 3.3 mm, wh 2.1 mm; × 20.

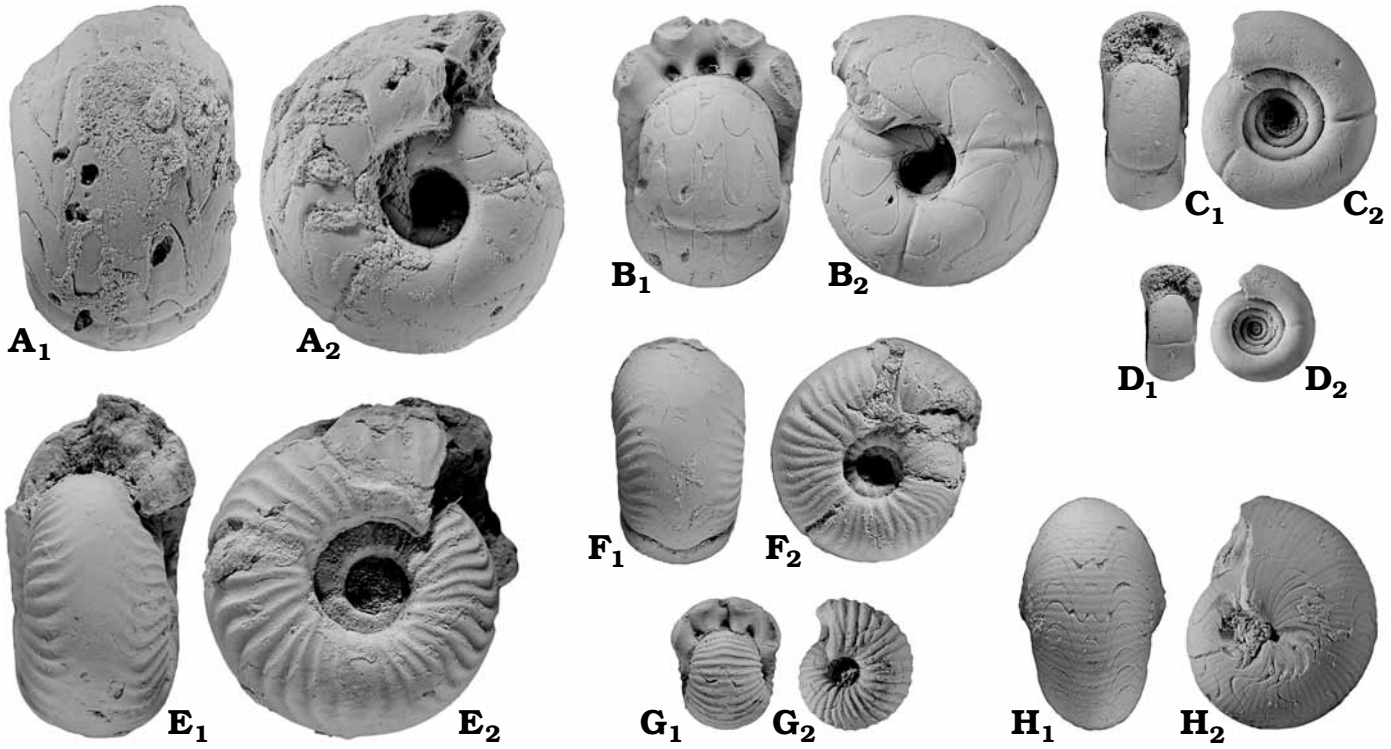

Fig. 23. **A**. *Ouaoufilalites ouaoufilalensis* sp. nov., holotype MB.C.3954. **B**. *Ouaoufilalites ouaoufilalensis* sp. nov., MB.C.3958. **C**. *Helicocyclus fuscus* sp. nov., holotype MB.C.3985. **D**. *Helicocyclus fuscus* sp. nov., MB.C.3986. **E**. *Pericyclus mercatorius* sp. nov., holotype MB.C.3962. **F**. *Pericyclus mercatorius* sp. nov., MB.C.3963. **G**. *Orthocyclus* (?) sp., MB.C.3967. **H**. *Bouhamedites enigmaticus* gen. et sp. nov.; holotype MB.C.3987. All × 3. All specimens figured in ventral (A_1, F_1, H_1), apertural (B_1, C_1, D_1, E_1, G_1), and lateral (A_2, B_2, etc.) views.

Material.—4 specimens between 4 and 8 mm diameter.

Diagnosis.— *Helicocyclus* with discoidal conch at 8 mm diameter (ww/dm 0.45). Umbilicus wide (uw/dm 0.45). Umbilical margin rounded. Conch smooth. Steinkerns with three deep protractive constrictions per volution. Suture line with symmetric, lanceolate adventive lobe and V-shaped lateral lobe.

Description.—The small evolute conchs have a depressed whorl section with widely rounded flanks and venter. Umbilical margin indistinct. The holotype has three deep constrictions, which begin some distance from the umbilicus, are protractive over flanks and venter, where they form a broad salient.

The suture line of the holotype (Fig. 24) has an external lobe with almost parallel-arranged, slightly sinuous flanks. The median saddle has a height of approximately one fourth of the widely rounded ventrolateral saddle. The adventive lobe is as wide as the external lobe; it is lanceolate and symmetric.

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/dm	ww/wh	uw/dm	IZR
holotype MB.C.3985	8.22	3.60	2.36	3.74	1.95	1.72	0.44	1.53	0.45	0.17
MB.C.3986	4.65	2.45	1.32	2.28	1.08	1.70	0.53	1.86	0.49	0.18

Comparisons.—*Helicocyclus fuscus* sp. nov. is the stratigraphically oldest representative of the genus. It differs in its smooth conch from the species *H. gracillimus* Schindewolf, 1951, *H. involutus* Kusina, 1977, and *H. tianshanicus* (Librovitch, 1927), which all possess numerous riblets. *H. divergens* Riley, 1996 has a much wider external lobe.

Family Pericyclidae Hyatt, 1900

Pericyclus Mojsisovics, 1882

Type species: *Goniatites princeps* de Koninck, 1844.

Pericyclus mercatorius sp. nov.

Figs. 23E, F, 25, 26.

Derivation of name: After mercatura (Lat. merchandise), because of the origin of the material.

Holotype: Specimen MB.C.3962 (coll. Klug), Fig. 23E.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality B east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

Material.—6 specimens (between 5 and 15 mm diameter) and thus rare in The Ksar Bouhamed fauna.

Diagnosis.—*Pericyclus* which is pachyconic at 8 mm diameter (ww/dm 0.65) and thickly discoidal at 15 mm (ww/dm 0.55). Umbilicus moderately wide (uw/dm 0.30 to 0.40). Umbilical margin rounded. Up to 35 rursiradiate, often dichotomising ribs per volution, which are strongest on the flanks and wedge out on the venter. Suture line with symmetrical adventive lobe.

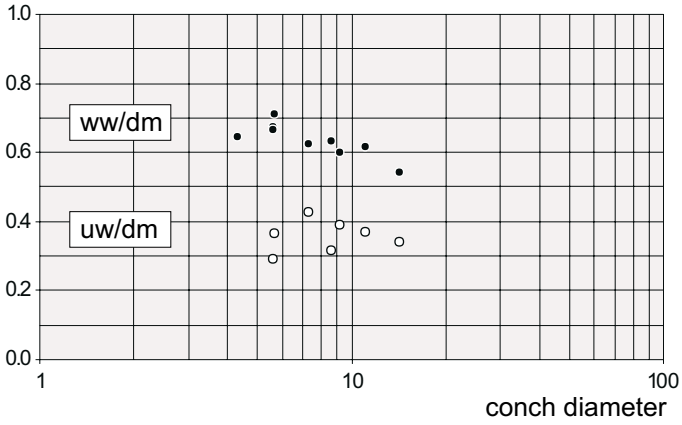

Fig. 25. Whorl width/ conch diameter and umbilical width/ conch diameter ratios of *Pericyclus mercatorius* sp. nov.

Description.—Apart from the general tendency in many Carboniferous goniatites to have more globose juveniles, no significant ontogenetic trend in the conch geometry of this species can be observed (Fig. 25). In all stages available for study, the whorl cross section is depressed with broadly rounded flanks and venter. The umbilical margin is also rounded, and the umbilical wall is rather steep.

Specimens smaller than 4 mm (inner whorls of paratype MB.C.3966) are smooth except for four or more steinkern constrictions. In larger specimens (e.g., the holotype MB.C.3962) a coarse ornament is expressed even on the steinkern, with approximately 30 to 35 sharp ribs which begin immediately at the umbilical margin. From there they run in backward direction and form a shallow lateral sinus and a barely visible ventrolateral salient. On the venter they turn back to form a deeply, rounded chevron-shaped sinus, but on the midventer they wedge out and thus are hardly visible on the midventer. Many of the ribs dichotomise on the umbilical margin. The constrictions of the steinkern become fewer during ontogeny. The holotype possesses only one, which parallels the ribs.

In the suture line of the holotype MB.C.3962 (Fig. 26), all elements are low and wide. The external lobe is V-shaped with sinuous flanks, and the median saddle is low (less than 0.20 of the external lobe depth). Both the broadly rounded ventrolateral saddle and the V-shaped adventive lobe are symmetrical.

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/ dm	ww/ wh	uw/ dm	IZR
holotype MB.C.3962	14.20	7.80	4.95	4.90	2.90	1.58	0.55	1.58	0.35	0.41
MB.C.3963	8.60	5.50	3.20	2.75			0.64	1.72	0.32	
MB.C.3964	5.65	4.05	2.05	2.10			0.72	1.98	0.37	
MB.C.3966	5.60	3.80	2.00	1.65	1.25	1.66	0.68	1.90	0.29	0.38
MB.C.3965	11.10	6.90	3.65	4.15	2.35	1.61	0.62	1.89	0.37	0.36
dto.	9.10	5.50	2.90	3.60	1.85	1.58	0.60	1.90	0.40	0.36
dto.	7.30	4.60	2.35	3.15	1.45	1.56	0.63	1.96	0.43	0.38
dto.	5.60	3.75	1.95		1.15	1.58	0.67	1.92		0.41

Comparisons.—*Pericyclus* is a genus with species which were described mainly in the 19th century and thus revision is required for most of them. *P. princeps* (de Koninck, 1844) has a very similar conch, but a narrower umbilicus (uw/dm less than 0.30) and has ribs which cross the venter. *P. ryckholti* (de Koninck, 1880) and *P. divisus* (de Koninck 1880) have a very narrow umbilicus (uw/dm less than 0.20) and faint ribs. *P. foordi* Crick, 1899 and *P. trapezoidalis* Crick, 1899 are based on large specimens (more than 100 mm in diameter) and thus difficult to compare. Finally, *P. latumbilicatus* Kusina, 2000 resembles the new species in its ornament, but has a wider umbilicus (uw/dm more than 0.45) than *P. mercatorius* sp. nov.

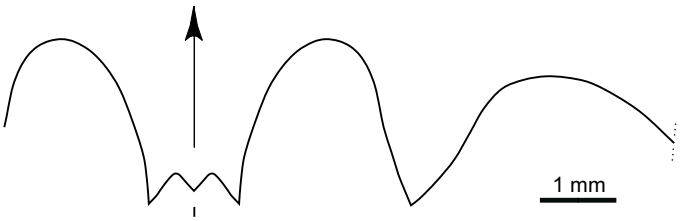

Fig. 26. Suture line of *Pericyclus mercatorius* sp. nov.; holotype MB.C.3962 at dm 11.4 mm, ww 7.1 mm, wh 4.7 mm; × 10.

Orthocyclus Kusina, 2000

Type species: *Ammonellipsites*? *raricostatus* Kusina, 1980.

Orthocyclus (?) sp.

Fig. 23G.

Material.—One small specimen (MB.C.3967) of 5 mm diameter is available for study. It is a strongly pachyconic conch (ww/dm 0.83) with a narrow umbilicus (uw/dm 0.22). It is strongly ornamented with 30 sharp ribs, which are linear across flanks and venter. Some of them are intercalated near the umbilicus. The suture shows a subparallel external lobe with concave flanks and a barely visible median saddle.

Bouhamedites gen. nov.

Derivation of name: After Ksar Bouhamed, where the fauna was found.

Type species: *Bouhamedites enigmaticus* sp. nov.

Diagnosis.—Pericyclid with small thickly discoidal conch. Umbilicus almost closed and umbilical margin broadly rounded. Aperture and whorl expansion rate moderately high (WER 2.0). Ornament with fine, slightly biconvex riblets. Suture line with wide, V-shaped external lobe and low median saddle. Ventrolateral saddle asymmetrical, widely rounded. Rounded adventive lobe.

Comparisons.—*Bouhamedites* gen. nov. displays a morphology that is not known from any other Middle or Late Tournaisian ammonoid, and hence assignment to the family Pericyclidae is uncertain. Some similarities exist with involute species of *Goniocyclus* Gordon, 1986, but in these, the ribs are much sharper and form an angular ventral sinus.

Occurrence.—So far only known from the vicinity of Jebel Ouaoufilal; Oued Znaïgui Formation, early Late Tournaisian.

Bouhamedites enigmaticus sp. nov.

Figs. 23H, 27.

Derivation of name: After the enigmatic conch morphology and ornament.

Holotype: Specimen MB.C.3987 (coll. Bockwinkel and Ebbighausen), Fig. 23H.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality B east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

Material.—One complete phragmocone, almost 10 mm in diameter.

Diagnosis.—*Bouhamedites* with pachyconic conch at 9 mm diameter (ww/dm 0.62). Umbilicus very narrow (uw/dm 0.05), umbilical margin rounded. Ornament with approximately 80 smooth riblets per volution, forming a shallow lateral and deeper sinus across the venter. Suture line with wide, V-shaped external lobe, low median saddle, broadly rounded ventrolateral saddle, and asymmetrical adventive lobe.

Description.—The almost involute, pachyconic conch is widest at the umbilicus, from where the flanks converge to a broadly rounded venter. The steinkern of the holotype displays approximately 80 shallow ribs on the venter which cause a regular undulation. They are strongest on the venter where they form shallow and wide sinuses. They wedge out in the midflank area. Their course is slightly biconvex with a barely visible lateral sinus and a low ventrolateral projection.

The holotype MB.C.3987 (Fig. 27) shows a suture line that differs markedly from all the other Late Tournaisian ammonoids. The external lobe is V-shaped and wide, and its prongs are narrowly rounded at their base. It is divided by a low median saddle. The ventrolateral saddle is widely rounded, and continues into the symmetric, rounded adventive lobe. On the last volution, the septa are periodically approximated.

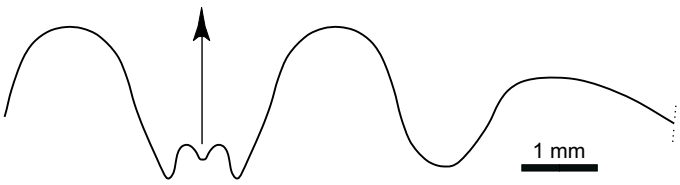

Fig. 27. Suture line of *Bouhamedites enigmaticus* gen. et sp. nov.; holotype MB.C.3987 at dm 8.9 mm, ww 5.6 mm, wh 4.9 mm; × 10.

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/ dm	ww/ wh	uw/ dm	IZR
holotype MB.C.3987	9.34	5.77	5.02	0.57	2.78	2.02	0.62	1.15	0.06	0.52

Comparisons.—*Bouhamedites enigmaticus* sp. nov. is clearly distinct from the other species in the Ksar Bouhamed fauna, and it is not clear that it belongs to the pericyclids. Superficially, the conch resembles *Irinoceras*, but the suture line is very different.

Family Girtyoceratidae Wedekind, 1918

Winchelloceras Ruzhencev, 1965

Type species: *Goniatites allei* Winchell, 1862.

Winchelloceras antiatlanteum sp. nov.

Figs. 28, 29, 30A–C.

Derivation of name: After the Anti-Atlas of Morocco.

Holotype: Specimen MB.C.3968 (coll. Klug), Fig. 30B.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality B east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

Material.—52 specimens, many of them are complete phragmocones, 5 to 17 mm in diameter.

Diagnosis.—*Winchelloceras* with thickly discoidal conch at 8 mm diameter (ww/dm 0.55) and at 15 mm diameter (ww/dm 0.45). Umbilicus narrow between 8 and 15 mm diameter (uw/dm 0.20 to 0.28), umbilical margin subangular. Steinkerns with four to six constrictions. Suture line with wide, V-shaped external lobe, low median saddle, broadly rounded ventrolateral saddle, and asymmetrical adventive lobe.

Description.—Specimens of all growth stages show a similar conch geometry with angular umbilical margin and convex flanks and venter (Fig. 28). As can be seen in the table of dimensions, there are two ontogenetic trends observable. Firstly the whorl width/ conch diameter ratio decreases from 0.60 to 0.45 between 6 and 16 mm diameter, and secondly the aperture becomes higher in larger growth stages, with the whorl expansion rate rising from 1.70 to 2.00. The umbilical width is a rather plastic character, with a uw/dm varying between 0.15

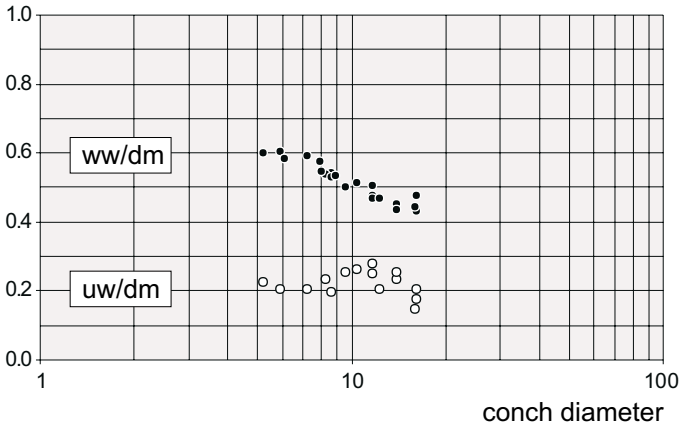

Fig. 28. Whorl width/ conch diameter and umbilical width/ conch diameter ratios of *Winchelloceras antiatlanteum* sp. nov.

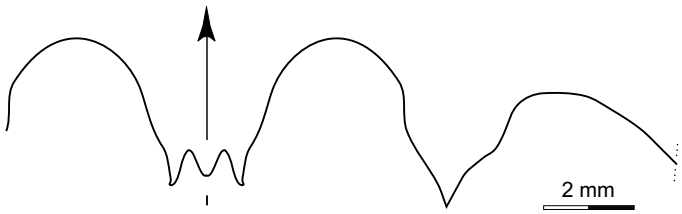

Fig. 29. Suture line of *Winchelloceras antiatlanteum* sp. nov.; MB.C.3977 at dm 13.9 mm, ww 6.3 mm, wh 7.0 mm; × 6.

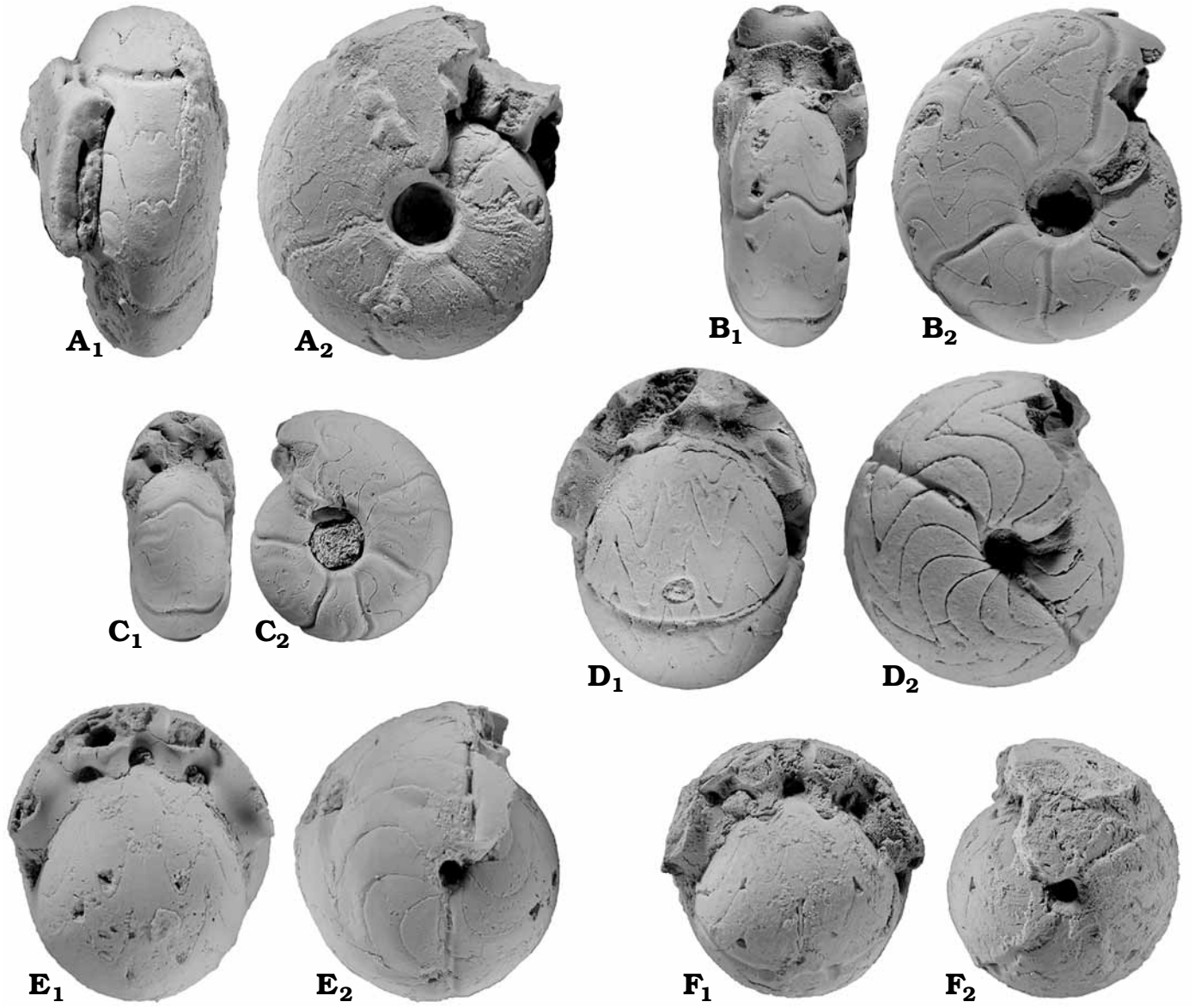

Fig. 30. **A**. *Winchelloceras antiatlanteum* sp. nov., MB.C.3977. **B**. *Winchelloceras antiatlanteum* sp. nov., holotype MB.C.3968. **C**. *Winchelloceras antiatlanteum* sp. nov., MB.C.3971. **D**. *Progoniatites maghribensis* sp. nov., holotype MB.C.3978. **E**. *Progoniatites maghribensis* sp. nov., MB.C.3981. **F**. *Progoniatites maghribensis* sp. nov., MB.C.3982. All × 3. All specimens figured in ventral (A_1), apertural (B_1, C_1, etc.), and lateral (A_2, B_2, etc.) views.

and 0.28, and there appears to be no dependence on the ontogenetic stage.

There are four to six constrictions per volution. They begin at the subangular umbilical edge and follow a biconvex course across the flank with low dorsolateral projection, very shallow lateral sinus, low ventrolateral projection, and deep ventral sinus across the venter. In the interspaces between the constrictions, a faint undulation, following the course of the constrictions can be seen.

In the holotype MB.C.3969 (Fig. 29), the suture line shows a wide and V-shaped external lobe with a low median saddle. The flanks of the external lobe are slightly sinuous, and the two prongs are very narrow. The wide and broadly rounded ventrolateral saddle is almost symmetrical, and the adventive lobe is symmetrical and V-shaped with gently curved flanks.

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/dm	ww/wh	uw/dm	IZR
MB.C.3969	16.20	7.10	7.40	3.40	4.75	2.00	0.44	0.96	0.21	0.36
holotype MB.C.3968	15.90	7.15	8.05	2.45	4.70	2.02	0.45	0.89	0.15	0.42
MB.C.3970	13.90	6.35	5.90	3.30	3.40	1.75	0.46	1.08	0.24	0.42
MB.C.3971	11.60	5.60	4.60	3.30	2.70	1.70	0.48	1.22	0.28	0.41
MB.C.3972	11.60	5.50	4.70	2.95	2.65	1.68	0.47	1.17	0.25	0.44
MB.C.3973	9.50	4.80	3.90	2.45	2.30	1.74	0.51	1.23	0.26	0.41
MB.C.3974	8.60	4.70	3.80	1.75	2.15	1.78	0.55	1.24	0.20	0.43
MB.C.3975	8.20	4.45	3.35	1.95	1.95	1.72	0.54	1.33	0.24	0.42
MB.C.3976	5.90	3.60	2.80	1.25	1.45	1.76	0.61	1.29	0.21	0.48

Comparisons.—It is difficult to compare the species of *Winchelloceras* of different sizes. Also it is not clear, which of the many specimens illustrated by Miller and Garner (1955) do in fact belong to *W. allei* (Winchell 1862). At least the holotype of this species has an almost closed umbilicus and is thus dissimilar to *W. antiatlanteum* sp. nov. The holotype of *W. ruzhencevi* Kusina, 1971 is of large size (69 mm). At this stage, the venter is acute, the steinkern has no constrictions, and the suture line has a much narrower ventrolateral saddle than *W. antiatlanteum* sp. nov. *W. minutum* Kusina, 1980 has a very narrow umbilicus (uw/dm 0.06) and also narrow sutural elements with an almost parallel-sided external lobe. *W. dzhaprakense* (Popov, 1965) has a compressed conch (ww/dm less than 0.30), and that of *W.*(?) *sonkulense* (Popov, 1965) is almost involute with closed umbilicus. *W. palentinum* Wagner-Gentis, 1982 is based on insufficient material, but the umbilicus is almost closed and the conch is more compressed than in *W. antiatlanteum* sp. nov. It is unclear if *W. delepinei* Kusina, 1971 belongs to this genus. The specimen was originally described by Delépine (1941) as "*Muensteroceras*"? ou "*Sagittoceras*"? sp. nov. from Erfoud is a lenticular and nearly involute conch.

Family Goniatitidae de Haan, 1825

Progoniatites gen. nov.

Glyphioceras Hyatt 1884; Schindewolf 1926: 89.
Glyphioceras Hyatt 1884; Schindewolf 1939: 467.
Pericycloides gen. nov.; Follot 1953: 14. (*nomen nudum*).
Goniatites de Haan 1825; Pareyn and Conrad 1968:570.
Glyphioceras Hyatt 1884; Conrad 1984: 100.
Zhifangoceras Sheng 1984; Kusina 2000: 22.

Derivation of name: After the close resemblance to the stratigraphically much younger genus *Goniatites* of the Viséan.

Type species: *Progoniatites maghribensis* sp. nov.

Diagnosis.—Goniatitidae with small globular conch. Aperture and whorl expansion rate low (WER 1.60). Suture line with narrow, V-shaped external lobe and moderately high median saddle. Ventrolateral saddle asymmetrical and subacute. Large, V-shaped adventive lobe.

Other species included.—*P. angustilobatum* (Schindewolf, 1926) from Thuringia, Germany, and *P. karensis* (Kusina, 2000) from the Pay Khoy, Russia, both also early Late Tournaisian in age.

Comparisons.—*Progoniatites* gen. nov. has a conch shape and a suture line which closely resembles *Goniatites* de Haan, 1825. The main difference is the shape of the ventrolateral saddle, which in *Goniatites* is truly acute, but only subacute with a narrowly rounded top in *Progoniatites*. *Zhifangoceras* Sheng, 1984 shows some similarities to *Progoniatites*, but its external lobe is much wider, the median saddle is higher (more than 0.60 of the external lobe depth, in contrast to 0.40 in *Progoniatites*), and the ventrolateral saddle is far more rounded. In this respect, it resembles *Pseudogirtyoceras* Wagner-Gentis, 1982, of which it may be a junior synonym. The conchs of *Zhifangoceras* are thickly discoidal, in contrast to the more globose conchs of *Progoniatites*.

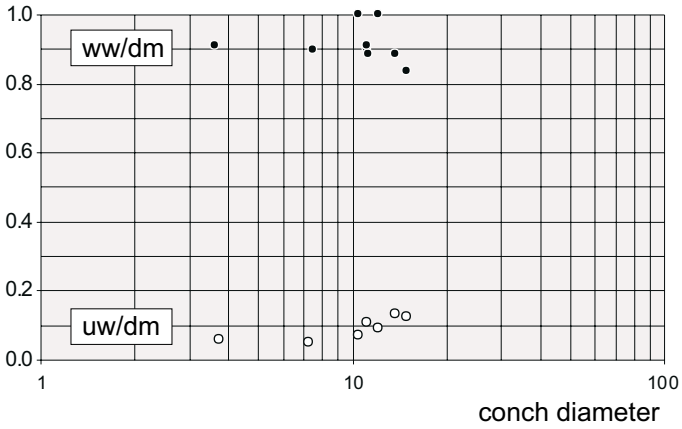

Fig. 31. Whorl width/conch diameter and umbilical width/conch diameter ratios of *Progoniatites maghribensis* sp. nov.

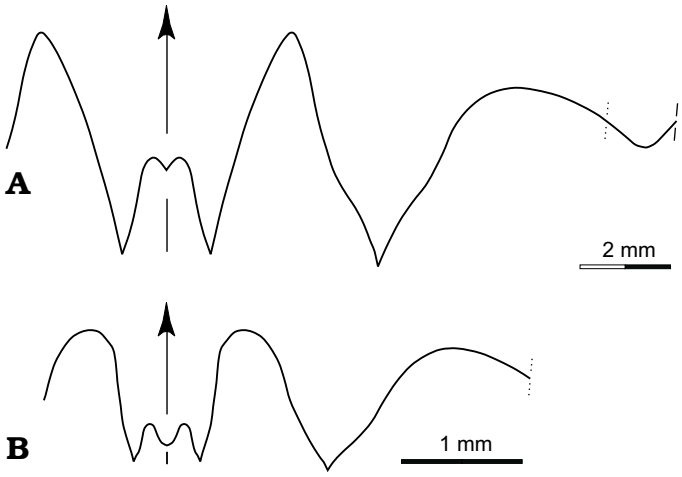

Fig. 32. Suture lines of *Progoniatites maghribensis* sp. nov. **A**. Holotype MB.C.3978 at dm 14.7 mm, ww 12.4 mm, wh 6.7 mm; × 6. **B**. MB.C.3984 at dm 3.7 mm, ww 3.3 mm, wh 1.75 mm; × 16.

Occurrence.—*Progoniatites* is known from the Tafilalt of Morocco, the Mouydir (Central Sahara) of Algeria (Follot 1953; Conrad and Pareyn 1968), Thuringia (Schindewolf 1926), and the South Urals (Kusina 2000). All occurrences have probably an early Late Tournaisian age.

Progoniatites maghribensis sp. nov.

Figs. 30D–F, 31, 32.

Derivation of name: After Maghrib, the Arabian name for north-west Africa.

Holotype: Specimen MB.C.3978 (coll. Klug), Fig. 30D.

Type locality and horizon: Taouz, Jebel Ouaoufilal, locality B east of Ksar Bouhamed (Tafilalt, Morocco); Oued Znaïgui Formation, early Late Tournaisian.

Material.—32 specimens (only few of which are complete and undistorted phragmocones), 8 to 18 mm in diameter.

Diagnosis.—*Progoniatites* with globose conch between 5 and 15 mm diameter (ww/dm 0.85 to 1.00). Umbilicus at 8 mm diameter very narrow (uw/dm 0.06) and little wider at 15 mm diameter (uw/dm 0.15). Umbilical margin rounded. Steinkerns with two or three constrictions. Suture line with V-shaped external lobe, moderate median saddle (40% of external lobe depth), and asymmetrical adventive lobe.

Description.—The conch width shows some variability (Fig. 31), but all measured specimens are globular, with width/conch diameter ratios between 0.84 and 1.01. The umbilicus is in all stages very narrow, but it opens slightly during ontogeny. In specimens between 10 and 15 mm conch diameter it measures between 0.08 and 0.14. The umbilical margin is rounded and the umbilical wall is steep. The steinkern is smooth, and only two linear constrictions per whorl across the flanks and venter.

The goniatitid suture of the holotype MB.C.3978 (Fig. 32) shows a narrow V-shaped external lobe with almost linear flanks, and a median saddle with a height of approximately 40% of the external lobe depth. The ventrolateral saddle is subacute with a very narrowly rounded top. Both flanks of the adventive lobe are convexly arched.

Dimensions.—(in mm).

	dm	ww	wh	uw	ah	WER	ww/dm	ww/wh	uw/dm	IZR
holotype MB.C.3978	14.80	12.50	6.80	1.95	3.05	1.59	0.84	1.84	0.13	0.55
MB.C.3981	13.68	12.20	5.86	1.91	2.81	1.58	0.89	2.08	0.14	0.52
MB.C.3982	11.96	12.08	5.56	1.18	2.57	1.62	1.01	2.17	0.10	0.54
MB.C.3979	11.00	10.00	5.30	1.25	2.30	1.60	0.91	1.89	0.11	0.57
MB.C.3980	10.40	10.50	5.10	0.80	2.20	1.61	1.01	2.06	0.08	0.57
MB.C.3983	7.20	6.70	3.20	0.40	1.25	1.46	0.93	2.09	0.06	0.61
MB.C.3984	3.70	3.30	1.75	0.25	0.65	1.47	0.89	1.89	0.07	0.63

Comparisons.—*P. maghribensis* sp. nov. can hardly be confused with any other of the described Tournaisian species. Poorly known "*Glyphioceras angustilobatum* Schindewolf, 1926" from nodules within the Rußschiefer of Zadelsdorf of Thuringia has a more compressed conch (ww/dm approximately 0.65) than *P. maghribensis* sp. nov., similarly as does *P. karensis* (Kusina, 2000) (ww/dm 0.55).

Some similarity to *P. maghribensis* sp. nov. is shown by species of *Zhifangoceras* Sheng, 1984: *Z. subglobosum* Sheng, 1984 (ww/dm 0.55) and *Z. zhifangense* Sheng, 1984 (ww/dm 0.40) have a much more discoidal conch than *P. maghribensis* sp. nov.

Acknowledgements

We are indebted to Michael R. House (Dorset) for reading the typescript and for many helpful suggestions. Wolfgang Gerber (Tübingen) provided the digital images of the specimens. Jennifer Clark and Elisabeth Bickford (Tübingen and Seattle) checked the text. The paper profited much from the careful reviews by Jerzy Dzik (Warsaw), William Kirchgasser (Potsdam, New York), Marcin Machalski (Warsaw), and Dieter Weyer (Berlin).

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