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RESEARCH PAPER

Early Toarcian (Jurassic) belemnites from northeastern Gondwana (South Riffian ridges, Morocco)

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Abstract A belemnite fauna collected in the lowermost Toarcian succession that crops out near Moulay Idriss (northern Morocco) is studied in this article. This is the first palaeontological study of Early Toarcian belemnites from Northern Africa, i.e., the northeastern margin of the Gondwana, in connexion with Tethys. Four species of the family Passaloteuthidae Naef, 1922, have been identified: Passaloteuthis bisulcata (de Blainville, 1827), Pseudohastites longiformis (Blake, 1876), Parapassaloteuthis zieteni (Mayer-Eymar, 1884) and Parapassaloteuthis sp. A. All species have been collected in lowermost Toarcian beds dated to the ammonite Polymorphum Chronozone (=Tenuicostatum Chronozone), which coincides with the belemnite Passaloteuthis bisulcata biozone. The discovery of a syntype of this zonal index is discussed. The identified species are common with Europe, thus suggesting that the onset of the belemnite provincialism in the Toarcian could

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Département de Géologie, Faculté des Sciences, Université Moulay Ismail, Zitoune, BP 11201, Meknes, Morocco e-mail: benzaggagh@gmail.com post-date the earliest Toarcian Polymorphum—Tenuicostatum Chronozone. However, records of Early Jurassic belemnites are still too sparse to recognize the establishment of provincialism and the timing of its onset.

Keywords Belemnites · Systematics · Biostratigraphy · Biogeography · Jurassic · Toarcian · Morocco

Kurzfassung Aus der untersten Toarcium-Abfolge in der Nähe von Moulay Idriss (Nord-Marokko) wird eine Belemnitenfauna beschrieben. Dies ist die erste paläontologische Studie von Belemniten aus dem frühen Toarcium von Nordafrika, d.h. vom nordöstlichen Rand Gondwanas, der mit der Tethys in Verbindung stand. Vier Arten der Familie Passaloteuthidae Naef, 1922 wurden bestimmt: Passaloteuthis bisulcata (de Blainville, 1827), Pseudohastites longiformis (Blake, 1876), Parapassaloteuthis zieteni (Mayer-Eymar, 1884) und Parapassaloteuthis sp. A. Alle Arten stammen aus den untersten Toarcium-Schichten, die der Ammoniten Polymorphum-Chronozone (=Tenuicostatum Chronozone) angehören. Sie entspricht der Belemniten Palassoteuthis bisulcata Biozone. Die Entdeckung eines Syntyps dieses Zonen-Indexfossils wird diskutiert. Die identifizierten Arten treten auch in Europa auf, was darauf hindeutet, dass der Belemniten-Provinzialismus im Toarcium erst nach der Polymorphum ? Tenuicostatum Chronozone des frühesten Toarcium einsetzte. Allerdings sind die Belemnitenfunde des frühen Jura noch zu spärlich, um die Etablierung des Provinzialismus und den Zeitpunkt seines Einsetzens zu erkennen.

Schlüsselwörter Belemniten · Taxonomie · Biostratigraphie · Biogeographie · Jura · Toarcium · Marokko

Introduction

Belemnites are an important cephalopod fossil group that has stimulated the interest of palaeontologists for both biostratigraphic and palaeobiogeographic purposes (Doyle 1987; Doyle and Bennett 1995). According to Doyle (1987), there is only a single Lower Jurassic record of belemnite occurrence in northern Africa (Coquand 1862). The Moulay Idriss area (northern Morocco) is well known for its lowermost Toarcian succession and is rather rich in cephalopods fossils (Elmi and Faugères 1974; Faugères 1975). The presence of belemnites in this area has been known for some decades (Faugères 1975; Bassoullet et al. 1991); there are, to our knowledge, no systematic studies of early Toarcian belemnites from this location. The present work is the first palaeontological study of Early Toarcian belemnites from Northern Africa.

Geological setting

The study area is located in the South Riffian ridges of Morocco, namely in the Dhar en Nsour mountains. This is a massive anticline with a Pliensbachian core located between the Saïs basin in the South and the external Prerif in the North (Fig. 1). The Jurassic succession exposed spans the Pliensbachian to the Upper Bajocian (Elmi and Faugères 1974) and was formed on the continental shelf of the Northern African margin, which was the northeastern part of Gondwana. The sedimentary succession was deposited in a marine basin located north of the land of central Morocco. This basin was palaeogeographically connected with the Tethys and with the protoatlantic sea of the Hispanic Corridor (Dercourt et al. 2000). Thick sedimentary successions were deposited from the Pliensbachian to late Bajocian when the whole domain emerged. After a brief Cretaceous (Late Albian) marine episode, the sea transgressed this area in the upper Miocene-lower Pliocene interval. This produced the thick Neogene cover, which rests over Jurassic beds by angular unconformity (Faugères 1975).

The fossils studied in the present article have been collected in 5 of the 16 outcrops studied. These crop out in two main sites: the former prison of Moulay Idriss and the Oued Lkhemmane tributary site (Figs. 2, 3).

The former prison is located around 0.5 km outside the east exit of the city of Moulay Idriss (localization 34"03'38.01"N 5"30'48.63"W). This is the sole locality in the area where the Pliensbachian-Toarcian transition is exposed. Here we have logged outcrop 14 (Fig. 2a), which is the thickest and most complete of the whole study area, with more than 65 m of lowermost Toarcian marls exposed. Belemnites have been collected in outcrop 14 and



Fig. 1 Location of the study area and geological sketch map of Moulay Idriss area (Chenakeb and Ben Dkik 2004, modified)

in the nearby outcrop 13 (Fig. 2b). Section 14 displays a rather monotonous succession mainly characterized by blue-gray marls with episodical intercalations of limestone beds. Detrital, siliciclastic fractions have been observed in some limestone beds.

The second site is located approximately 3 km east of the prison where road P7014 crosses a little tributary of the Oued Lkhemmane. The only outcrop (over seven investigated) where the belemnites have been found (outcrop 7) is around 100 m upstream (localization 34''03'47.74''N 5''28'42.54''O) (Fig. 2c).

The stratigraphic correlation of the studied sections (Fig. 4) has been realized by means of ammonites (Bardin et al. in prep).

Biostratigraphy

All belemnite specimens have been found in beds ascribed to the lowermost Toarcian ammonite *polymorphum* zone, which, according to Page (2003), is chronologically equivalent to the *tenuicostatum* zone. These zones are

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Fig. 2 Lithological succession of the investigated area with belemnite occurrences and ammonoid biostratigraphy. **a–c** Stratigraphic logs of the three belemnite-rich sections presenting more than one calcareous bed. See Fig. 4 for stratigraphic correlation



Fig. 3 Views of outcrops 14 and 7 (pictures taken in 2011) with indication of limestone beds and topographic map of the investigated region

considered chronozones by Page (2003), and the index species must not be written in italics (e.g., Tenuicostatum Chronozone). The former has been defined on the basis of ammonite faunas of the Mediterranean areas whereas the latter on ammonites of northwestern Europe. In terms of belemnite biostratigraphy, Doyle (1990) defined the belemnite *Passaloteuthis bisulcata* biozone stressing that its upper part coincides with the ammonite Tenuicostatum Chronozone, whereas its base was unidentified but probably coincides with the ammonite Margaritatus Chronozone. Combémorel (1997) then split Doyle's *Passaloteuthis bisulcata* biozone, which spans the entire late Pliensbachian, and a chronologically restricted

P. bisulcata biozone, whose range corresponds to the earliest Toarcian ammonite Tenuicostatum Chronozone.

The problem of the types of *Passaloteuthis bisulcata* (de Blainville, 1827)

Doyle (1990) considered the specimen originally figured by de Blainville (1827, pl. 2, fig. 7, here reproduced in fig. 5c) as the holotype of the *Passaloteuthis bisulcata*. It is worth noting that all the specimens studied by de Blainville were believed lost during the WWII bombing of Caen, and, as a consequence, Doyle (1990) noted that a neotype from the same locality should be designated. However, the notion of holotype should not be used in this case because, in agreement with the code, all specimens originally



Fig. 4 Correlation of the outcrops studied in the Moulay Idriss area. Beds below bed IV of outcrop 14 are not figured

studied by de Blainville should be syntypes. By using the word holotype before the year 2000, Doyle (1990) automatically designated the specimen figured by de Blainville (1827) as the lectotype (ICZN art.74.5 in ICZN 1999). However, all original specimens are not lost because there is at least one (MNHN B44621 figured here, Fig. 5a, b) from the lower Toarcian of Basse-Normandie in the de Desnoyers collection housed in the Muséum National d'Histoire Naturelle (Paris, France). There are probably some other specimens in the d'Orbigny collection (housed in the same institution) that de Blainville studied that have not yet been inventoried. As a consequence, all specimens originally studied by de Blainville are paralectotypes, and creation of a neotype as suggested by Doyle (1990) is not necessary. However, among all the specimens observed by de Blainville, there is a fair possibility that some may belong to the Toarcian-Aalenian species Mesoteuthis

rhenana (Oppel, 1856). Because of this, some authors (Riegraf et al. 1998 and Riegraf 2000) considered *Belemnites bisulcatus* de Blainville, 1827 as a species of *Mesoteuthis*, namely *Mesoteuthis bisulcata* (de Blainville, 1827). Further research within the d'Orbigny and Desnoyers collections should be conducted in order to find out whether *P. bisulcata* type material is monospecific or not.

Systematic palaeontology

The belemnite classification used herein follows Riegraf et al. (1998). The character terminology follows Doyle and Kelly (1988) and Combémorel (1988) and is summarized in Fig. 6. The belemnites were determined by one of us (MTS), while field study and ammonite biostratigraphy were carried out by the other authors. All studied specimens are housed in the UPMC (Université Pierre et Marie Curie, Paris, France).

All belemnites were collected during the year of 2011; more than the half of the specimens (58 %) were collected in outcrop 7. The whole collection is composed of 44 specimens, from nearly complete specimens to stem section fragments. External features such as lateral lines or apical furrows are often hardly visible. The poor preservation of 12 of the studied specimens does not allow their identification at either the generic or specific level.

Systematic descriptions

Phylum Mollusca Linnaeus, 1758
Class Cephalopoda Cuvier, 1797
Subclass Coleoidea Bather, 1888
Order Belemnitida MacGillivray, 1840
Suborder Belemnitina MacGillivray, 1840
Family Passaloteuthidae Naef, 1922
Genus *Passaloteuthis* Lissajous, 1915 (=Holcoteuthis Stolley, 1919)

Type species: *Belemnites bruguierianus* d'Orbigny, 1842 (junior subjective synonym of *Belemnites bisulcatus* Blainville, 1827) by original designation.

Passaloteuthis bisulcata (de Blainville, 1827) Figure 7a–e; Table 1

1827 Belemnites bisulcatus de Blainville, p. 79, pl. 2, fig. 7.

1990 *Passaloteuthis bisulcata* (de Blainville, 1827); Doyle, p. 19, pl.1, fig. 1–8; pl. 2, fig. 1–4; pl. 3, fig. 1–4 (*cum syn.*)

Type specimens. The lectotype is the original of de Blainville (1827, pl. 2, fig. 7) from the middle Lias ("Domérien" = Upper Pliensbachian) of Caen (Calvados,



Fig. 5 *Passaloteuthis bisulcata* (Blainville 1827). a-b Paralectotype (specimen MNHN B44621). c Original figuration of de Blainville (1827, pl. 2, fig. 7)

France) by automatic designation by Doyle (1990) (see above). All the other specimens studied by de Blainville are paralectotypes. Most of them are probably lost but at least one specimen exists within the collection of the Muséum National d'Histoire Naturelle (Paris, France) (MNHN B44621 Fig. 5a, b).

Material. One specimen (UPMC-175) from outcrop 7 (bed IV), one specimen (UPMC-185) from outcrop 12 (bed I), 2 specimens (UPMC-176-177) from outcrop 13 (both from bed 0) and 7 specimens (UPMC-178-184) from outcrop 14 (1 from bed Ia, one from bed IIa, 2 from bed IIIc, 1 from bed XIa and 2 from bed XIIa).

Description. Small to medium slender rostra, weakly subhastate to cylindriconical profile and outline. The transverse section is circular to subquadrate. The total length is seven to nine times Dv. There are no well-defined features on the rostrum. The apex is moderately acute. The

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phragmocone penetrates one-third to one quarter of the rostrum, and the apical line is goniolineate.

Remark. P. bisulcata could be confused with *Pseudohastites longiformis* (Blake, 1876), but it does not display welldefined lateral lines. It could also be confused with *P. milleri* (Phillips, 1867), which is more cylindrical, with a shorter and less conical apical area. Our specimens can be identified with *P. bisulcata* "var. C" (Werner, 1912), which is smaller than the other morphotypes. Some authors considered it as a distinct species, i.e., *Passaloteuthis laevigata* (Zieten, 1831).

Occurrence. Lowermost Toarcian belemnite *P. bisulcata* biozone (=ammonite Polymorphum Chronozone) of South Riffian ridges of Morocco. Upper Pliensbachian to lowermost Toarcian (Tenuicostatum Chronozone) of Britain and mainland Europe.

Genus Parapassaloteuthis Riegraf, 1980

Type species: *Belemnites zieteni* Mayer-Eymar, 1884 by original designation.

Parapassaloteuthis zieteni (Mayer-Eymar, 1884) Figure 7h-k; Table 1

1884 *Belemnites Zieteni* Mayer-Eymar; Mayer-Eymar, p. 47.

1990 *Parapassaloteuthis zieteni* (Mayer-Eymar, 1884); Doyle, p. 25, pl. 4, fig. 2, 3, 5, 7–9.

Type specimen. A neotype was appointed by Schlegelmilch (1998 pl.2, fig. 8) because the original specimen figured by Zieten (1830, pl. XXI, fig. 7) from the Upper Lias of Wurttemberg (Germany) seems to be lost.

Material. Three specimens (UPMC-170-172) from outcrop 7 (two from bed III and one from bed IV), one specimen (UPMC-173) from outcrop 14 (bed IIIc) and one specimen (UPMC-174) from outcrop 15 (bed I).

Description. Small cylindriconical to conical rostra. The outline is conical and symmetrical, and the profile is slightly ventrally inflated. The transverse section is subquadrate. The total length is usually around four times Dv. There is no ventral groove; the apex is acute and recurved in profile. The phragmocone penetrates one-third to one half of the rostrum, and the apical line is cyrtolineate.

Remark. Pr. zieteni could easily be confused with *Parapassaloteuthis* sp. A (possibly a new species, see below) because they both have a broadly similar shape. However, *Pr.* sp A is much bigger, and its apex is not recurved.

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Fig. 6 Descriptive morphology of belemnite hard parts. **a** Transversal section, **b** sagittal section, **c** coronal section, **d** transversal section morphology, **e** outline morphology, **f** apical morphology, **g** apical line morphology. *Al* alveolus, *Apl* apical line, *Ar* architheca (proostracum not shown), α alveolar angle, *C* conotheca, *Dl* lateral diameter at *l*, *Dv*

Occurrence. Lowermost Toarcian belemnite *P. bisulcata* biozone (=ammonite Polymorphum Chronozone) of the South Riffian ridges of Morocco. Upper Pliensbachian to lowermost Toarcian (Tenuicostatum Chronozone) of Britain and mainland Europe.

Parapassaloteuthis sp. A Figure 8a–i; Table 1

Material. Eleven specimens (UPMC-154-165) from outcrop 7 (six from bed II, four from bed III and one from bed IV), three specimens (UPMC-166-168) from outcrop 14 (two from bed IIIa and one from bed XIIa) and one specimen (UPMC-169) from outcrop 15 (bed I).

Description. Medium to large robust rostra. Both the outline and the profile are symmetrical and cylindriconical to conical, but some specimens may have a slightly inflated venter. The transverse section is circular to slightly subquadrate in smaller specimens. The total length is around four to five times Dv. There are no visible features such as grooves or a lateral line; the apex may be striated for some specimens. The apex is acute and tends to become slightly rounded in the larger specimens. The phragmocone penetrates one half of the rostrum, and the apical line is cyrtolineate.

Remarks. Despite the similar shape, *Pr.* sp. A cannot be confused with *Pr. zieteni* because of its much bigger size and unrecurved apex. *Pr. robusta* (Simpson, 1885) has a similar size, but a well-defined quadratic section. *Pr.* sp. A

could be confused with *Passaloteuthis bisulcata* (Blainville, 1827), but its phragmocone penetrates one half instead of one-third of the rostrum, and the apex does not display the distinctive two dorsoapical furrows of *P. bisulcata*. One specimen (UPMC-162, fig. 8H-I) displays several cusps on the rostrum, which are quite congruent in both form and depth, with bite marks, a consequence of shark or large fish attacks (Mazuch and Kostak 2005, fig. 8J). The preservation of the studied specimens is insufficient for describing a new species.

post-phragmocone height, En endotheca (=phragmocone), L rostrum

total length, l post-phragmocone length, Pc protochonque, R rostrum

(=amphitheca), Se septum, Si siphuncle. All size measurements are

expressed in mm and the angle in degrees

Genus *Pseudohastites* Naef, 1922 [=*Catateuthis* Nal'nyaeva, 1967 (in Saks and Nal'nyaeva 1967); *Passaloteuthis* (*Propassaloteuthis*) Riegraf, 1980].

Type species: *Belemnites scabrosus* Simpson, 1866; by original designation.

Pseudohastites longiformis (Blake, 1876) Figure 7f, g; Table 1

1876 *Belemnites longiformis* Blake (in Tate & Blake), p. 320, pl. IV, fig. 8.

1990 Pseudohastites longiformis (Blake, 1876); Doyle, p. 24, pl. 3, fig. 5–9 (cum syn.)

Holotype. BMNHCI 1877 from the Natural History Museum, London, "*spinatus*" beds (*spinatum* zone), Domerian, Eston, Cleveland (England)

Material. One single specimen (UPMC-186) from bed VI of outcrop 14.



Fig. 7 Belemnite species of the genera *Passaloteuthis, Parapassaloteuthis* and *Pseudohastites.* **a–e** *Passaloteuthis bisulcata* (de Blainville 1827) mor. C, **a–b** lateral and ventral views of specimen UPMC-177 from Polymorphum Chronozone, outcrop 13, bed 0; **c–e** backlit lateral, lateral and ventral views of specimen UPMC-180 from Polymorphum Chronozone, outcrop 13, bed XIa. **f–g** *Pseudohastites*

Description. Small to medium slender rostra, weakly subhastate profile and outline. The transverse section is compressed and subquadrate. The total length is usually around nine times Dv, but some specimens are shorter and more robust than the norm. Lateral lines are well developed, forming two depressions separated by a ridge. The apex is acute. The phragmocone penetrates one-third to one quarter of the rostrum, and the apical line is ortholineate.

longiformis (Blake, 1876), lateral and ventral views, Polymorphum Chronozone, outcrop 14, bed VIa (UPMC-186). **h–k** *Parapassaloteuthis zieteni* (Mayer-Eymar, 1884), **h–i** lateral and ventral views of specimen UPMC-173, Polymorphum Chronozone, outcrop 114, bed IIIc; **j–k** lateral and ventral views of specimen UPMC-170, Polymorphum Chronozone, outcrop 7, bed III

Remarks. The studied specimen corresponds to what Doyle (1990) called a robust morph; therefore, the *l*/Dv ratio is closer to 8 than 9 (see Table 1).

Occurrence. Lowermost Toarcian belemnite *P. bisulcata* biozone (=ammonite Polymorphum Chronozone) of the South Riffian ridges of Morocco. Upper Pliensbachian to lowermost Toarcian (Tenuicostatum Chronozone) of Britain and mainland Europe.

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Table 1	Measurements	of the	studied	belemnite	specimens
					· · · · · · · · ·

Species	UPMC collection numbers	Outcrop	Bed number	L	l	Dl	Dv	Dv/Dl	<i>L</i> /Dv	а
Parapassaloteuthis sp. A	UPMC-154	7	II	_	51.71	17.07	17.94	1.050966608	_	_
Parapassaloteuthis sp. A	UPMC-155	7	II	64.71	36.39	16.44	17.8	1.082725061	3.936131387	23°
Parapassaloteuthis sp. A	UPMC-156	7	II	82.15	35.79	16.03	16.34	1.01933874	5.02753978	23°
Parapassaloteuthis sp. A	UPMC-157	7	II	68.85	46.56	15.02	15.05	1.001997337	4.583888149	26°
Parapassaloteuthis sp. A	UPMC-158	7	II	_	50.43	14.12	13.62	0.964589235	_	_
Parapassaloteuthis sp. A	UPMC-159	7	Π	91.83	44.48	16.12	16.31	1.0117866	5.630288167	26°
Parapassaloteuthis sp. A	UPMC-160	7	Π	_	_	_	_	_	_	_
Parapassaloteuthis sp. A	UPMC-161	7	III	71.76	46.75	17.44	17.85	1.023509174	4.020168067	26°
Parapassaloteuthis sp. A	UPMC-162	7	III	56.66	42.21	12.97	14	1.079414032	4.368542791	_
Parapassaloteuthis sp. A	UPMC-163	7	III	_	52.02	12.92	13.67	1.058049536	_	_
Parapassaloteuthis sp. A	UPMC-164	7	III	_	34.38	12.12	10.96	0.904290429	_	_
Parapassaloteuthis sp. A	UPMC-165	7	IV	_	31.91	10.5	10.09	0.960952381	_	_
Parapassaloteuthis sp. A	UPMC-166	14	IIIa	69.94	39.57	13.64	14.32	1.049853372	4.884078212	25°
Parapassaloteuthis sp. A	UPMC-167	14	IIIa	56.93	33.27	12.71	13.71	1.078678206	4.152443472	26°
Parapassaloteuthis sp. A	UPMC-168	14	XIIa	_	39.13	12.7	13.98	1.100787402	_	_
Parapassaloteuthis sp. A	UPMC-169	15	Ι	64.08	48.46	15.53	16.31	1.05022537	3.928877989	30°
Parapassaloteuthis zieteni	UPMC-170	7	III	_	_	_	_	_	_	_
Parapassaloteuthis zieteni	UPMC-171	7	III	_	_	_	_	_	_	_
Parapassaloteuthis zieteni	UPMC-172	7	IV	28.14	15.81	6.39	5.99	0.937402191	4.403755869	24°
Parapassaloteuthis zieteni	UPMC-173	14	IIIc	_	_	_	_	_	_	_
Parapassaloteuthis zieteni	UPMC-174	15	Ι	_	28.51	9.04	9.72	1.075221239	_	_
Passaloteuthis bisulcata mor. C	UPMC-175	7	IV	_	19.5	6.08	4.97	0.817434211	_	_
Passaloteuthis bisuclcata mor. C	UPMC-176	13	0	41.2	27.24	6.06	5.45	0.899339934	6.798679868	30°
Passaloteuthis bisuclcata mor. C	UPMC-177	13	0	38.52	27.89	9.46	8.56	0.904862579	4.5	16°
Passaloteuthis bisuclcata mor. C	UPMC-178	14	Ia	41.9	30.88	12.02	11.17	0.929284526	3.485856905	25°
Passaloteuthis bisuclcata mor. C	UPMC-179	14	IIa	_	_	_	_	_	_	_
Passaloteuthis bisuclcata mor. C	UPMC-180	14	XIa	38.08	28.93	8.21	7	0.852618758	5.44	29°
Passaloteuthis bisuclcata mor. C	UPMC-181	14	XIIa	_	23.72	7.85	6.77	0.862420382	_	_
Passaloteuthis bisuclcata mor. C	UPMC-182	14	XIIa	_	23.09	6.22	5.71	0.918006431	_	_
Passaloteuthis bisuclcata mor. C	UPMC-183	14	IIIc	_	20.89	5.66	5.04	0.890459364	_	_
Passaloteuthis bisuclcata mor. C	UPMC-184	14	IIIc	_	_	_	_	_	_	_
Passaloteuthis bisuclcata mor. C	UPMC-185	12	Ι	_	_	_	_	_	_	_
Pseudohastites longiformis	UPMC-186	14	VIa	28.2	19.51	3.68	4.02	1.092391304	7.663043478	_
Passaloteuthidae gen. sp. ind.	UPMC-187	7	Ι	40.17	30.23	12.2	13.08	1.072131148	3.292622951	23°
Passaloteuthidae gen. sp. ind.	UPMC-188	7	Ι	27.34	17.97	8.66	7.63	0.881062356	3.15704388	_
Passaloteuthidae gen. sp. ind.	UPMC-189	7	III				7.34			22°
Passaloteuthidae gen. sp. ind.	UPMC-190	7	III	_	_	8.22	7.16	0.871046229	_	
Passaloteuthidae gen. sp. ind.	UPMC-191	7	III	-	-				_	_
Passaloteuthidae gen. sp. ind.	UPMC-192	7	III	_	_	_ 9.04	_ 8.65		_	_
Passaloteuthidae gen. sp. ind.	UPMC-193	7	III			_	_	_		
Passaloteuthidae gen. sp. ind.	UPMC-194	7	IV	_ 43.54	25.18	9.93	10.3	1.037260826	4.38469285	25°
Passaloteuthidae gen. sp. ind.	UPMC-195	13	Π	_	_	_	_	_	_	_
Passaloteuthidae gen. sp. ind.	UPMC-196	14	IIIa	24.52	16.96	5.14	4.57	- 0.889105058	4.770428016	
Passaloteuthidae gen. sp. ind.	UPMC-197	14	VIa	38.74	19.54	7.54	6.39	0.847480106	5.137931034	20°
Passaloteuthidae gen. sp. ind.	UPMC-198	14	XIIa	_	_	7.83	6.91	0.882503193	_	21°

The values in italics correspond to estimated values. Parameters are illustrated in Fig. $\boldsymbol{6}$



Fig. 8 a–j: *Parapassaloteuthis* sp. A, a–c sagittal section, lateral and ventral views of specimen UPMC-166 from Polymorphum Chronozone, outcrop 14, bed IIIa; d–e lateral and ventral views of specimen UPMC-157, from Polymorphum Chronozone, outcrop 7, bed II; f–g lateral and ventral views of specimen UPMC-159, from

Biogeography

According to Doyle and Bennett (1995), most records of Early Jurassic "belemnites" actually correspond to aulacocerids of the family Xiphoteuthididae, and Early Jurassic, pre-Toarcian, true belemnites were restricted to Europe. However, Iba et al. (2012) have recently questioned this scenario on the basis of specimens from the Hettangian of Japan, which have been assigned to the family Sinobelemnitidae and to Belemnitina. Iba et al. (2012) support the idea of a Triassic origin of true belemnites because Sinobelemnitidae are known from the Late Triassic of China. In any case, Doyle (1987) noted that in the early Jurassic it is difficult to recognize well-defined biogeographical Polymorphum Chronozone, outcrop 7, bed II; **h–i** lateral and ventral views of specimen UPMC-162, from Polymorphum Chronozone, outcrop 7, bed III, showing marks that are compared with **j**, *i.e.*, experimental plasticine cast of a rostrum showing shark-bite marks (Mazuch and Kostak 2005)

provinces because of the sparsity of belemnite data. Doyle (1987) and Doyle and Bennett (1995) stressed that while Arctic endemic taxa can be recognized, there is no evidence for regional differentiation indicating a distinct Tethyan belemnite fauna within Europe before the Toarcian. At the generic level, the Early Toarcian belemnites of Moulay Idriss were widespread in the Boreal Hemisphere during the Early Jurassic (Doyle 1987; Doyle and Mariotti 1991). The genus *Passaloteuthis* is known from the early Pliensbachian to Toarcian in Britain, mainland Europe, the former USSR, Turkey (Western Pontides), the Spitzbergen, East Greenland and North America. The genus *Parapassaloteuthis* is recorded in Britain, mainland Europe, the former USSR and East Greenland from the late Pliensbachian to early Jurassic.

Finally, the genus *Pseudohastites* has been reported in Britain, mainland Europe, the former USSR and Turkey (Western Pontides) from early the Pliensbachian to earliest Toarcian. These genera are not recorded among the belemnites mentioned by Coquand (1862) from Algeria, which need an accurate systematic study. The three recognized species, *Passaloteuthis bisulcata*, *Pseudohastites longiformis* and *Parapassaloteuthis zieteni*, are reported from Britain and mainland Europe. *P. milleri* and *Pr. zieteni* occur in Slovakia (Cincurova 1967, 1971), in areas that were located on the northern margin of Tethys (Dercourt et al. 2000), and also from northern Russia (Saks and Nal'nyaeva 1967, 1970, 1975).

Despite the intervening epioceanic Tethyan palaeoenvironments, the distribution of the identified species would suggest close relationships between the South Riffian basin of Northern Morocco and European seas. This also would suggest that the onset of the belemnite provincialism in the Toarcian post dates the *Passaloteuthis bisulcata* biozone or, in terms of ammonite biostratigraphy, the earliest Toarcian Polymorphum—the Tenuicostatum Chronozone.

The fauna of the Moulay Idriss area cannot be compared with the Early Jurassic belemnites mentioned by Coquand (1862) from the Constantine region (Algeria), which was also located on the southern margin of the Tethys (Dercourt et al. 2000). Coquand (1862) briefly mentioned unidentified belemnite species and a form that probably corresponds to the genus *Nannobelus* (Doyle, 1987). The fauna from the Constantine region deserves further sampling and a systematic study.

Conclusions

As already stressed by Doyle (1987), Early Jurassic belemnite records are too sparse. The present study offers, for the first time, a palaeontological study of Early Jurassic belemnites from northern Africa, i.e., the northeastern margin of the Gondwana, in connection with Tethys. The taxa (with the exception of Parapassaloteuthis sp. A) identified in the South Riffian basin of Northern Morocco correspond to genera and species already described in the literature. They make up part of the belemnite assemblage that characterizes the Passaloteuthis bisulcata biozone, which correlates with the ammonite polymorphum zone (equivalent of the ammonite Tenuicostatum Chronozone). Common species within Europe would suggest that the provincial differentiation of belemnite faunas took place after the earliest Toarcian. However, compared to ammonoids and other invertebrate fossil groups, belemnites have been poorly studied and probably not sampled intensively enough to reliably recognize the establishment of provincialism and the timing of its onset.

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References

- Bassoullet, J.P., G. Lachkar, F. Baudin, K. Benshili, P. Blanc, M. Boutakiout, F. Depèche, S. Elmi, and C. Ruget. 1991. Stratigraphie intégrée dans le Toarcien du Maroc (Rides sud-rifaines et Moyen Atlas). Bulletin de la société géologique de France 162: 825–839.
- Bather, F.A. 1888. Shell-growth in Cephalopoda (Siphonopoda). Annals and Magazine of Natural History (Series 6) 1: 298–310.
- Blainville, M.H.D. de. 1827. Mémoire sur les Bélemnites considérées zoologiquement et géologiquement, Paris, 136.
- Chenakeb, M., and H. Ben Dkik. 2004. Carte géologique 428 au 1/50000 de Beni Ammar. Notes et Mémoires du service géologique du Maroc.
- Cincurova, E. 1967. Zur Kenntnis der Belemniten der Slowakei. Sbornik Slovenskeho Ndrodneho Muzea. Pfirodne Vedy. Bratislava 13: 3–10.
- Cincurova, E. 1971. Stratigrafia liasu na zaklade belemnitov v Zapnadynch Karpatoch. *Sbornik Slovenskeho Ndrodneho Muzea*. Pfirodne Vedy. *Bratislava* 17: 3–102.
- Combémorel, R. 1988. Les bélemnites de Madagascar. Documents des laboratoires de géologie Lyon 104: 1–239.
- Combémorel, R. 1997. Bélemnites. In: Cariou E. and P. Hantzpergue, eds. Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations paralléles et distribution des invertébrés et microfossiles. Bulletin du Centre Recherche Elf, Exploration et Production, (Mémoires) 17: 157–167.
- Coquand, H. 1862. Géologie et Paléontologie de la région sud de la province de Constantine. Mémoires de la société d'émulation de la provence 2: 5–366.
- Cuvier, G. 1797. Tableau élémentaire de l'histoire naturelle des animaux. Baudouin, Paris, 1–710.
- Dercourt, J., M. Gaetani, B. Vrielynck, E. Barrier, B. Biju-Duval, M.F. Brunet, J.P. Cadet, S. Crasquin and M. Sandulescu. 2000. *Atlas Peri-Tethys, palaeogeographical maps*. Comité de la Carte Géologique du Monde/Committe of the Geological Map of the World, Paris, 24 maps and explanatory notes: I–XX, 1–269.
- Doyle, P. 1987. Lower Jurassic Lower Cretaceous belemnite biogeography and the development of the Mesozoic Boreal Realm. *Palaeogeography, Palaeoclimatology, Palaeoecology* 61: 237–254.
- Doyle, P. 1990. *The British Toarcian (Lower Jurassic) Belemnites*. London: Monograph of the Palaeontographical society, 1–49.
- Doyle, P., and S.R.A. Kelly. 1988. The Jurassic and Cretaceous belemnites of Kong Karls Land, Svalbard. Norsk Polarinstitutt. Skrifter 189: 1–76.
- Doyle, P., and N. Mariotti. 1991. Jurassic and Lower Cretaceous Belemnites from North-Western Anatolia (Turkey). *Geologica Romana* 27: 347–379.
- Doyle, P., and M.R. Bennett. 1995. Belemnites in Biostratigraphy. *Palaeontology* 38: 815–829.
- Elmi, S., and J.C. Faugères. 1974. Chronographie et interprétation séquentielle de la série Lias-Dogger du flanc NW du Dehar-en-Nsour (Rides prérifaines, Maroc septentrional). Notes du service géologique du Maroc 264: 69–79.
- Faugères, J.C. 1975. Le Toarcien du Jbel Dehar en N'sour (rides prérifaines, Maroc): précisions biostratigraphiques et remarques paléontologiques sur les ammonites (genre *Bouleiceras*,

Hildaites) de la zone à Serpentinus. Bulletin de la société géologique de France 17: 117–122.

- Iba, Y., S. Sano, J. Mutterlose, and Y. Kondo. 2012. Belemnites originated in the Triassic—a new look at an old group. *Geology* 40: 911–914.
- ICZN 1999. International Code of Zoological Nomenclature (Fourth edition). The Natural History Museum. Cromwell Road, London. 1–306.
- Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed 10, tome 1, Laurentii Salvii, Stockholm, Sweden 1–824.
- Lissajous, M. 1915. *Quelques remarques sur les bélemnites Jurassiques*. Macon: Bulletin de la Société d'Histoire Naturelle de Macon. 32.
- MacGillivray, W. 1840. A manual of geology. London: Scott Webster and Geary. 239.
- Mayer-Eymar, K. 1884. Grundzüge der Klassification der Belemniten. Zeitschrift der Deutschen Geologischen Gesellschaft 35: 640–643.
- Mazuch, M. and M. Kostak. 2005. Rare evidences of shark predation in Upper Cretaceous belemnites. 2nd International Symposium -Coleoid Cephalopods Through Time - Prague 2005, short papers/Abstract volume, 92–93.
- Naef, A. 1922. Die fossilen Tintenfische: eine palaozoologische Monographic. Jena, 1–322.
- Orbigny, A. d' 1840–1842. Paléontologie française. Terrains crétacés. I. Céphalopodes. Paris. 1–120, (1840); 121–430, (1841); 431–662, (1842).
- Page, K.N. 2003. The lower Jurassic of Europe: Its subdivision and correlation. *Geological Survey of Denmark and Greenland Bulletin* 1: 23–59.
- Phillips, J. 1865-1909. A monograph of British Jurassic Belemnitidae. Monograph of the Palaeontographical Society, London: (1) 1865, 1–28; (2) 1866, 29–52, pis 1–7; (3) 1867, 53–88, pis 8–20; (4) 1869, 89–108, pis 21–7; (5) 1870, 109–28, pis 28–36; (6) 1909, title page and index.

- Riegraf, W. 1980. Revision der Belemniten des Schwäbischen Jura, Teil 7. Palaeontographica, A 169: 128–206.
- Riegraf, W., N. Janssen, and C. Schmitt-Riegraf. 1998. Cephalopoda dibranchiata fossiles (Coleoidea) II. In Westphal F. ed., *Fossilium Catalogus Animalia*. Leiden: Backhuys Publishers 135: 1–519.
- Riegraf, W. 2000. The belemnites described by Baron Ernst Friedrich Von Schlotheim(1764–1832). Paläontologische Zeitschrift 281–303.
- Saks, V.N., and T.I. Nal'Nyaeva. 1967. Contribution to the systematics of Jurassic and Cretaceous belemnites. 6-26. In *Problems of paleontologic substantiation of detailed Mesozoic stratigraphy* of Siberia and the Far East USSR, ed. Saks V.N. Leningrad [In Russian].
- Saks, V.N., and T.I. Nal'Nyaeva. 1970. Early and Mid Jurassic Belemnites of northern U.S.S.R. Nannobelinae, Passaloteuthinae and Hastitidae. *Trudy Instituta geologii i geofiziki Sibirskogo* otdeleniâ Akademii Nauk SSSR 110: 1–228. [In Russian].
- Saks, V.N., and T.I. Nal'Nyaeva. 1975. The Early and Middle Jurassic Belemnites of northern U.S.S.R. Megateuthinae and Pseudodicoelitinae. *Nauka*, Leningrad, 1–191 [In Russian].
- Schlegelmilch, R. 1998. Die Belemniten des süddeutschen Jura : ein Bestimmungsbuch für Geowissenschafter und Sammler Stuttgart/ Jena. 1–151.
- Simpson, M. 1866. Inferior Oolite-Lias Belemnites of the Yorkshire Coast. Geological and Natural History Repertory and Journal of Prehistoric Archaeology and Ethnology 215: 216.
- Simpson, M. 1885. The fossils of the Yorkshire Lias (First edition). London. 1–256.
- Stolley, E. 1919. Die Systematik der Belemniten. Jahresbericht des Niedersdchsischen Geologischen Vereins 11: 1–59.
- Tate, R., and J.F. Blake. 1876. The Yorkshire Lias. London. 1-475.
- Werner, E. 1912. Über die Belemniten des Schwäbischen Lias und die mit ihnen verwandten Formen des Braunenjura (Acoeli). Palaeontographica 59: 103–146.
- Zieten, K.H. von 1830–33. Die Versteinerungen Wurttembergs. Stuttgart. 1–102.