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First description of the early Devonian ammonoid *Mimosphinctes* from Gondwana and stratigraphical implications

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Abstract *Mimosphinctes* is an ammonoid genus that occurs in many localities that formerly surrounded the Prototethys. In spite of the great exposures and abundance of fossils, unequivocal and well-documented records of this genus from Gondwana were missing. Here, a recently discovered specimen from the eastern Anti-Atlas of Morocco is described and the taxon *Mimosphinctes karltschanzi* n. sp. is introduced. Based on this discovery, the state of the art of ammonoid stratigraphy in the eastern Anti-Atlas is shortly discussed with a focus on the timing of the Daleje Event.

Keywords Ammonoidea · Morocco · Emsian · Stratigraphy · Morphometrics · Daleje event

Introduction

During the early Emsian stage (Devonian), ammonoids evolved from bactritids (Erben 1964, 1965; Kröger and Mapes 2007; De Baets et al. 2013a; Klug et al. 2015a). Still during the early Emsian stage (Zlichovian regional stage), ammonoids radiated at an impressive rate and generated species with a broad range of conch morphologies (Erben 1966; Montesinos and Garcia-Alcade 1996; Monnet et al. 2011; Baets et al. 2013a; Klug et al. 2015a) including gyroconic (*Anetoceras*, *Erbenoceras*) via platyconic (*Gracilites*, *Mimagoniatites*) to oxyconic forms (*Celaeceras*, *Weyeroceras*). Similarly, the disparity of ornamentation became varied very early in the evolution and ranged from smooth forms (*Mimagoniatites*, *Weyeroceras*) to such with simple rursiradiate ribs (*Anetoceras*, *Erbenoceras*) via fine ribs (*Chebbites*, *Gyroceratites*, *Teicherticeras*) to ribbed forms with intercalatory and bifurcating ribs, such as *Mimosphinctes*, which is the subject of this article. The latter genus is remarkable because superficially, it resembles the stratigraphically much younger perisphinctids of the Jurassic in its more intricate ribbing patterns.

The fossil record of these early evolutionary stages is limited to a moderate number of localities: western Algeria (Termier and Termier 1950; Petter 1959; Göddertz 1987); Australia (Teichert 1948; Erben 1965); Belgium (De Baets et al. 2013c); Czech Republic (Barrande 1865; Chlupáč and Turek 1983); southern China (Guangxi: Shen 1975; Ruan 1981; Kuang and Zhou 1992; Sichuan: Ruan 1996; Yunnan: Liao et al. 1979; Yu and Ruan 1988); Germany (Erben 1960, 1964, 1965; De Baets et al. 2013b); France (Erben 1960, 1962; Feist 1970; De Baets et al. 2009); Kazakhstan (Kaplun and Senkevich 1974); Morocco (Hollard 1963, Klug 2001, Becker et al. 2008, De Baets et al. 2010); Kirgisistan (Kiselev and Starshinin 1987, Nikolaeva et al. 2015); Russia (Bogoslovsky 1961, 1969; Caucasus: Nikolaeva 2007; Gorny Altai: Yolkin et al. 2000; Novaya Zemlya: Bogoslovskiy 1972, Yatskov 1990, 1994); Spain (Kullmann 1960; Montesinos Lopez and Truyols-Massoni 1987, Pyrenees: Kullmann and Calzada 1982); Tibet (Ruan 1984); Turkestan (Bogoslovskiy 1980); Turkey (Erben 1962); USA. (Miller 1938, House 1965); Uzbekistan (Bogoslovsky 1980, 1984, Becker et al. 2010); Vietnam/Laos (Mansuy 1921, Tóng-Dzuy 1993); Yakutia (Yatskov and Kuz'min 1992). Among those localities, *Mimosphinctes* was reported from China (Guangxi), Germany, Kirgisistan,

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Morocco (Anti-Atlas, southern Atlas; but without illustrations or other proof, so not testable; Massa 1965; Hollard 1974), Russia (Caucasus, Urals; Plotnikova 1979), Turkestan, Uzbekistan. Some of these occurrences are undoubted, in other cases; however, their documentation is poor or generic assignment doubtful or wrong.

Many localities yielded only one or a few species, while outcrops in a few countries yielded many taxa. In the past decades, the eastern Anti-Atlas (Morocco) proved to be particularly rich in well-preserved and abundant early Emsian ammonoids of a surprising diversity (e.g., Hollard 1963; Becker and House 2000; Klug 2001; Klug et al. 2008, 2013; De Baets et al. 2010, 2013b; Aboussalam et al. 2015).

Most of the early Emsian ammonoids were found in the so-called *Erbenoceras* Limestone (Klug 2001; =*Anetoceras* Limestone of Bultynck and Walliser 1999; see also De Baets et al. 2010), the underlying claystones (Faunule 2; Klug et al. 2008; *Metabactrites-Erbenoceras* Shale of Becker and Aboussalam 2011), and the overlying *Mimagoniatites* Limestone (Aboussalam et al. 2015). Above the latter limestone layers, marls are poorly exposed at several localities; these marls did not yield determinable ammonoids in decades of sampling of several workgroups: "The light-grey limestones at the top of the *Mimagoniatites* Limestone have no goniatites. The alleged occurrence of a *Mimosphinctes* at Jebel Amelane (Massa 1965, p. 66; Bultynck and Hollard 1980), the index genus of LD III-E sensu Becker and House (2000), has never been substantiated by subsequent findings (De Baets et al. 2010; Aboussalam et al. 2015). Currently there are no Tafilalt goniatite faunas, which fall in the *laticostatus* Zone" (Aboussalam et al. 2015: 926). However, Hollard (1967, p. 214) noted *Mimosphinctes cantabricus* in the Skoura region, from a Devonian northwards extension of the Anti-Atlas region at the foot of the High Atlas. Subsequently, Hollard (1974, p. 12) mentioned *Mimosphinctes cantabricus* also from the Jebel Sardar, an isolated Early Devonian outcrop west of the Maider. These materials were never illustrated or described in detail and are thus considered questionable. Additionally, Klug (2001) reported a specimen of *?Mimosphinctes* sp., which was collected from scree of Faunule 2 (i.e., much older than normal for the genus); probably, these specimens were misinterpreted specimens of *Chebbites*. In March 2016, Karl Tschanz (Zurich) discovered a reasonably well-preserved *Mimosphinctes* at Jebel Mdouar (Figs. 1, 2), which is described here together with its stratigraphic occurrence.

Materials and methods

The single specimen PIMUZ 32468 was discovered by Karl Tschanz (Zurich) in the marls overlying the *Mimagoniatites* Limestone (Fig. 3). These strata underlie the thick Daleje Shale equivalents, which were deposited after the Daleje transgression in the late Emsian Stage. PIMUZ 32468 is stored in the Palaeontological Institute and Museum at the University of Zurich.

The left side of the specimen was exposed and displays the weathering facets characteristic of aeolian erosion. The right side of the specimen was still embedded in calcareous marls. Both the sparitic filling of the phragmocone and the calcitic replacement shell are strongly recrystallized, making the fossil highly fragile. The body chamber could be prepared with an air scribe, while the inner whorls had to be prepared with a sandblaster (hence the somewhat eroded surface of the inner whorls).

Parameters and ratios were measured and calculated following Korn (1997, 2010) and Klug et al. (2015b). Raw data are given in Table 1. Abbreviations: dm, conch diameter; dm2, conch diameter of the preceding whorl; uw, umbilical width; ah, apertural height; ww, whorl width; prim, primary ribs per quarter whorl; sec, secondary ribs per quarter whorl.

The PCA is based on the variance/covariance matrix using the following ratios: WER (whorl expansion rate, normalized by dividing all values by 2.6), UWI (umbilical width index, uw/dm), AHI (apertural height index, ah/dm; nearly identical to the whorl height index in this genus because in most species, wh = ah), WWI (whorl width index, ww/dm), rib-ratio primaries/secondaries (ratio of primary to secondary ribs). For the PCA, the data were normalized. Both the normality tests and the PCA were carried out using PAST (Hammer et al. 2001). The results of the normality tests and the variance/covariance matrix are given in Tables 2 and 3.

Systematic palaeontology

Suborder Agoniatitina Ruzhencev, 1957.

Superfamily Mimoceratoidea Steinmann and Döderlein, 1890.

Family Mimosphinctidae Erben, 1953.

Subfamily Mimosphinctinae Erben, 1953.

Genus *Mimosphinctes* Eichenberg, 1931.

Type species: *Mimosphinctes tripartitus* Eichenberg, 1931, p. 185 (OD).

Genus definition (Klug, 2001: p. 402): "Shell small to moderate in size, advolute to evolute and thinly discoidal. Whorls laterally flattened and rounded venter. Embryonic shell ornamented. Moderate to moderately high whorl expansion rate (1.8–2.3). Rectiradiate or rursiradiate sculpture with prominent ventrally bi- or trifurcating, mostly coarse ribs (20–100 per whorl); additional ribs often inserted ventrolaterally and ventrally, coarse growth lines with only a shallow external sinus, which fade out dorsolaterally. Suture line with a small internal lobe (Table 4).

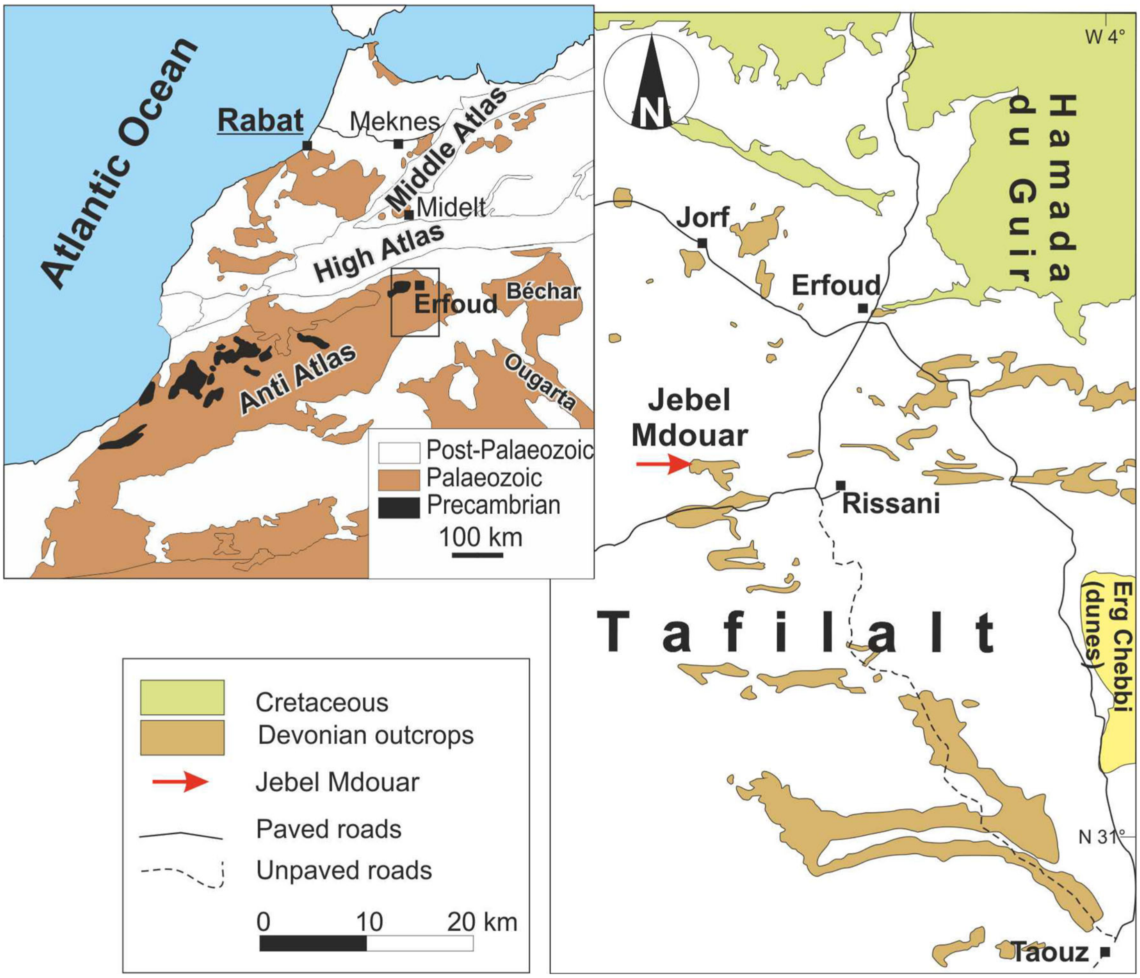


Fig. 1 Map of the Tafilalt, showing the position of Jebel Mdouar. Modified after Klug (2002) and Klug et al. (2016)

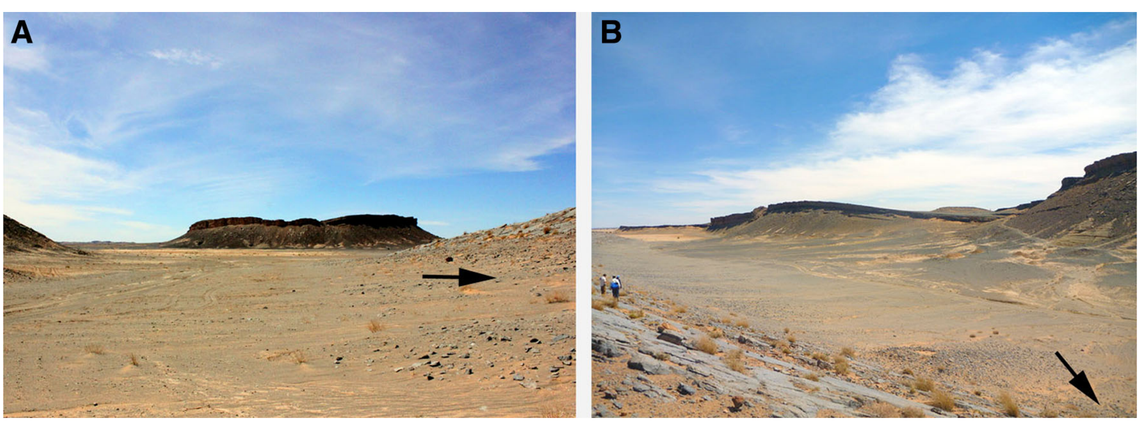


Fig. 2 A, Jebel Mdouar seen from the east. The arrow points to the spot where the type specimen of *Mimosphinctes karltschanzi* n. sp. was discovered. B, Photo taken almost from the same spot, but directed to the east. The persons are standing on the *Mimagoniatites* Limestone, which also contains huge specimens of *Deiroceras hollardi* Kröger, 2008 and other cephalopods. The overlying nodular marls crop out only sporadically and are followed by the Daleje Shale equivalents of the Amerboh Group

Discussion: This genus contains species that can superficially be subdivided in such with a greater number of secondary ribs (*M. discordans*, *M. erbeni* and *M. rudicostatus*) and such with a lower number of coarser secondaries. Also, the coiling differs slightly, particularly in the presence or absence of whorl overlap. These differences

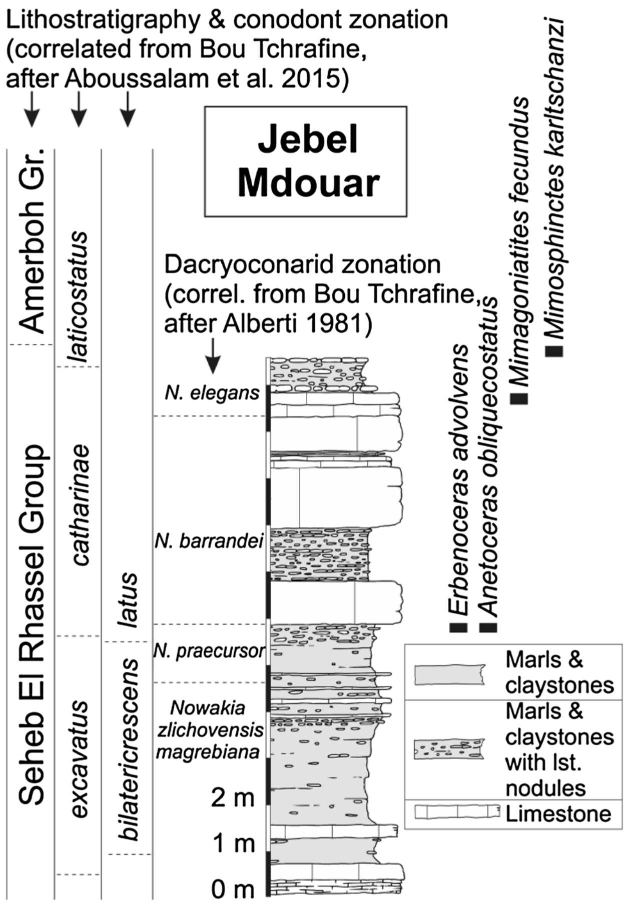


Fig. 3 Lithostratigraphy of the early Emsian of Jebel Mdouar. Modified after Klug (2001) incorporating information of Hollard (1981), Alberti (1981) and Aboussalam et al. (2015)

are subject of ongoing research. Becker et al. (2010) suggested that forms without a dorsal imprint zone and without dorsal lobe should be assigned to a different genus, which will be carried out in another article that is in preparation. Apart from *Erbenoceras khanakasuense* Yatskov, 1990, this applies for example to the German holotype of *Mimosphinctes erbeni* (=*Mimosphinctes* n. sp. A of Erben 1964, 1965). Since this form lacks evidence of rib bifurcation, it probably does not belong to *Mimosphictes*. Consequently, it is not included in Table 1 and the PCA.

Included species

Mimosphinctes bipartitus Eichenberg, 1931: p.185, Lst., Harz (Germany).

Mimosphinctes cantabricus Kullmann, 1960: p.483, Emsian, Palencia (Spain).

Convoluticeras discordans Erben, 1965: p.300, elegans to cancellata Zone, Rhenish Mountains (Germany).

Mimosphinctes erbeni Bogoslovskii, 1980 auct. (=*Mimosphinctes* n. sp. in Becker et al. 2010): p.55, Dzhaus Beds, Zeravshan (Uzbekistan).

Erbenoceras khanakasuense Bogoslovsky, 1978: pl.44 Figs. 2, 3, 4., Dzhaus Beds, Zeravshan (Tajikistan).

Teicherticeras primigenitus Erben, 1965: p.284, Hunsrück Slate, Hunsrück (Germany).

Teicherticeras rotatile Wang in Xian et al., 1980: p.26, Tangdin Fm., Guangxi (China).

Teicherticeras rudicostatum Bogoslovskii, 1980: p.58, Dzhaus Beds, Zeravshan (Uzbekistan).

Mimosphinctes tenuicostatus Bogoslovskii, 1963: p.32, *Anetoceras* range zone, North Urals (Russian Federation).

Mimosphinctes tripartitus Eichenberg, 1931: p.185, Lauterberg Lst., Harz (Germany).

Mimosphinctes zlichovensis Chlupáč and Turek, 1977: p.304, upper Zlichov Lst., Praha-Zlichov (Czech Republic).

Mimosphinctes karltschanzi n. sp.: Marls above *Mimagoniatites* Limestone, Jebel Mdouar, Morocco.

Mimosphinctes karltschanzi n. sp.

Holotype: PIMUZ 32468 by monotypy.

Derivatio nominis: After Karl Tschanz (Zürich), who discovered the holotype, helped with fieldwork, and to acknowledge his contributions on Mesozoic fossils of Switzerland.

Stratum typicum: Marls overlying the *Mimagoniatites* Limestone, uppermost Seheb El Rhassel Group. The age of these marls very likely corresponds to the Gyroceratites laevis Zone, the stratigraphically latest ammonoid zone of the early Emsian Stage (Zlíchovian; Weddige 1996). In contrast to Klug (2001), *G. laevis* does not enter in the Tafilalt below the *Anetoceras* Limestone; this older *Gyroceratites* is either identical with *G. heinricherbeni* De Baets et al., 2012 or a related, very early species of the genus. Generic assignment, however, is corroborated by its coiling and the characteristical 'Ritzstreifen' on the internal mould (see Klug 2001: Fig. 11.13).

Locus typicus: Jebel Mdouar, northern Tafilalt; c. 15 km west of Rissani, Morocco.

Diagnosis: *Mimosphinctes*, which has, diameters over 10 mm, a conch with a whorl expansion rate around 2.0, an umbilical width index around 0.5, an apertural height index mostly under 0.3, and a primary to secondary rib-ratio of about 0.3.

Description: The single specimen and thus holotype PIMUZ 32468 has a diameter of 71.8 mm. With this size, it belongs to the largest specimens known from this genus. At all diameters, its conch is extremely discoidal (WWI 0.11 to 0.21), very evolute to evolute (UWI 0.48 to 0.67) and has a mostly moderate to high whorl expansion rate (WER c. 1.5 to 2.1). Terminal growth is indicated by a decrease in WER, an increase in UWI, and a reduced whorl height at a diameter over 60 mm. The whorls do not overlap. The embryonic conch is not or only imperfectly preserved; it is not possible to discern the initial chamber, mainly due to

Table 1 Measurements of representatives of all known species of *Mimosphinctes*

Taxon	Number	Locality	dm	dm2	uw	ah	ww	WER	uw/dm	ah/dm	ww/dm	Prim/s	Prim	s
M. bipartitus	33267	Luofu, Guangxi	24	18.09	12.55	5.17		1.76	0.52	0.22		0.43	10	23
M. bipartitus	33267	Luofu, Guangxi	18.09	12.55	8.677	4.06		2.08	0.48	0.22		0.58	11	19
M. bipartitus	33267	Luofu, Guangxi	12.55	8.68	6.462	3.51		2.1	0.51	0.28			10	
M. cantabricus	HT GPIT Ce 1160/98	Palencia	48.2	38.2	21.5	15.5	10	1.59	0.45	0.32	0.21	0.25	7	**28**
M. cantabricus	HT GPIT Ce 1160/98	Palencia	23	18	15.6	7.3	5	1.63	0.68	0.32	0.22			
M. cantabricus	GPIT Ce 1160/616	Palencia	65	52.4	33	19	12.6	1.54	0.51	0.29	0.19	0.25	8	32
M. cantabricus	GPIT Ce 1160/616	Palencia	24.5	20.3	11.5	5.3	4.2	1.46	0.47	0.22	0.17			
M. cantabricus	GPIT Ce 1160/79	Palencia	27	21.3	13	8.7	5.7	1.61	0.48	0.32	0.21	0.33	10	30
M. cantabricus	GPIT Ce 1160/30	Palencia	47	36.5	23	14.7	10.5	1.66	0.49	0.31	0.22			
M. discordans	Pl. 11, Figs. 14, 15	Choteč	30	19.8	12.7	10.2		2.3	0.42	0.34	**0.2**	0.25	8	**32**
M. discordans	Pl. 11, Figs. 14, 15	Choteč	19.8	12.7	8	7.1		2.43	0.40	0.36	**0.2**	0.25	7	**28**
M. discordans	Pl. 11, Figs. 14, 15	Choteč	12.7	8	5.7	4.7		2.52	0.45	0.37				
M. discordans	Pl. 11, Figs. 14, 15	Choteč	8	5.7	3.9	2.3		1.97	0.49	0.29				
M. discordans	Pl. 27, Fig. 1, NMP-BR 397	Choteč	42	28	19.5	14		2.25	0.46	0.33	**0.2**	0.18	8	45
M. discordans	Pl. 27, Fig. 1, NMP-BR 397	Choteč	28	19.5	13	8.5		2.06	0.46	0.30	**0.2**	0.21	8	**38**
M. discordans	Pl. 27, Fig. 1, NMP-BR 397	Choteč	19.5	13	10	6.5		2.25	0.51	0.33				
M. discordans	Pl. 27, Fig. 1, NMP-BR 397	Choteč	13	10	7	3		1.69	0.54	0.23				
M. erbeni	3755/11	Uzbekistan	55.5	43.1	28.4	15.7	9.1	1.66	0.51	0.28	0.16	0.27	9	33
M. erbeni	3755/11	Uzbekistan	43.1	30.9	21.6	12.2	7.2	1.95	0.50	0.28	0.17			
M. erbeni	3755/12	Uzbekistan	50	35.5	25.5	14.5	7.8	1.98	0.51	0.29	0.16			
M. erbeni	3755/2	Uzbekistan	47.7	32.4	22.3	15.3		2.17	0.47	0.32				
M. erbeni	3755/2	Uzbekistan	40	27.7	19.1	12.3		2.09	0.48	0.31				
M. erbeni	3755/2	Uzbekistan	35.5	24	16.8	11.5	5.4	2.19	0.47	0.32	0.15	0.23	7	31
M. erbeni	3755/10	Uzbekistan	22.8	15.2	10.5	7.6	4.4	2.25	0.46	0.33	0.19			
M. erbeni	3755/6	Uzbekistan	15.8	10.2	7.5	5.6	3.5	2.4	0.47	0.35	0.22			
M. erbeni	HT	Uzbekistan	31.8	21.2	15.2	10.6	**6.9**	2.25	0.48	0.33	0.22			
M. khanakasuense	Figure 2: 8	Uzbekistan	30	20	13.5	9.6		2.25	0.45	0.32	0.2	0.81	17	23
M. rotatile	33277	Luofu, Guangxi	38.8	28.6	19.2	10.2	6.8	1.84	0.49	0.26	0.18	**0.2**	8	
M. rotatile	33278	Luofu, Guangxi	55	40	28.2	15		1.89	0.51	0.27			10	
M. rotatile	33279	Luofu, Guangxi	24	17	12	7		1.99	0.5	0.29			9	
M. rotatile	33280	Luofu, Guangxi	20	14.2	10	5.8		1.98	0.5	0.29			9	
M. rudicostatus	3304/301	Uzbekistan	53.2	37	26	16.2	11	2.07	0.49	0.31	0.21	**0.2**		
M. rudicostatus	3304/302	Uzbekistan	43	29.4	19.9	13.6	8.4	2.14	0.46	0.32	0.2	0.17	8	47
M. rudicostatus	3304/302	Uzbekistan	33.2	22.9	15.3	10.3	7	2.10	0.46	0.31	0.21			
M. rudicostatus	HT 3304/160	Uzbekistan	41.5	28.9	19.4	12.6	7.3	2.06	0.47	0.30	0.18	0.15	6	**40**
M. rudicostatus	3304/303	Uzbekistan	25.1	16.7	11.2	8.4	5.6	2.26	0.45	0.34	0.22			

Table 1 continued

Taxon	Number	Locality	dm	dm2	uw	ah	ww	WER	uw/dm	ah/dm	ww/dm	Prim/s	Prim	s
M. tenuicostatus	HT 1859/206	N Urals	26	17	11.6	9	5.2	2.34	0.45	0.35	0.2	0.27	8	30
M. tenuicostatus	HT 1859/206	N Urals	17	12	8.8	5	3.4	2.01	0.52	0.29	0.2	0.39	9	23
M. tripartitus	GPIT Ce 1160/50	Palencia	24.5	15.7	11.5	8.8	5	2.44	0.47	0.36	0.20	0.42	8	**19**
M. tripartitus	GPIBo/Gö 311	Harz	15.7	10.4	7	5.3		2.28	0.45	0.34		0.4	8	**20**
M. tripartitus	GPIBo/Gö 311	Harz	23	15.4	10.7	7.6	5.2	2.23	0.47	0.33	0.23			
M. tripartitus	GPIBo/Gö 311	Harz	33.9	23.1	15.4	10.8		2.15	0.45	0.32				
M. zlichovensis	HT L15453	Zlichov	27	17	12	10		2.52	0.44	0.37		0.33	8	24
M. zlichovensis	L17709	Zlichov	57	40	**29**	**17**		2.03	0.51	0.3				
M. zlichovensis	ICh5422	Zlichov	16	10.2	8	5.8		2.46	0.5	0.36				
M. zlichovensis	ICh5421	Zlichov	12.3	7.5	5.1	4.8		2.69	0.411	0.39				
M. zlichovensis	ICh5406	Zlichov	36	25	16	11		2.07	0.44	0.31				
M. karltschanzi	PIMUZ	Mdouara	**71.75**	**55.15**	**38.25**	16.6	14.3	**1.69**	**0.53**	**0.23**	**0.2**	0.29	7	24
M. karltschanzi	PIMUZ	Mdouara	**55.15**	38.25	27.75	16.9	10.7	2.08	0.50	0.31	0.19			
M. karltschanzi	PIMUZ	Mdouara	38.25	27.75	18.95	10.5	8	1.9	0.5	0.28	0.21		10	
M. karltschanzi	PIMUZ	Mdouara	27.75	18.95	14.1	8.8	5.3	2.14	0.51	0.32	0.19		9	
M. karltschanzi	PIMUZ	Mdouara	18.95	14.1	10.05	4.85	3.9	1.81	0.53	0.26	0.21			
M. karltschanzi	PIMUZ	Mdouara	14.1	10.05	6.7	4.05	1.6	1.97	0.48	0.29	0.11			
M. karltschanzi	PIMUZ	Mdouara	10.05	6.7	6	3.35	1.5	2.25	0.6	0.33	0.15			
M. karltschanzi	PIMUZ	Mdouara	6.7	6	4.5	0.7		1.25	0.67	0.10				
M. karltschanzi	PIMUZ	Mdouara	**6**	**4.5**	**3.7**	**1.5**		**1.78**	**0.62**	**0.25**				
M. karltschanzi	PIMUZ	Mdouara	**4.5**	**3.7**		**0.8**		**1.48**		**0.18**				

Data from the literature: *M. bipartitus*—Ruan (1981); *M. cantabricus*—Kullmann (1960); *M. discordans*—Barrande (1865) and Erben (1965); *M. erbeni*—Bogoslovsky (1980); *Erbenoceras khanakasuense*—Becker et al. 2010; *M. rotatile*—Ruan (1980); *M. rudicostatus*—Bogoslovsky (1980); *M. tenuicostatus*—Bogoslovsky (1969); *M. tripartitus*—Kullmann (1960) and Göddertz (1989); *M. zlichovensis*—Göddertz (1989); *M. karltschanzi* n. sp.—own measurements. Uncertain values and estimates in bold face. For the PCA, only the most complete datasets were used (grey background), sometimes using estimates to complete the set; where possible, the holotype (HT) was included

Table 2 Variance/covariance matrix of the PCA incorporating conch ratios of the majority of the known species of *Mimosphinctes*

PC	Eigenvalue	% Variance
1	0.0147414	51.973
2	0.0120779	42.582
3	0.00105501	3.7196
4	0.000302115	1.0651
5	0.000187368	0.66059

M. khanakasuense is excluded here because it differs so strongly from all the other species of the genus in its ribbing (primary to secondary ratio)

the eroded surface on both sides. The ontogenetically earliest preserved whorl has a diameter of about 0.8 mm and thus was at least close to the embryonic part. Septa are poorly preserved; on the second and third whorl, weak traces of a simple lateral lobe are discernible. The characteristic ribbing is preserved on the last two whorls. One quarter whorl carries 7–10 primary ribs, which have a slightly rursiradiate course. Ventrolaterally, they almost disappear and pass into the double to triple amount of secondary ribs. Their orientation is clearly rursiradiate and ventrally, they form a broadly rounded and moderately deep hyponomic sinus. Only very faint traces of growth lines are preserved between the last primary ribs; their course appears to be identical to that of the ribs.

Comparison: The conch morphology is particularly similar to the species *Mimosphinctes cantabricus* and *M. bipartitus* in some respects (Fig. 5). In terms of whorl expansion rate, *M. karltschanzi* resembles *M. rotatile*, *M. rudicostatus* and *M. erbeni* (Fig. 6). Especially towards larger diameters, the similarity in umbilical width index is marked, although the new species mostly has the highest values of all included specimens. Since the holotype is

Table 3 Results of the test for normal distribution of data

Test	WER	UWI	AHI	WWI	prim/s
Shapiro–Wilk W	0.9383	0.975	0.9245	0.8318	0.9252
p (normal)	0.1829	0.8223	0.09418	0.001642	0.09763
Jarque–Bera JB	1.44	0.1527	2.268	6.804	2.611
p (normal)	0.4869	0.9265	0.3217	0.0333	0.271
p (Monte Carlo)	0.2522	0.9267	0.1074	0.02	0.0923
Chi^2	4.9091	0.90909	0.54545	10.727	3.4545
p (normal)	0.026716	0.34036	0.46018	0.0010557	0.063078
Chi^2 OK ($N > 20$)	YES	YES	YES	YES	YES
Anderson–Darling A	0.497	0.2741	0.5939	1.858	0.5512
p (normal)	0.1903	0.6292	0.1085	6.419E − 05	0.1374

M. khanakasuense is excluded here because it differs so strongly from all the other species of the genus in its ribbing (primary to secondary ratio)

among the largest specimens assigned to the genus *Mimosphinctes*, it is not surprising that the adult modification of its conch geometry is more distinct compared to all other species of the genus. At diameters exceeding 30 mm, the new species has the lowest number of secondary ribs per primary rib. Particularly *M. discordans*, *M. erbeni*, *M. primigenitus*, *M. rudicostatum* and *M. tenuicostatus* have much finer secondary ribs than the new species (this character might be useful to split the genus in the future). The specimen of *M. bipartitus* figured by Eichenberg (1931, pl. IX Fig. 4) appears to have even less secondary ribs, although the venter is poorly preserved. Specimens of *M. tripartitus* figured on the same plate have a greater apertural height and it is arguable whether or not *M. tripartitus* and *M. bipartitus* are conspecific. In the specimens of the Figs. 3a–c, the primary ribs hardly weaken at the transition to the secondaries. In contrast, the specimen in Eichenberg's Fig. 3d is similar to the new species with respect to the almost smooth conch surface between the primaries and secondaries. *Mimosphinctes cantabricus* has a distinctly lower whorl expansion rate. In contrast, *M. tripartitus* and *M. zlichovensis* are overall very similar in their conch-parameters, but their whorl expansion rates mostly exceed 2.2, their umbilici are narrower and the apertures higher than in the new species. The imprint zone of the new species is very low and resembles '*Erbenoceras' khanakasuense* in this respect, but the new species has much coarser and much less primary ribs. The new species will be included in a new taxon Gen. aff. *Mimosphinctes* sensu Becker et al. (2010), but this is the subject of ongoing research. In any case, this genus is in need of further revision including both the introduction of one or two new genera and synonymizing some of the species, where sometimes the main difference might be of taphonomic origin.

Geographical distribution: The genus *Mimosphinctes* (in its current state) and at least the subfamily has a wide distribution from the western Variscan Sea (Germany, Bohemia, northern Spain) via the epicontinental shelf of northern Gondwana (southern Morocco) to the Urals, Caucasus, Central Asia (Uzbekistan, Kirgisia) and southern China, thus ranging from middle latitudes in the southern hemisphere to roughly the palaeo-Tropic of Cancer. Thus far, the genus is unknown from the American part of Laurentia, southern and eastern Gondwana (southern America, southern Africa, Australia, Antarctica).

Stratigraphical distribution: Early Emsian Stage, latest Zlichovian Regional Stage, *Mimosphinctes* Zone of Becker and House (1994).

Discussion

In consideration of the excellently exposed Emsian sediments and the abundance of *Mimosphinctes* in Spain (Kullmann 1960; Montesinos Lopez and Truyols-Massoni 1987; Montesinos López 1991; Truyols-Massoni 1998), it appears surprising that this genus is so rare in Morocco (Aboussalam et al. 2015). It is likely a taphonomic or collection bias that accounts for its rarity, because the marls overlying the *Mimagoniatites* Limestone are commonly deeply weathered and either covered by alluvial sediments or by scree of the underlying (usually tectonically tilted) *Mimagoniatites* Limestone.

With the herein described, newly found specimen of *Mimosphinctes*, the last missing piece of ammonoid biostratigraphy of the Emsian Stage of Morocco (cf. Aboussalam et al. 2015) can now be added: All biostratigraphically significant species or groups of

Table 4 Ammonoid stratigraphy of the Emsian Stage of the eastern Anti-Atlas (Morocco)

Stage	Lithostratigraphic units (beds)	Index ammonoids	Additional ammonoids
Late Emsian	Upper *Anarcestes* Lst.	*Anarcestes lateseptatus*	*Amoenophyllites doeringi*, *Anarcestes* spp., *Chlupacites praeceps*, *Mimagoniatites bohemicus*
	Lower *Anarcestes* Lst. (*Sellanarcestes* Marls)	*Sellanarcestes wenkenbachi*	*Achguigites tafilaltensis*, *Anarcestes* spp., *Chlupacites praeceps*, *Paranarcestes pictus*, *Sellanarcestes neglectus*
	Middle and upper Daleje Shale	*Latanarcestes noeggerathi* auct.	*Latanarcestes latisellatus*, *Rherisites tuba*, *Praewerneroceras hollardi*
	Lower Daleje Shale	*Gyroceratites gracilis*	*Rherisites tuba*[a]
	Base Daleje Shale	*Gyroceratites laevis*	–
Early/late Emsian	Marls above Mimagoniatites Lst.	*Mimosphinctes karltschanzi*	–
Early Emsian	*Mimagoniatites* Lst.	*Mimagoniatites fecundus*	–
	Upper *Erbenoceras* Lst.	*Klugites gesinae*	*Erbenoceras solitarium*, *Weyeroceras angustum*
	Lower *Erbenoceras* Lst.	*Anetoceras obliquecostatum*	*Anetoceras obliquecostatum*, *Erbenoceras advolvens*, *Irdanites korni*, *Metabactrites formosus*, *Teicherticeras* cf. *senior*
	Lower *Devonobactrites* Shale (early Faunule 2)	*Erbenoceras advolvens*	*Anetoceras* sp., *Irdanites kaufmanni*, *Ivoites ernsti*, *Metabactrites formosus*, *Gyroceratites* cf. *heinricherbeni*, *Chebbites* spp.
	Deiroceras Lst.	*Chebbites reisdorfi*	–

This table was assembled using own field data as well as published data from Becker and House (1994), Klug (2001, 2002), Klug et al. (2008), De Baets et al. (2010), Aboussalam et al. (2015) and this paper. It is unclear whether the *Gyroceratites laevis*, *G. gracilis* and *Latanarcestes noeggerathi* (auct.) zones are entirely justified and to which degree the occurrences overlap. In that respect, this table is an attempt to summarize the state of research; at the same time, the lack of biostratigraphic data have to be stressed as well as the need for further research

[a] Aboussalam et al. (2015, p. 926) noted that *Rherisites tuba* enters in the Daleje Shale Equivalent before the first anarcestids (W of Hamar Laghdad), which justifies a new *Rh. tuba* Zone. They also emphasised that the true *Lat. noeggerathi* is a younger species (holotype from the Wissenbach Slate) than the oldest anarcestids commonly given that name

morphologically similar species that are known from other important occurrences of Early Devonian ammonoids are herewith documented from the northern African Emsian Stage as well. It remains to be clarified what is the succession in greater detail. In Morocco, *Gyroceratites* occurs already in older sediments below the *Erbenoceras* (or *Anetoceras*) Limestone, but the form described as *G. laevis* in Klug (2010) is probably more closely related or identical to *G. heinricherbeni*, which has been described from roughly coeval strata of the Hunsrück Slate (De Baets et al. 2013b). In contrast, the more derived species *G. laevis* and the stratigraphically somewhat younger *G. gracilis* (Becker and House 1994), which are also the index forms for the ammonoid level following *Mimagoniatites fecundus*, are neither found in the carbonates of the *Mimagoniatites* Limestone nor in the overlying marls, but as haematitic internal moulds in the claystones of the overlying Daleje Shale Equivalents. In contrast, in the Barrandian area, *G. circularis* appears to co-occur with *Mimagoniatites* (Chlupáč and Turek 1983; Becker and House 1994). In Spain, *G. pallantinianum* occurs in the Cancellata Zone (Montesinos López 1991). Possibly, the lack of clarity in the distinction between these younger species of *Gyroceratites* contributed to this confusion, although some are easy to identify (Walliser 1962; De Baets et al. 2013b). According to Aboussalam et al. (2015: p. 969), the layers at the transition between the early and the late Emsian Stage (i.e., between the Zlíchovian and the Dalejan Regional Stages) are free of ammonoids. With the herein described newly found specimen, the ammonoid succession appears as follows in the eastern Anti-Atlas:

As far as the Daleje Event is concerned (House 1985), its precise dating is hampered by inter-regional differences in sedimentary facies and its gradual onset (e.g., Chlupáč and Kukal 1988: p. 125; Walliser 1997; Carls and Valenzuela-Ríos 2007; Becker 2007; Carls et al. 2009; Ferrová et al. 2012; Tonarová et al. 2017). House (1985) defined the beginning of the transgression by the disappearance of auguritids and some mimosphinctids, but regarding biostratigraphic data from Morocco, this is

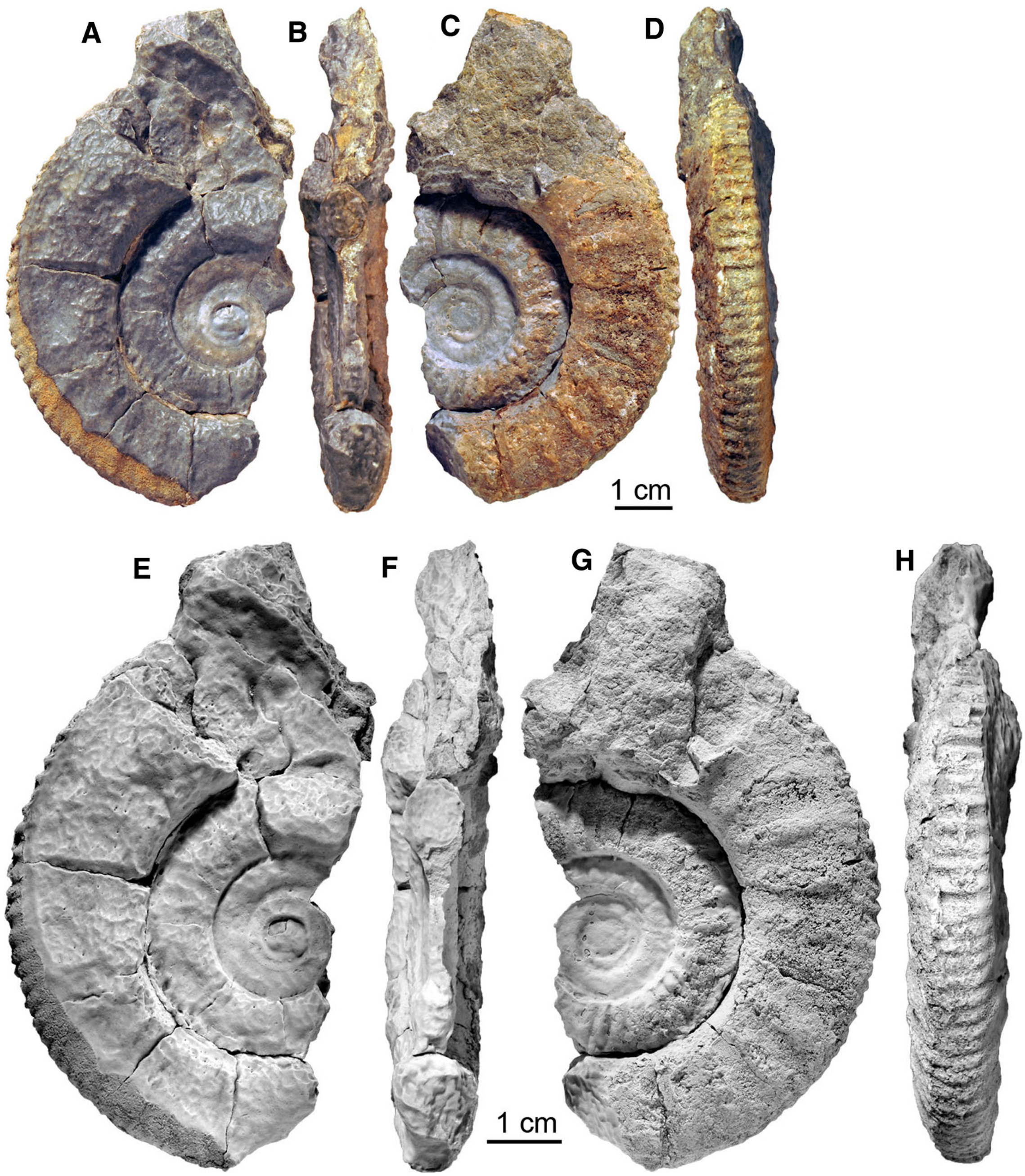
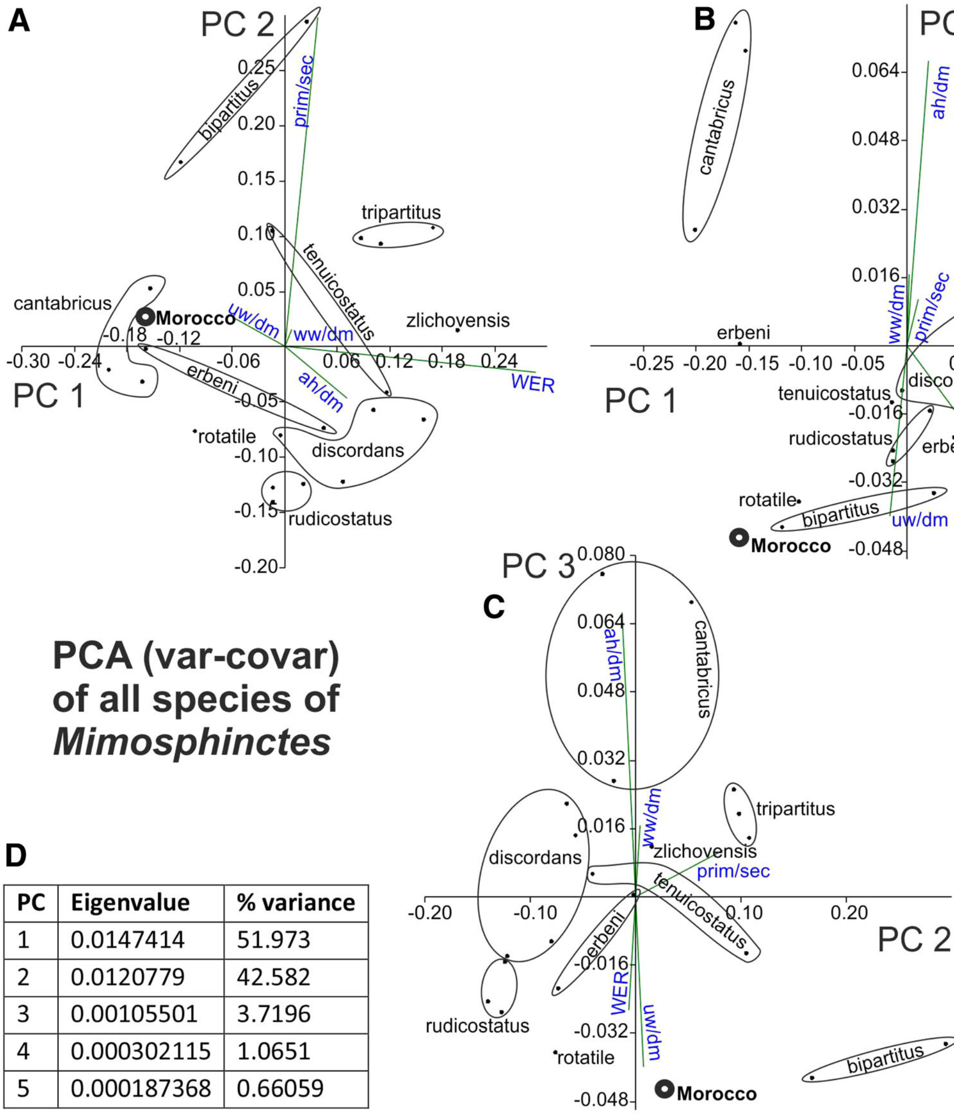


Fig. 4 Holotype of *Mimosphinctes karltschanzi* n. sp., PIMUZ 32468, from the marls overlying the *Mimagoniatites* Limestone of the uppermost Seheb El Rhassel Group of Jebel Mdouar. **a**–**e** Colour images to show the presence of replacement shell and the corroded inner whorls. **a**, **e** Left lateral view. **b**, **f** Dorsal view. **c**, **g** Right lateral view. **d**, **h** Ventral view

much more complicated, because the extinctions of these ammonoid taxa occurred not from one layer to the next but rather covered an interval varying strongly in thickness and probably also time (incomplete fossil record, sampling bias, etc.).

The new discovery of *Mimosphinctes* in Morocco documented in this paper will help to refine the inter-regional correlations, but it raises the question for the timing of the Daleje transgression. In the Tafilalt, the clay content is much higher in the marls covering the *Mimagoniatites* Limestone (which form the top of the ridges composed of mostly Pragian to early Emsian carbonates), but does this correlate with the Daleje transgression or would the correct correlation be the base of the actual Daleje Shales above



PC	Eigenvalue	% variance
1	0.0147414	51.973
2	0.0120779	42.582
3	0.00105501	3.7196
4	0.000302115	1.0651
5	0.000187368	0.66059

Fig. 5 Principal Component Analysis based on the variance–covariance matrix of ratios of all published species of *Mimosphinctes*. For data see Tab. 2. **a** PC 1 and 2. **b** PC 1 and 3. **c** PC 2 and 3. **d** Table with Eigenvalues and the percentage of variance of each principal component. The fat *circle* with the label "Morocco" indicates the position of *Mimosphinctes karltschanzi* n. sp. *M. khanakasuense* is excluded here because it differs so strongly from all the other species of the genus in its ribbing (primary to secondary ratio: Fig. 6)

the marls? From the changes in clay content around the early to late Emsian boundary, it appears like the Daleje transgression started off gently, thereby reducing the carbonate content gradually. Aboussalam et al. (2015: p. 927) stated that it is important to distinguish the first Daleje Transgression of Ferrová et al. (2012: *elegans* Zone), which is the Upper Zlíchov Event of García-Alcalde (1997). The main Daleje Transgression near the *elegans-cancellata* boundary is that of Chlupáč and Kukal (1988) and that of southern Morocco, which is indeed gradual, with two pulses where first the marls and then the thick monotonous claystones were deposited.

Conclusion

For the first time, a reasonably preserved specimen of the ammonoid genus *Mimosphinctes* is described in detail from the early Emsian Stage of Morocco. Although this specimen resembles various species of the genus in several respects, the differences justify the introduction of the new species *M. karltschanzi*.

The herein documented find is of interest since it does have significance for biostratigraphic correlations because the genus occurs near the Zlíchovian/Dalejan boundary around much of the Prototethys. It also raises

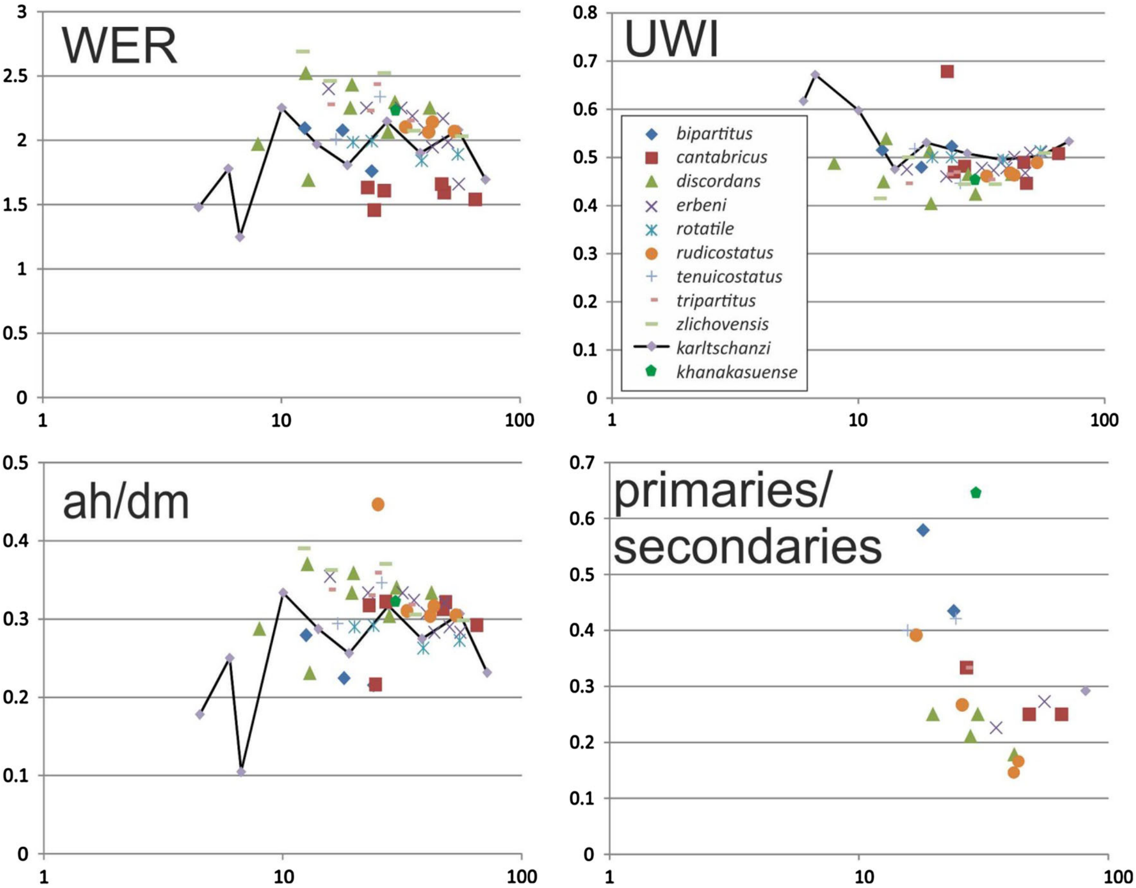


Fig. 6 Biplots of the main conch-parameters WER, uw/dm, ww/dm, primary/secondary rib-ratio

the question for the timing of the eustatic Daleje transgression. A detailed ammonoid succession of the Emsian Stage is given for the eastern Anti-Atlas. Future research needs to incorporate other fossil groups in a more quantitative way to refine correlations in the Emsian Stage.

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