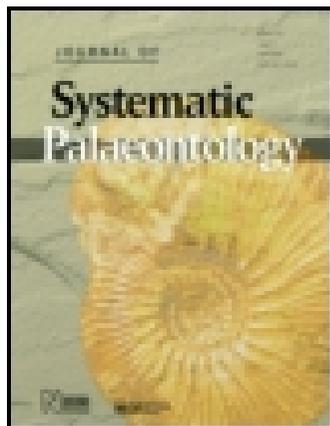


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Lower Toarcian (Jurassic) ammonites of the South Riffian ridges (Morocco): systematics and biostratigraphy

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A rich ammonite fauna from the Lower Toarcian (Lower Jurassic) of the South Riffian ridges (northern Morocco), collected bed-by-bed from 14 new outcrops, is described. The fauna is nearly exclusively composed of already-known taxa, allowing correlation from the chronozone down to the zonule level. Fourteen species are described, among them the new species *Dactylioceras (Dactylioceras) laticostatum* sp. nov. The stratigraphical interval studied spans the first chronozone of the Toarcian, the Polymorphum Chronozone, but it remains unclear whether the Toarcian Oceanic Anoxic Event is represented in the studied succession. The Early Toarcian is mainly characterized by representatives of the family Dactylioceratidae, which are abundant but commonly crushed or deformed. Two new descriptors are proposed to describe the shell shape of crushed or incomplete specimens and have been used together with the classical ones for the taxonomic treatment of this group. A hypothesis about dimorphism in *Dactylioceras (Orthodactylites) semicelatum* (Simpson, 1843) and *Dactylioceras (Dactylioceras) laticostatum* sp. nov. is proposed.

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Keywords: Jurassic; Toarcian; systematics; biostratigraphy; ammonites; dimorphism

Introduction

The Early Toarcian is characterized by a minor extinction event envisaged to have been caused by the spread of anoxia (Hallam 1987; Aberhan & Fürsich 1997, 2000; Harries & Little 1999; Fürsich *et al.* 2001; Wignall *et al.* 2005), which is inferred from the widespread development of anoxic facies (Jenkyns 1988) characterizing an oceanic anoxic event (OAE). To assess the extent of the extinction in ammonites, some authors have taken into account palaeogeographical domains (Macchioni & Cecca 2002; Cecca & Macchioni 2004; Dera *et al.* 2011) because palaeobiogeographical parameters are essential for understanding palaeobiodiversity dynamics (Jablonski 2008). The palaeobiography of the NW Tethyan Realm during the Early Toarcian is a complex mosaic of emerged landmasses and epicontinental seas (Dercourt *et al.* 2000). In addition to this spatial dimension, refined taxonomic and stratigraphical data are required to perform studies on palaeobiodiversity changes. Despite the rich literature on Pliensbachian and Toarcian ammonites, problems with taxonomy and correlations between different palaeogeographical domains remain unresolved.

The present paper deals with the ammonite fauna, which has been collected bed-by-bed, in natural outcrops

of the South Riffian ridges (Fig. 1). The fauna is significant because it spans the range of the ammonite Polymorphum (= Tenuicostatum) Chronozone in whose upper part, the Semicelatum Subchronozone, the Early Toarcian extinction event has been recognized (Hallam 1987; Macchioni & Cecca 2002). Furthermore, a detailed palaeontological study of this fauna, the dactylioceratids in particular, from the South Riffian ridges was needed.

Geological and stratigraphical setting

The Jurassic succession of the South Riffian ridges has been described by Faugères (1974, 1975), Elmi & Faugères (1974) and Bassoullet *et al.* (1991). It was formed on the northern shelf of the Northern African margin (Dercourt *et al.* 2000). The best exposures of the Jurassic crop out around the town Moulay Idriss, which is located some 30 km north of Meknès (Fig. 1), in the Dehar-en-Nsour mountain. This is a massive anticline with a Pliensbachian core. The youngest Jurassic rocks are dated to the Upper Bajocian, when the whole domain emerged. After a brief Cretaceous (Late Albian) marine episode, the basin was once more invaded by the sea in the Early Miocene–Early Pliocene. This produced the thick Neogene cover, which rests on Jurassic beds with an angular unconformity (Faugères 1975).

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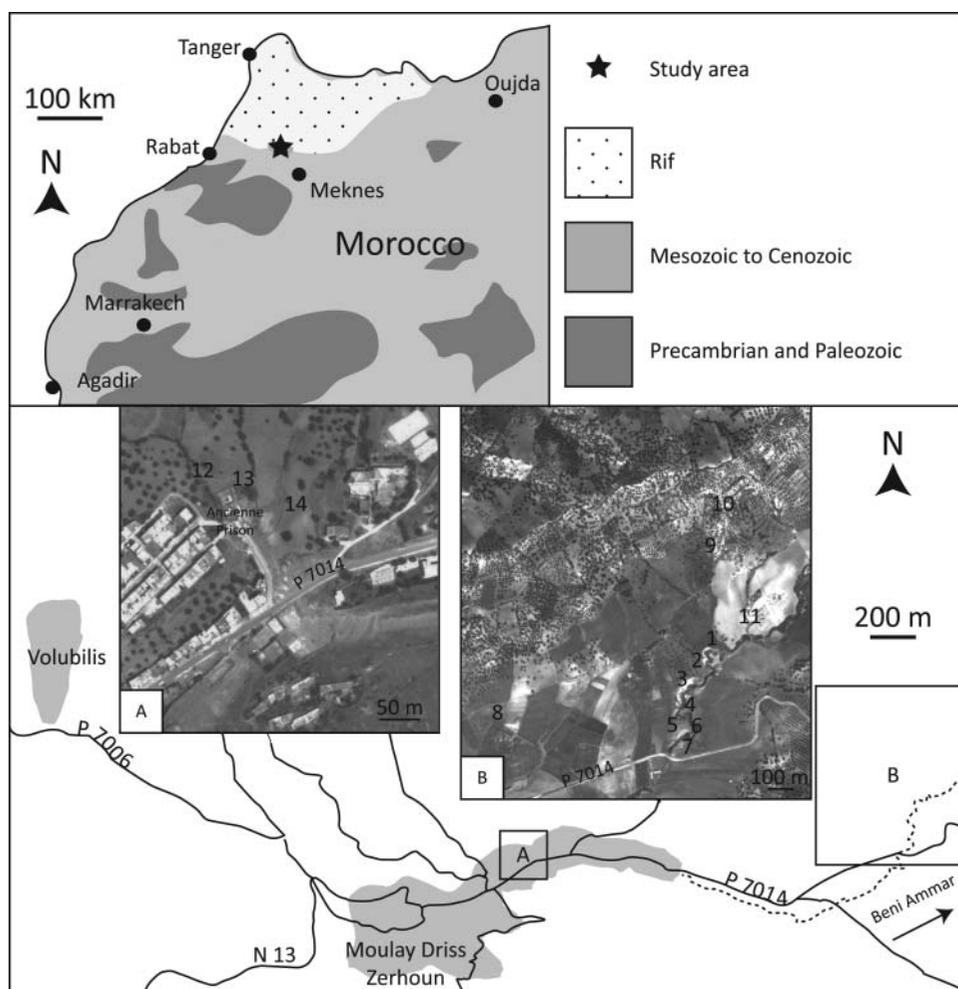


Figure 1. Location of the study area in northern Morocco and of the studied outcrops, 1 to 14. **A, B**, position of corresponding aerial photographs on the map.

According to Elmi & Faugères (1974), the Pliensbachian–Toarcian boundary is marked by a change in ammonite faunas: *Pleuroceras* Hyatt, 1867, *Tauromeniceras* Mouterde, 1967, and *Lioceratoides* Spath, 1919 characterize the Late Pliensbachian, whereas *Dactylioceras* (*Eodactylites*) Schmidt-Effing, 1972 marks the beginning of the Toarcian. This change is paralleled by a lithological transition between Upper Pliensbachian sandy calcareous beds and lowermost Toarcian blue-grey marls. The latter forms a monotonous succession, almost 150 m thick, with thin calcareous beds up to a massive, 5 m-thick calcareous bed containing Middle Toarcian faunas. Faugères (1975) described four outcrops spanning the entire Lower Toarcian and recognized both the *Tenuicostatum* and *Serpentinum* chronozones. He also figured some Early Toarcian ammonites, younger than the ones studied in the present paper, namely several specimens of representative taxa of the *Serpentinum* Chronozone (e.g. *Bouleiceras* Thévenin, 1906 and *Hildaïtes* Hyatt, 1867). Faugères' stratigraphical

columns suggest that our studied outcrops would span all or nearly all the *Tenuicostatum* Chronozone.

According to the palaeobiogeographical provinces defined by Page (2003), in this paper we use some biostratigraphical units defined on faunas corresponding to the Subboreal and Submediterranean provinces, whereas our outcrops would belong to the Mediterranean province. The first biozonation for the Pliensbachian–Toarcian transition and for the Early Toarcian was based on faunas from England that belong to the Subboreal province. Stratigraphical correlations between faunas of these provinces have yet to be resolved (Macchioni 2002) and we use a synthesis (Table 1) proposed by Page (2003) for our discussion.

Location of the outcrops

We have logged 14 outcrops (Fig. 1; see Supplemental Appendix 1 for GPS coordinates). Four of the outcrops

Table 1. Stratigraphical correlations between zonations established in Subboreal, Submediterranean and Mediterranean provinces, modified from Page (2003).

Stage	Subboreal Province			Submediterranean Province			Mediterranean Province			
	Chronozone	Subchronozone	Biohorizon	Chronozone	Subchronozone	Zonule	Chronozone	Subchronozone	Zonule	
Toarcian	Bifrons	Commune	<i>ovatum</i>	Bifrons	Sublevisoni	Sublevisoni	Bifrons	Sublevisoni	Sublevisoni	
			<i>falciferum</i>			Douvilliei				Falciferum?
	Serpentinum	Exaratum	<i>pseudoserpentinum</i>	Serpentinum	Falciferum	Pseudoserpentinum	Elegantulum	Levisoni	Levisoni	Sublevisoni
			<i>elegans</i>			Strangewayysi				
			<i>exaratum</i>			Elegantulum				
	Tenuicostatatum	Paltum	Semicelatatum (I)	<i>elegantulum</i>	Tenuicostatatum	Semicelatatum (II)	Semicelatatum	Polymorphum	Semicelatatum (II)	Striatus
				<i>antiquum</i>			Tenuicostatatum			
				<i>semicelatatum</i>			Crosbeyi			
				<i>tenuicostatatum</i>			Paltum			
				<i>clevelandicum</i>						
Pliensbachian	Spinatum	Hawskerense	<i>crosbeyi</i>	Spinatum	Paltum	Hawskerense	Emaciatum	Elisa	Elisa	
			<i>paltum</i>							Hawskerense

were described by Faugères (1975). His second and third outcrops could correspond to our outcrops 1 to 7 (Fig. 1). Outcrop 7 is located approximately 3 km east of Moulay Idriss, close to the road P7014 just beside a small bridge, at an altitude of 617 m. Outcrops 8–11 are located a few hundred metres north and west of outcrops 1 to 7. Finally, outcrops 12–14 are located behind the ‘ancienne prison’ (the old jail) around 0.5 km outside the eastern part of Moulay Idriss. Bassoulet *et al.* (1991) studied an outcrop near Moulay Idriss which, according to one of the co-authors of this study (F. Baudin, pers. comm.), is located very close to the village. The stratigraphical succession described by Bassoulet *et al.* (1991) suggests that it could correspond to our outcrop 14.

Lithostratigraphy

The entire Lower Toarcian stratigraphical succession consists of marls with scattered limestone beds (Fig. 2). Lateral continuity is reduced because their thickness can change from one section to another. Based on lithostratigraphical and faunal arguments, we conclude that all other studied sections correspond to portions of the succession exposed in outcrop 14, which is the thickest (65 m). Therefore, only this section is described in detail. Correlations between the different outcrops are given in Figure 2. To facilitate the reading of the following text, we refer to our beds by quoting two numbers, the first (Arabic numeral) corresponds to one of the studied outcrops and the second (Roman numeral) to the bed (e.g. 14-II means outcrop 14, bed 2).

We have distinguished three lithological units in outcrop 14:

Unit A (from bed Ia to IIIc). This unit corresponds to the lowest part of the succession studied and is visible in outcrop 14 only. It consists of an almost 20-m thick succession of alternating marls and limestones resting on top of Pliensbachian limestones. The unit is characterized by grey, bluish marls. Fossils have been found only in the marly limestone beds at the top of the unit. Beds Ia and IIa are 0.5 m thick, whereas beds IIIa and IIIc are 0.15 m thick. The succession is covered for almost four metres above bed IIIc.

Unit B. This is represented by four metres of reddish to brown marls overlain by eight metres of grey-blue marls.

Unit C (from bed IVa to bed Xa). This is the most calcareous unit of the entire succession. The vertical lithological transitions between marls and limestones are gradual and not clear cut. Some beds (e.g. 14-Va) contain a high detrital fraction with sandstone and wood debris. The alteration turns the limestone colour from yellow to red. In the upper part of the unit, calcareous nodules rest above the more marly part of some beds (i.e. 7-IIIa, 7-IVa, 7-Va,

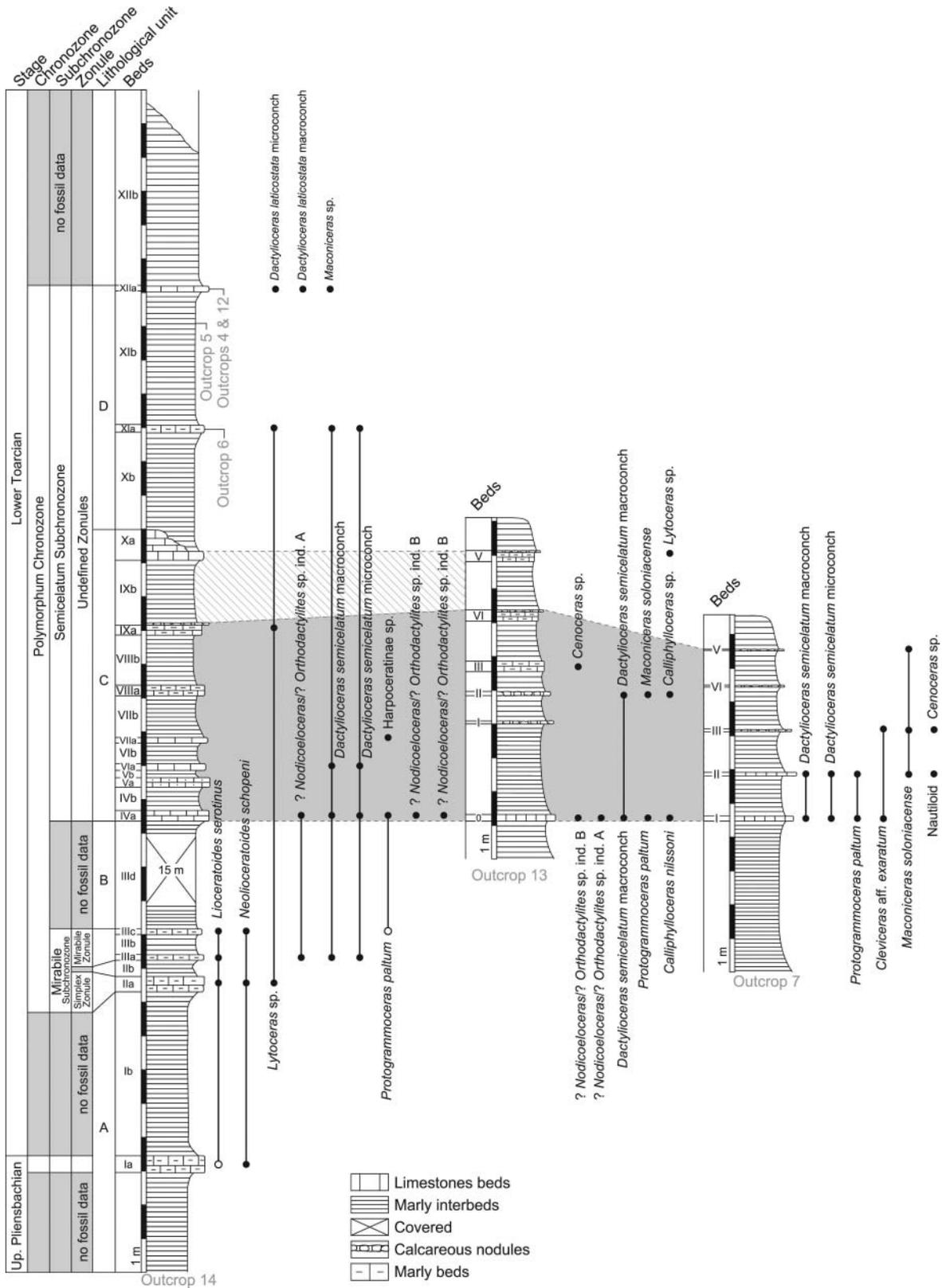


Figure 2. Lithological sections at outcrops 7 (right), 13 (middle) and 14 (left) with the stratigraphical distributions of the identified ammonite species. Outcrops 4, 5, 6 and 12 are single, fossiliferous limestone beds correlated to the beds of outcrop 14. Open circles correspond to uncertain identification. Grey area indicates lithostratigraphical correlation.

13-IVa, 13-Va, 14-IXa). This unit is also exposed in outcrops 7 and 13. Outcrops 7, 13 and 14 differ in thickness and number of limestone beds. This is consistent with observed variations in lateral thickness within an outcrop (e.g. bed 7-IIIa disappears laterally; bed 14-Xa shows a wide thickness variation).

Unit D (from bed XIa to bed XIIa). This ensemble is composed of two limestone beds (14-XIa and 14-XIIa) separated by four metres of marls. Because of the identical faunal contents, outcrop 6 has been correlated with bed 14-XIa, and outcrops 4, 5, and 12 with bed 14-XIIa. Above these beds is the transition between grey marls and yellow to brown marls that do not contain limestone beds. According to Faugères (1975), the next limestone beds occur higher, in the Lower Toarcian succession, and are dated to the Levisoni Chronozone (= Serpentinum Chronozone).

Faunal lists

Almost all limestone beds are fossiliferous. Faunas mostly consist of cephalopods (ammonites, belemnites and nautili) but benthic organisms (bivalves, gastropods) can be relatively common in some beds. Wood debris occurs in particular beds. Shells are well preserved, albeit calcified by epigenesis. Marls occurring 10 cm above or below a limestone bed can also contain fossils with the same preservation. Otherwise, fossils found in the marly interbeds generally are mostly unidentifiable pyritized ammonite nuclei. Belemnites collected in the studied outcrops have been described in a separate paper (Sanders *et al.* 2013). The assignment of the faunas to biostratigraphical units is indicated in the following faunal lists. This is thoroughly discussed in the Biostratigraphy section.

Acronyms. The numbers in brackets indicate the number of specimens. Letters M and m after the species name mean macroconch and microconch morphs, respectively.

UPMC: Université Pierre et Marie Curie, Paris, France.

Outcrop 4

Semicelatum Subchronozone.

Bed Ia. Ammonites: *Dactylioceras laticostatum* sp. nov. M (five specimens), *Dactylioceras* sp. (3), *Microdactylites* sp. (2), *Maconiceras* sp. (1). Bivalves: *Chlamys* sp. (1), *Plicatula* sp. (1).

Outcrop 5

Semicelatum Subchronozone.

Bed Ia. Ammonites: *Dactylioceras laticostatum* sp. nov. M (1) and m (2), *Dactylioceras* sp. (7).

Outcrop 6

Semicelatum Subchronozone.

Bed Ia. Ammonites: *Juraphyllites* (*Harpophylloceras*) *eximius* (Hauer, 1854) (1), *Lytoceras* sp. (1),

Dactylioceras (*O.*) *semicelatum* M (5), *Dactylioceras* (*O.*) *semicelatum* m (23), *Dactylioceras* sp. (18), *Maconiceras soloniacense* (Lissajous, 1906) (1), unidentified Harpoceratinae (6). Bivalves: *Chlamys* sp. (1).

Outcrop 7

Semicelatum Subchronozone.

Four metres below bed Ia. Wood debris.

Bed Ia. Ammonites: *Dactylioceras* (*O.*) *semicelatum* M (51), *Dactylioceras* (*O.*) *semicelatum* m (17), *Dactylioceras* sp. (31), *Protogrammoceras paltum* (Buckman, 1922) (1), *Cleviceras* aff. *exaratum* (Young & Bird, 1828) (1), unidentified Harpoceratinae (5), unidentified nuclei (7). *Passaloteuthidae* gen. sp. indet. (2). Bivalves: *Agerchlamys* sp. (1), *Chlamys* sp. (1). Gastropods: ‘*Amberleya*’ sp. (1).

Bed IIa. Nautiloid (1). Ammonites: *Dactylioceras* (*O.*) *semicelatum* M (10), *Dactylioceras* (*O.*) *semicelatum* m (4), *Dactylioceras* sp. (8), *Protogrammoceras paltum* (1), *Maconiceras soloniacense* (1), unidentified Harpoceratinae (6), unidentified nuclei (3). *Parapassaloteuthis* sp. A (7). Gastropods: *Pseudomelania* (*Oonia*) sp. (1). Wood debris.

Between beds IIa and IIIa. Gastropods: *Pseudomelania* (*Oonia*) sp. (3), undetermined aporrhaid (1). Bivalves: *Entolium* (*E.*) *corneolum* (1).

Bed IIIa. Nautiloids: *Cenoceras* sp. (3). Ammonites: *Maconiceras soloniacense* (2), *Cleviceras* aff. *exaratum* (1), unidentified Harpoceratinae (6). Gastropods: *Pseudomelania* (*Oonia*) sp. (12). *Parapassaloteuthis* sp. A (4), *Parapassaloteuthis zietenii* (2), *Passaloteuthidae* gen. sp. indet. (5). Bivalves: *Chlamys* sp. (1), *Plicatula* sp. (1), *Grammatodon* (*G.*) sp. (1). Wood debris.

Bed Iva. *Parapassaloteuthis* sp. A (1), *Parapassaloteuthis zietenii* (2), *Passaloteuthis bisulcata* mor. C (1), *Passaloteuthidae* gen. sp. indet. (1). Gastropods: *Pseudomelania* (*Oonia*) sp. (12). Bivalves: ?*Chlamys* sp. (1). Wood debris.

Bed Va – *Maconiceras soloniacense* (1).

Outcrop 8

Semicelatum Subchronozone.

Bed Ia. Gastropods: nerineid (1). Bivalves: unidentified lucinid (1).

Outcrop 12

Semicelatum Subchronozone.

Bed Ia. Ammonites: *Dactylioceras laticostatum* sp. nov. M (17) and m (5), *Dactylioceras* sp. (12), unidentified Harpoceratinae (1), *Microdactylites* sp. (1). *Passaloteuthis bisulcata* mor. C (2), *Passaloteuthis bisulcata* mor. C (1). Bivalves: *Eopecten* sp. (2), *Agerchlamys* sp. (2), *Chlamys* sp. (1). Wood debris.

Outcrop 13

Semicelatum Subchronozone.

Bed Ia. Ammonites: *Calliphylloceras nilssoni* (Hébert, 1866) (1), *Dactylioceras (O.) semicelatum* M (6), *Dactylioceras* sp. (9), *?Nodicoeloceras/?Orthodactylites* sp. ind. A (2), *?Nodicoeloceras/?Orthodactylites* sp. indet. B (1), *Protogrammoceras paltum* (1), unidentified Harpoceratinae (4). *Passaloteuthis bisulcata* mor. C (2). Gastropods: *Pseudomelania (Oonia)* sp. (7). Wood debris.

Bed IIIa. Ammonites: *Calliphylloceras* sp. (1), *Dactylioceras (O.) semicelatum* M (2), *Dactylioceras* sp. (2), *Maconiceras soloniacense* (1). *Passaloteuthidae* gen. et sp. indet. (1). Gastropods: *Ataphrus* sp. (2), *Pseudomelania (Oonia)* sp. (1). Bivalves: *Plicatula* sp. (1), *Nicaniella (N.)* sp. (1).

Bed Iva. Nautiloids: *Cenoceras* sp. (1). Wood debris.

Bed Via. Ammonites: *Lytoceras* sp. (1). Gastropods: *Pseudomelania (Oonia)* sp. (1). Wood debris.

Outcrop 14

Emaciatum Chronozone.

Bed Ia. Ammonites: *Lioceratoides* sp. (1), *Neolioceratoides* sp. (1). *Passaloteuthis bisulcata* mor. C (1). Bivalves: *?Chlamys* sp. (1). Brachiopods: unidentified terebratulid (3). Wood debris.

Polymorphum Chronozone – Mirabile Subchronozone – Simplex Zonule.

Bed IIa. Ammonites: *Lytoceras* sp. (1), *Dactylioceras simplex* Fucini, 1935 (1), *Dactylioceras* aff. *simplex* (2), *Dactylioceras* sp. (6), *Lioceratoides serotinus* (Bettoni, 1900) (5), *Neolioceratoides schopeni* (Gemmellaro, 1886a) (5), unidentified Harpoceratinae (1), unidentified nucleus (1). *Passaloteuthis bisulcata* mor. C (1). Gastropods: *Pseudomelania (Oonia)* sp. (3). Bivalves: *Mesosaccella* sp. (1). Wood debris.

Mirabile Subchronozone – Mirabile Zonule.

Bed IIIa. Ammonites: *Dactylioceras (O.) semicelatum* M (5), *Dactylioceras (O.) semicelatum* m (3), *Dactylioceras* sp. (9), *?Nodicoeloceras/?Orthodactylites* sp. indet. A (1), *Lioceratoides serotinus* (1). *Parapassaloteuthis* sp. A (2), *Passaloteuthidae* gen. et sp. indet. (1). Gastropods: *Pseudomelania (Oonia)* sp. (1). Bivalves: *Eopecten* sp. (1), *Chlamys* sp. (2), *'Lingula'* sp. (1), *Grammatodon (G.)* sp. (1), *Mesosaccella* sp. (1). Brachiopods: unidentified terebratulid (1). Wood debris.

Bed IIIc – Ammonites: unidentified Dactylioceratinae (1), *Lioceratoides serotinus* (5), *Neolioceratoides schopeni* (2), *Protogrammoceras* cf. *paltum* (1), unidentified nuclei (7). *Parapassaloteuthis zietenii* (1), *Passaloteuthis bisulcata* mor. C (2). Gastropods: *Pseudomelania (Oonia)* sp. (3). Bivalves: Pectinid (1). Wood debris.

Semicelatum Subchronozone.

Bed Iva. Ammonites: *Dactylioceras (O.) semicelatum* M (8), *Dactylioceras (O.) semicelatum* m (5), *Dactylioceras* sp. (2), *?Nodicoeloceras/?Orthodactylites* sp. indet. A (1), *?Nodicoeloceras/?Orthodactylites* sp. indet. B (1), *Protogrammoceras paltum* (1), unidentified Harpoceratinae (1).

Bed Via. Ammonites: *Dactylioceras (O.) semicelatum* M (3), *Dactylioceras (O.) semicelatum* m (1), *Dactylioceras* sp. (1). *Pseudohastites longiformis* (1), *Passaloteuthidae* gen. et sp. indet. (1).

Bed VIIa. Ammonites: unidentified Harpoceratinae (1).

Bed XIa. Ammonites: *Dactylioceras (O.) semicelatum* M (3), *Dactylioceras (O.) semicelatum* m (1), *Dactylioceras* sp. (4), unidentified Harpoceratinae (2). *Passaloteuthis bisulcata* mor. C (1). Bivalves: *Eopecten* sp. (2).

Bed XIIa – Ammonites: *Juraphyllites (Meneghiniceras) lariense* (Meneghini, 1875) (2), *Dactylioceras latocostatum* M (24) and m (5), *Dactylioceras (O.) semicelatum* m (1), *Dactylioceras* sp. (7), unidentified Harpoceratinae (1), *Maconiceras* sp. (1). *Parapassaloteuthis* sp. A (1), *Passaloteuthis bisulcata* mor. C (2), *Passaloteuthidae* gen. et sp. indet. (1). Bivalves: *Eopecten* sp. (1). Wood debris.

Biostratigraphy

Due to faunal differences observed in different palaeogeographical domains, there are problems in correlation of Lower Toarcian ammonite zonal schemes, as discussed by Page (2003, 2008). The ammonite biostratigraphy in the areas of Page's provinces was established by Howarth (1955, 1973, 1980, 1992) and Dean *et al.* (1961) for the NW European province, and by Gabilly *et al.* (1971), Gabilly (1976) and Elmi *et al.* (1994, 1997) for the Sub-mediterranean province. In the Mediterranean province, ammonite biostratigraphy suffers from numerous correlation problems due to the large number of zonal schemes proposed in different countries for Early Toarcian faunal successions: Guex (1973) for the Moyen-Atlas (Morocco); Elmi *et al.* (1974) for Algeria; Rivas (1972), Goy (1974), Comas-Rengifo & Goy (1978), Jiménez & Rivas (1979), Braga (1983) and Jiménez (1986) for the Betic Cordillera (Spain); Faraoni *et al.* (1994), Macchioni (2002) and Sassaroli & Venturi (2012) for the Apennines (Italy).

In the present paper, we follow the ammonite biozonation summarized by Page (2003) for the Mediterranean province (Table 1). Furthermore, we recognize some of Goy & Martínez's (1990) zonules. As clarified by Page (2003), a zonule corresponds to a succession of ammonite species whose biostratigraphical rank is lower than a sub-zone. Zonules defined by Morard (2004) in the Moroccan Middle Atlas cannot be recognized in the South Riffian ridges because of faunal differences.

We list below, after the index species of the biostratigraphical unit under discussion, 'characteristic taxa' and 'recognized taxa'. The first list contains the characteristic taxa of the unit according to the literature. These taxa may or may not be exclusive to the biostratigraphical unit. The second lists the species found in our study area, which are known to be part of the assemblage defining a biostratigraphical unit.

A synthesis of the stratigraphical occurrences of the identified species is presented in Figure 2.

Polymorphum Chronozone; Mirabile Subchronozone

Simplex Zonule

Stratigraphical range. 14-IIa.

Index species. According to Jiménez & Rivas (1979), Goy *et al.* (1988) and Elmi *et al.* (1994), the base of the Polymorphum Chronozone is defined by the first occurrence of *D. polymorphum* Fucini, 1935, although other authors use the first occurrence of the subgenus *Eodactylites* Schmidt-Effing, 1972 (Ferretti 1967, 1970; Mouterde 1971; Guex 1973; Elmi *et al.* 1974; Bilotta *et al.* 2010).

Characteristic taxa. Species of the subgenus *Eodactylites*, *Fontanelliceras fontanellense* (Gemmellaro, 1886a), *Naxensiceras* Fucini, 1931 spp., *Lioceratoides* spp. and most commonly *L. serotinus*, *Neolioceratoides schopeni*, *Juraphyllites libertus* (Gemmellaro, 1884), *Meneghiniceras* spp.

Recognized taxa. *D. (E.) simplex*, *L. serotinus*, *N. schopeni*.

Comments. In the South Riffian ridges, the Pliensbachian–Toarcian boundary has been drawn by Elmi & Faugères (1974) and Faugères (1975, 1976) between two fossiliferous beds supposed to occur in all outcrops: the ‘*Dactylioceras* bed’ and, 10 metres below, a bed containing *Pleuroceras*, *Tauromeniceras*, *Lioceratoides* and rare specimens of *Amaltheus*. The ‘banc à *Dactylioceras*’ could occur at the base of our unit A, which is partly covered by road P7014. However 14-IVa and 7-Ia, which are lateral equivalents, are commonly well exposed and are the richest in *Dactylioceras* specimens. These beds could be considered the equivalent of Faugères’ (1975) ‘banc à *Dactylioceras*’. Nevertheless, specimens of 14-IVa and 7-Ia do not belong to the subgenus *Eodactylites* but to the subgenus *Orthodactylites* Buckman, 1926, whereas Faugères (1975) quoted *Dactylioceras (Eodactylites)* gr. *mirabile* Fucini, 1935 from his ‘banc à *Dactylioceras*’. Unfortunately, Faugères did not figure the specimens.

The Polymorphum Chronozone is usually characterized by the occurrence of *Eodactylites*. However, in many successions authors assigned *Dactylioceras* specimens to this subgenus on the basis of their stratigraphical occurrence with the characteristic taxa of the chronozone, more than on the basis of their morphological characters (see synonymy list and discussion of *D. (O.) semicelatum* in the Systematic palaeontology section below). Despite the absence of the most abundant *Eodactylites* species (i.e. *E. mirabile* and *E. pseudocommune*), the presence of *Lioceratoides serotinus*, *Neolioceratoides schopeni* and *Dactylioceras (Eodactylites) simplex* permits recognition of the Simplex Zonule in our study area.

Some authors have rejected the use of the Simplex Zonule. According to Braga *et al.* (1982), *D. (E.) simplex* would not be a good index species because of its scarcity and sporadic occurrence. We agree that this species is not as abundant as other species of *D. (Eodactylites)* but it occurs in most successions of the Submediterranean and Mediterranean provinces (*sensu* Page 2003) and has a wide palaeogeographical distribution (e.g. Chile, according to Hillebrandt & Schmidt-Effing 1981). Finally, as remarked by Rocha *et al.* (2012), some *Eodactylites* species (i.e. *E. mirabile*, *E. polymorphum* and *E. pseudocommune* Fucini, 1935) occur below the Pliensbachian–Toarcian boundary. Hence we support the use of the Simplex Zonule because of its clear biochronological relevance for identification of the base of the Toarcian stage.

Mirabile Zonule

Stratigraphical range. 14-IIIa to 14-IIIc.

Characteristic taxa. *Dactylioceras (Eodactylites) mirabile*, *Dactylioceras (Orthodactylites) semicelatum*, *Lioceratoides serotinus* (Bettoni, 1900), *Neolioceratoides schopeni*, *Protogrammoceras paltum*.

Recognized taxa. *D. (O.) semicelatum*, *L. serotinus*, *N. schopeni*, *P. paltum*.

Comments. In this interval, Goy & Martinez (1990) recognized *D. mirabile*, *Lioceratoides*, *Neolioceratoides* and the first *P. paltum*. In our opinion, the forms that these authors have assigned to *D. mirabile* belong to *D. semicelatum*. The first representatives of *D. (O.) semicelatum* occur in this zonule, as observed by Elmi *et al.* (1974) in Algeria. The dactylioceratid specimen figured by Goy & Martinez (1990) from this zonule in the Iberian range is here interpreted as *D. (O.) semicelatum*. This species appears in the south Riffian area earlier than in the NW European domain and some Mediterranean areas. In this interval, the last *Lioceratoides* and *Neolioceratoides* have been found together with dactylioceratids bearing tubercles in the inner whorls. The latter forms are provisionally assigned to *?Nodicoeloceras/?Orthodactylites* sp.

Semicelatum Subchronozone (II) (Page 2003) = Madagascariense Subzone (Guex 1973) = Bassanii Subchronozone (see Bilotta *et al.* 2010)

Stratigraphical range. Outcrops 4, 7, 12, 14, beds IVa to 14 XIIa.

Index species. *Dactylioceras (Orthodactylites) semicelatum*.

Characteristic taxa. *Protogrammoceras paltum*, *P. madagascariense* (Thévenin, 1908), *Dactylioceras (Orthodactylites)* spp.

Recognized taxa. *D. (O.) semicelatum*, *P. paltum*.

Comments. This subchronozone, defined by Gabilly *et al.* (1971) for the Mediterranean province, is different from the one defined by Howarth (1973) for the NW European province. To distinguish them, the former is usually written with a number one in brackets, and the latter with a number two (Page 2003).

In the Moulay Idriss area the fauna of the Semicelatum Subchronozone consists of numerous *D.* (*Orthodactylites*) specimens assigned to *D.* (*O.*) *semicelatum*. However, this subchronozone has been hard to recognize for three reasons: (1) the morphological characters of *Orthodactylites* do not match the morphologies of *D.* (*Orthodactylites*) *croseyi* Simpson, 1843, *D.* (*O.*) *clevelandicum* Howarth, 1973, and *D.* (*O.*) *tenuicostatum* Young & Bird, 1822, which are the index species of the zonules recognized in the NW European areas; (2) the absence of typical Tethyan taxa (i.e. *Protogrammoceras madagascariense* (Thévenin, 1908) and *Hildaites striatus*) hampers any correlation with Mediterranean successions; and (3) according to the literature, *Cleviceras exaratum* and *Maconiceras soloniacense* should appear in the Serpentinum Chronozone. On the contrary, *Juraphyllites* (*Harpophylloceras*) *eximium* and *J.* (*Meneghiniceras*) *lariensis* occur in the upper part of our succession, respectively in beds 6-I (= 14-XI) XI and 14-XII. These species are not recorded after the Polymorphum (= *Tenuicostatum*) Chronozone (Meister 1993; Cecca & Macchioni 2004).

The great thickness of our succession (65 m) suggests that the early occurrences of *Cleviceras* and *Maconiceras* could be artefactual. The thickness of the beds assigned to the Polymorphum Chronozone varies from 15–23 m in the Iberian Range (Comas-Rengifo *et al.* 2010) and Moyen Atlas (Morard 2004). Reduced thicknesses, about 3 m, have been reported from England (Howarth 1962), and up to 6 m in the Betic Cordillera (Jimenez & Rivas 1991). Compared to successions described in the literature, the thickness in the Moulay Idriss area is the most expanded lowermost Toarcian succession. This produces the opposite effect to condensation concerning the stratigraphical succession of the range intervals of the ammonite species.

Faugères (1975) found several specimens of *Bouleiceras*, *Hildaites* and *Harpoceratoides* Buckman, 1909 in a layer that he named ‘assise à *Bouleiceras*’. These fossils indicate the Serpentinum (equivalent to Levisoni) Chronozone, which follows the Polymorphum Chronozone (Page 2003). The thickness of the Lower Toarcian succession reported by Faugères, and the correlation of his ‘banc à *Dactylioceras*’ with our levels 7-Ia, 13-Ia, and 14-IVa would suggest that 14-XIIa (Fig. 2) overlaps the lower part of Faugères’ ‘assise à *Bouleiceras*’. On this basis, the part of the succession studied in the present work would be included in the Serpentinum Chronozone. The occurrence of *Cleviceras* aff. *exaratum*, *Maconiceras soloniacense* and *Dactylioceras* (*Dactylioceras*) *laticostatum* sp.

nov. tends to support this idea. However, no *Hildaites* (which usually marks the base of the Levisoni Chronozone), with the exception of the species *H. striatus*, have been found in the outcrops described in the present paper. The sole *Hildaites* specimen that we have found comes from approximately 50 m higher than the last bed described here (14-XIIa, Fig. 2), i.e. in the part of the succession assigned by Faugères (1975) to the Serpentinum Chronozone.

In conclusion, we lack sound biostratigraphical arguments to assign the interval 14-IVa to XIIa to the Serpentinum/Levisoni Chronozone and we assign it therefore to the Polymorphum Chronozone, Semicelatum Subchronozone.

Systematic palaeontology

Two ammonite families are well represented in the Toarcian sediments of our study area: Dactylioceratidae Hyatt, 1867 and Hildoceratidae Hyatt, 1867. Rare specimens of the superfamily Phylloceratoidea Zittel, 1884 and of the family Lytoceratidae Neumayr, 1875 have also been found.

All specimens are housed in the palaeontological collections of the University Pierre et Marie Curie (Paris).

Features used to characterize the taxa discussed below are: *Da*: diameter of the adult shell; *D*: diameter; *Uw*: umbilical width; *Wh*: whorl height; and *Wb*: whorl breadth. Ribbing and other parameters used to describe the shell shapes of Dactylioceratidae are illustrated and discussed in the section dedicated to this taxon. All measurements (Fig. 3) of the studied specimens are reported in the Supplemental Material.

Subclass **Ammonoidea** Zittel, 1884

Order **Phylloceratida** Arkell, 1950

Superfamily **Phylloceratoidea** Zittel, 1884

Family **Juraphyllitidae** Arkell, 1950

Genus ***Juraphyllites*** Müller, 1939

Type species. *Phylloceras diopsis* Gemmellaro, 1884.

Occurrence. Upper Sinemurian to Lower Toarcian.

Description. Moderately evolute whorls. The ornamentation is made of weak ribs that start from the ventral side of the flanks and cross the venter. A keel can appear in the last part of the body chamber.

Remarks. *Meneghiniceras* Hyatt, 1900 and *Harpophylloceras* Spath, 1927 are usually considered as genera of the family Juraphyllitidae. However, because they are considered to have been derived from *Juraphyllites* Müller, 1939, we follow Géczy & Meister (1998) in treating them as subgenera (but see also Macchioni in Pavia & Cresta 2002).

Subgenus ***Meneghiniceras*** Hyatt, 1900

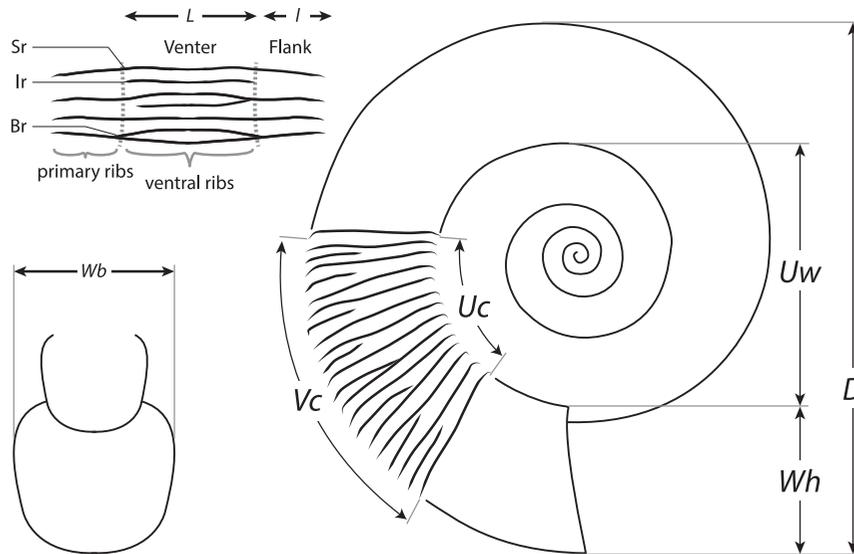


Figure 3. Morphometric scheme of an ammonite shell. *D*: diameter; *U*: umbilicus length; *Wh*: whorl height; *Wb*: whorl breadth; *Dc*: dorsal curve length; *Vc*: ventral curve length; *L*: average length of ventral ribs; *l*: average length of primary ribs. Different sets of measurements are taken depending on taxonomic group. Rib nomenclature: Sr: simple rib; Ir: intercalatory rib; Br: branching rib.

Type species. *Phylloceras lariense* Meneghini, 1867.

Occurrence. Sinemurian to Lower Toarcian.

Description. This subgenus is characterized by a keel consisting of a row of successive clavi on the adult body chamber. Whorls are subquadratic.

Juraphyllites (Meneghiniceras) lariense
(Meneghini, 1875)
(Fig. 4A, B)

1875 *Ammonites (Phylloceras) lariensis* Meneghini: 80, pl. 17, fig. 2.

1974 *Meneghiniceras lariense* (Meneghini); Fantini-Sestini: 217, figs 1, 2 (*cum syn.*).

1976 *Meneghiniceras lariense* (Meneghini); Howarth: 1, text-fig. 2.

1997 *Meneghiniceras lariense* (Meneghini); Dommergues *et al.*: 9, pl. 1 fig. 2.

2004 *Meneghiniceras lariense* (Meneghini); Morard: 194, pl. 1, fig. 2a, b.

2005 *Juraphyllites (Meneghiniceras) lariense* (Meneghini); Dommergues *et al.*: 417, fig. 6.4.

2005 *Meneghiniceras eximius* (Hauer) var. *lariense* (Meneghini); Schweigert: 6, fig. 3.

Types. Syntypes studied by Meneghini (1875) are lost. A neotype was selected by Pinna (1969, p. 17, pl. 6, fig. 2).

Material. 14-XIIa: UPMC-472, 485.

Occurrence. Lower Pliensbachian (Davoei Chronozone) to Lower Toarcian (Polymorphum Chronozone) in Spain,

Italy, Turkey, Tunisia and Morocco. Lower Toarcian (Semicelatum Subchronozone) in our succession.

Description. Our specimen is a part of an adult body chamber. However, we can observe some diagnostic characters of the species: a succession of weak clavi, and a whorl shape slightly higher than long.

Subgenus ***Harpophylloceras*** Spath, 1927

Type species. *Ammonites eximius* Hauer, 1854.

Occurrence. Lower Pliensbachian (Ibex Chronozone) to Lower Toarcian (Polymorphum Chronozone).

Description. Venter with a continuous keel. The ventrolateral edge of the whorl is angular.

Juraphyllites (Harpophylloceras) eximius
(Hauer, 1854)
(Fig. 4C, D)

1854 *Ammonites eximius* Hauer: 863, pl. 2, figs 1–4.

1938 *Rhacophyllites (Harpophylloceras) eximius* (Hauer); Roman: 12, pl. 1, fig. 6.

1973 *Juraphyllites libertus* (Gemmellaro); Guex: pl. 1, fig. 3.

1974 *Harpophylloceras eximius* (Hauer); Fantini-Sestini: 219.

1989 *Juraphyllites (Harpophylloceras) eximius* (Hauer); Meister: 31, pl. 3, figs 1–3.

1994 *Harpophylloceras eximius* (Hauer); Faraoni *et al.*: pl. 3 fig. 10.

?1996 *Harpophylloceras eximius* (Hauer); El Hariri *et al.*: 543, pl. 67, figs 3, 4.

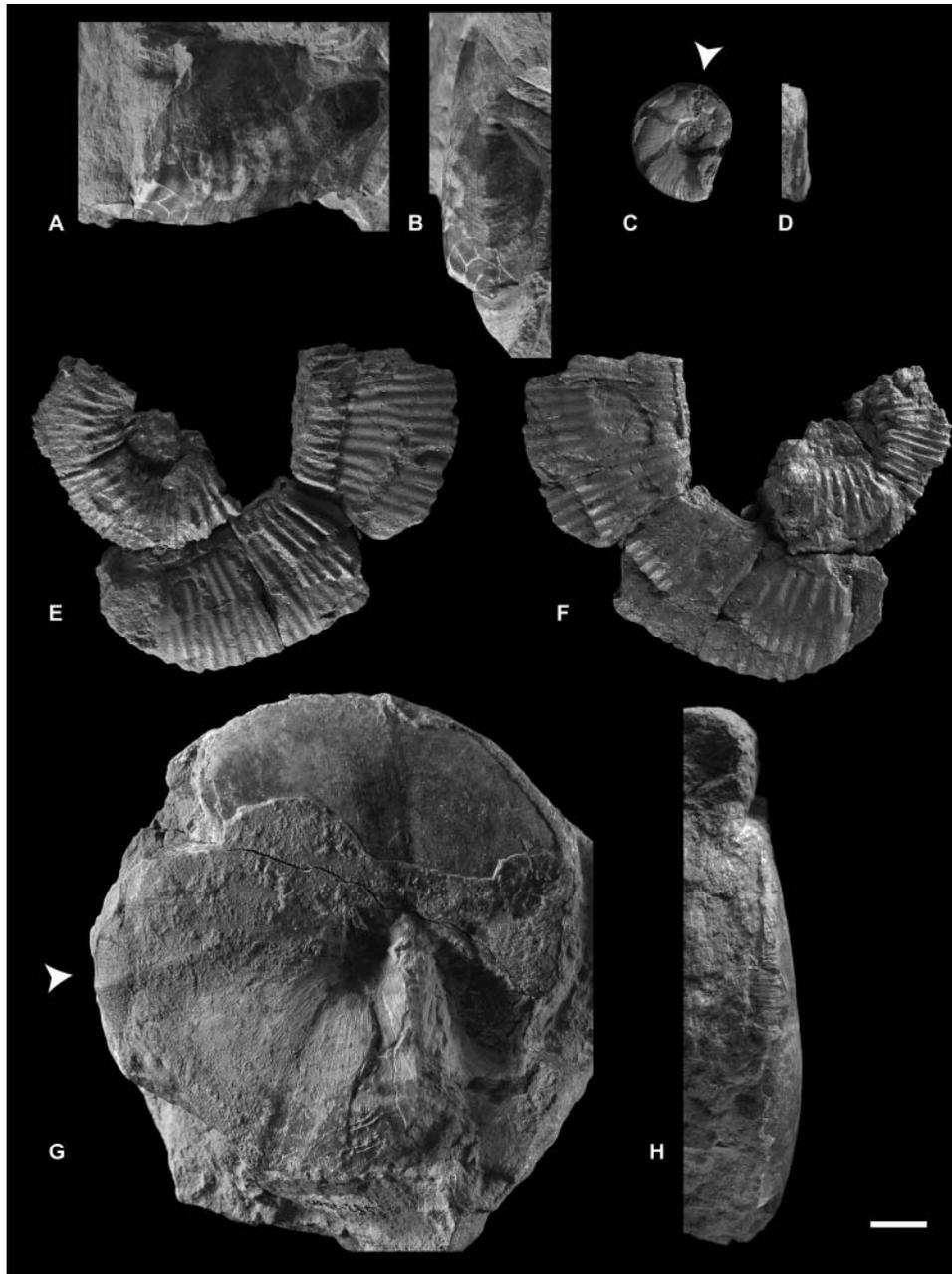


Figure 4. **A, B,** *Juraphyllites (Meneghiniceras) lariense* (Meneghini, 1875), UPMC-485, 14-XIIa. **C, D,** *Juraphyllites (Harpophylloceras) eximius* (Hauer 1854), UPMC-700, 6-Ia. **E, F,** *Dactylioceras (Eodactylites) simplex* Fucini 1935, UPMC-282, 14-IIa. **G, H,** *Calliphylloceras nilssoni* (Hébert 1866), UPMC-235, 13-Ia. Arrows indicate the beginning of the body chamber. Scale bar = 1 cm.

2005 *Juraphyllites (Harpophylloceras) eximius* (Hauer); Dommergues *et al.*: 415, figs 6.7, 6.9.

2005 *Meneghiniceras eximius* (Hauer); Schweigert: 6, pl. 1 fig. 1.

?2005 *Meneghiniceras eximius* (Hauer); Schweigert: 6, pl. 1 figs 2–9.

2007 *Meneghiniceras (Harpophylloceras) eximius* (Hauer); Fauré *et al.*: 483, figs 5.A1, A2.

2007 *Juraphyllites (Harpophylloceras) gr. eximius* (Hauer); Géczy & Meister: pl. 8, fig. 1 (*cum syn.*).

2011 *Juraphyllites (Harpophylloceras) eximius* (Hauer); Meister *et al.*: 117.e7, figs 5.2, 5.7.

Types. Fantini-Sestini (1974) selected the specimen figured by Hauer (1854, pl. 2, figs 1–4) as the lectotype of the species.

Material. 6-Ia: UPMC-700.

Occurrence. Lower Pliensbachian (Ibex Chronozone) to Lower Toarcian (Polymorphum Chronozone) in Morocco,

Hungary, Italy, Switzerland, Germany and England. Lower Toarcian (Semicelatum Subchronozone) in our succession.

Description. This small-sized specimen is moderately evolute, with flat flanks and a very weak keel on the venter. Five to six constrictions occur per whorl, more pronounced on the inner mould. Weak ribs start at mid flank, or at the upper third, and cross the venter without any discontinuity. The width of a single constriction matches almost three ribs.

Remarks. Schweigert (2005) considered *Harpophylloceras* to be a synonym of *Meneghiniceras*. Some juveniles seem to show morphological characters intermediate between *J. (H.) eximius* and *J. (M.) lariense*. The former could be an immature form of the latter.

Family **Phylloceratidae** Zittel, 1884
Subfamily **Calliphylloceratinae** Spath, 1927
Genus **Calliphylloceras** Spath, 1927

Type species. *Phylloceras disputabile* Zittel, 1869.

Occurrence. Hettangian to Middle Albian.

Description. Phylloceratidae with pseudoconstrictions, i.e. ridges on the shell corresponding to grooves in the inner mould. The ridges are developed in the upper half of the flank.

Calliphylloceras nilssoni (Hébert, 1866)
(Fig. 4G, H)

1845 *Ammonites calypso* d'Orbigny: 342, pl. 110, figs 1–3.

1866 *Ammonites nilssoni* Hébert: 527, fig. 3.

1966 *Calliphylloceras nilssoni* (Hébert); Kollarova-Andrusovova: 31, pl. 1, fig. 1.

1966 *Calliphylloceras nilssoni mediojurassica* (Hébert); Kollarova-Andrusovova: 31, pl. 2, fig. 4.

?1969 *Calliphylloceras nilssoni* (Hébert); Pinna: pl. 6, fig. 11.

2000 *Calliphylloceras nilssoni* (Hébert); Joly: 85, pl. 19, figs 6–9, text-figs 177–181 (*cum syn.*).

Types. The specimen selected by Joly (in Fischer 1994, pl. 32, fig. 3) is the lectotype of this species.

Material. 13-Ia: UPMC-235.

Occurrence. This species occurs in the Toarcian of Slovakia, France and Spain. Lower Toarcian (Semicelatum Subchronozone) in our succession.

Description. This species is a very involute form with flat flanks and a rounded venter. The test shows striae which are rectiradiate near the umbilical edge and strongly projected forward on the flanks and on the venter.

Our specimen shows five to six constrictions on the last whorl.

Remarks. The studied specimen shows some resemblances with *Calliphylloceras bicolae* (Meneghini, 1874). According to Joly (2000, p. 87) these species differ because of a slightly different inclination of pseudoconstrictions and a different whorl section.

Suborder **Ammonitina** Hyatt, 1889
Superfamily **Eoderoceratoidea** Spath, 1929
Family **Dactylioceratidae** Hyatt, 1867
Subfamily **Dactylioceratinae** Hyatt, 1867

Remarks. We refer the reader to the historical review of the taxonomy of this subfamily by Jiménez & Rivas (1991). The subfamily Dactylioceratinae includes ammonites with evolute to serpenticone whorls. The shell is characterized by a supplementary layer called the inner shell (Guex 1970; Howarth 1975). Sculpture consists of ribs and tubercles in some taxa. Ribbing consists of simple, branching and intercalatory ribs (Fig. 3). Simple ribs run on the entire circumference of the whorl. Ribs can branch at variable height of the flank (usually from the upper third up to the limit between the flank and the venter); the unbranched portion is called the primary rib and the branched ribs are called secondary ribs. The unbranched portions of branching ribs together with simple ribs (i.e. all ribs occurring on the whorl flank) are counted as the number of primary ribs, or *Npr*. Intercalatory ribs are free ribs that do not belong to a branch and only run on the venter. Secondary and intercalatory ribs are called ventral ribs; their number is *Nvr*. Because rib density can change abruptly during ontogeny, *Npr* and *Nvr*, which are traditionally counted per whorl or per half-whorl, have been replaced by counts at different portions of the whorl by taking variable angles.

In the material studied, three groups of Dactylioceratinae have been easily distinguished from the others: *D. (Eodactylites) simplex*, *?Nodicoeloceras/?Orthodactylites* sp. indet. A, and *?Nodicoeloceras/?Orthodactylites* sp. indet. B. The other Dactylioceratinae belong to the subgenus *Orthodactylites* and have been assigned to the species *Dactylioceras (Orthodactylites) semicelatum* and *Dactylioceras (Dactylioceras) laticostatum* sp. nov., both with their macroconch and microconch (i.e. antidimorphs). With respect to previous palaeontological studies on this subfamily, these specific assignments are supported by the introduction of new morphological parameters:

$$Dprm = \frac{Uc}{Npr}, \quad (1)$$

which is the mean of the distance, or interspace, between two primary ribs on a given portion of the whorl. *Uc* is the

length of a given portion of the whorl at the umbilical edge (Fig. 3)

$$D_{vrm} = \frac{V_c}{N_{vr}}, \quad (2)$$

which is the mean of the distance, or interspace, between two ventral ribs on a given portion of the whorl V_c is the length of the venter for a given portion of the whorl (Fig. 3).

D_{prm} and D_{vrm} have been introduced to quantify rib densities of ventral and lateral regions.

The parameter C is used for deformed or incomplete specimens and is equivalent to the umbilicus width (U_w) of well-preserved specimens $C = U_w/V_c$.

A new parameter is introduced to reconstruct the shape of the whorl in crushed specimens: $S = l/L$, where l is the mean length of primary ribs and L the mean length of ventral ribs on a given portion of the whorl (Fig. 3). Some additional information on the use of these parameters (D_{vrm} , D_{prm} , S , C) is provided in the Supplemental Material.

These parameters have been introduced to help taxonomic assignment. Their use permits quantitative comparison of more specimens and provides more objective diagnostic criteria to distinguish taxa. A linear discriminant analysis using the R MASS package (<http://cran.r-project.org/web/packages/MASS/index.html>) has been performed to verify if the a priori recognized groups could be distinguished on the basis of the quantitative representation of their shapes. Holotypes of the most important species of *Dactyloceras* were included in the analysis (i.e. *D. semicelatum*, *D. clevelandicum* and *D. crosbeyi*). The raw variables used are L , l , D_{vrm} , D_{prm} , Da and Wh/D . This analysis found new axes corresponding to linear combinations of raw variables that maximize between-group variance and minimize within-group variance (Abdi 2007). A subsample of specimens has been used to perform a cross-validation of the groups. The results show an error rate equal to zero (Table 2). This means that their morphologies do not overlap. The different morphologies (species and antidimorphs), discussed below, can be considered objectively different.

Genus *Dactyloceras* Hyatt, 1867

Type species. *Ammonites communis* Sowerby, 1815.

Description. Evolute Dactyloceratinae with simple, bifurcating and intercalatory ribs.

Dimorphism. In ammonites dimorphism is reflected in size and, often, ornamental differences. It is usually interpreted as sexual polymorphism (Davis *et al.* 1996). When adult and fully grown specimens are available, the sexual nature of the dimorphism can be inferred in a given species. In *Dactyloceras*, late ontogenetic shell modifications

are well identified (Howarth 1973). They consist of both reduction of rib interspaces and the formation of a shell thickening in the vicinity of the apertural border. The second feature is not always observable on the external part of the shell but always forms a large pseudo-constriction on the internal mould.

Dimorphism in Dactyloceratidae has been studied by several authors. First, Lehmann (1968) recognized dimorphism in *Dactyloceras athleticum* (Simpson, 1855) and *D. ernsti* (Lehmann, 1968). The most important arguments were a bimodal distribution in the adult diameter of these two species and a different spacing of the first septa. Howarth (1973) was opposed to this hypothesis, claiming that the numerous adult specimens collected in the Grey Shales Formation show a unimodal diameter distribution. Jiménez & Rivas (1991), supported by Morard (2004), proposed dimorphic relationships between the four most important species of the subgenus *Eodactylites*, i.e. two microconch and macroconch couples: *D. (E.) polymorphum*–*D. (E.) pseudocommune* and *D. (E.) simplex*–*D. (E.) mirabile*. Guex (1973) recognized several dimorphic couples: *Zugodactylites*–*Gabillytes*, *Catacoeloceras*–*Mucrodactylites*, *Porpoceras* and *Nodicoeloceras*–*Collina*. He claimed that there are no criteria allowing the distinction of dactyloceratid macroconchs and microconchs. Nevertheless, some trends are observable: compared to microconchs, macroconchs are larger and develop a stronger ribbing.

Davis *et al.* (1996) proposed several criteria to identify dimorphism in Jurassic Ammonoids. These included the observation of significant differences between the suspected antidimorphs and the similarity of their palaeogeographical and stratigraphical distributions. In this paper, we have used these two criteria to recognize dimorphic couples for three different species: *D. (Eodactylites) simplex*, *D. (Orthodactylites) semicelatum* and *D. (Dactyloceras) laticostata*. Difference in adult size is the most important feature to recognize dimorphism in our populations. Macroconchs range from 70 to 90 mm in *D. semicelatum* and from 65 to 80 mm in *D. laticostata*. Microconchs range from 40 to 55 in *D. semicelatum* and from 45 to 55 in *D. laticostata*. The specimens of *D. (E.) simplex* are too rare and incomplete to be measured.

There is no significant disjunction in the palaeogeographical and stratigraphical distributions of Dactyloceratidae whose dimorphism has been recognized several times, as reported above. Concerning the faunas under study, antidimorphs have been found in almost all beds except beds 13-Ia and 13-IIIa.

The last step consists of recognizing the sexual nature of the dimorphism. In living cephalopods, a difference in adult size is common. A similar pattern in ammonites has been considered as a clue for inferring sexual dimorphism. In our populations, size distributions of antidimorphs are different (Fig. 5) and comparable with those observed by

Table 2. Results of linear discriminant analysis on specimens belonging to the subgenera *Orthodactylites* Buckman, 1926 and *Dactylioceras* Hyatt, 1867. Numbers correspond to well-classified specimens. The error rate is equal to zero, meaning that the species are well discriminated by parameters used to describe their morphologies (i.e. *S*, *Dvrm*, *Dprm*, *Da*, *l*, *L*, *Wh/D*).

	<i>Dactylioceras clevelandicum</i> holotype	<i>Dactylioceras crosbeyi</i> holotype	<i>Dactylioceras semicelatum</i> macroconch	<i>Dactylioceras semicelatum</i> microconch	<i>Dactylioceras laticostatum</i> microconch	<i>Dactylioceras laticostatum</i> macroconch
<i>Dactylioceras clevelandicum</i> holotype	1	0	0	0	0	0
<i>Dactylioceras crosbeyi</i> holotype	0	1	0	0	0	0
<i>Dactylioceras semicelatum</i> macroconch	0	0	8	0	0	0
<i>Dactylioceras semicelatum</i> microconch	0	0	0	5	0	0
<i>Dactylioceras laticostatum</i> microconch	0	0	0	0	5	0
<i>Dactylioceras laticostatum</i> macroconch	0	0	0	0	0	6

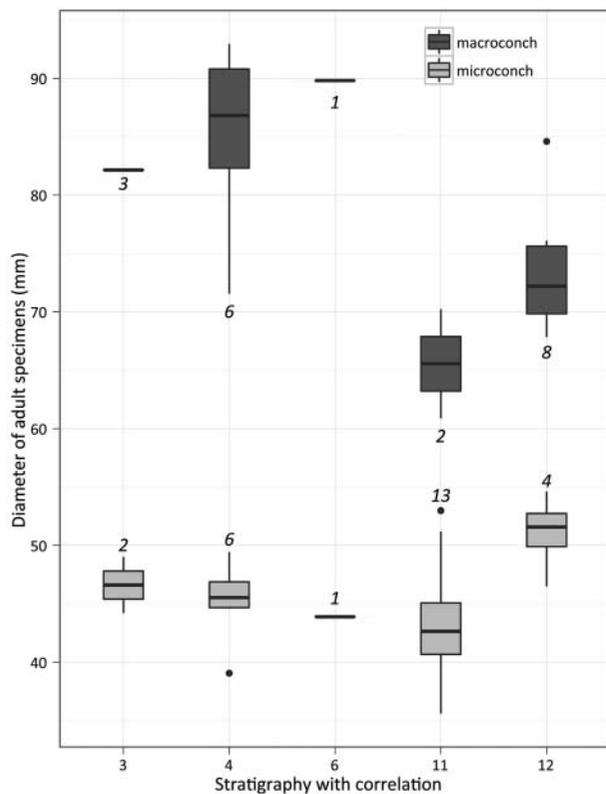


Figure 5. Boxplot of diameter (mm) of adult shells against bed numbers of outcrop 14 (stratigraphy). These boxplots include specimens from the other outcrops which have been plotted according to established correlations. Dark grey: macroconchs; light grey: microconchs; italics: number of specimens. Hinges correspond to first and third quartiles, thick horizontal bars to medians, and vertical bar the maximum range of values. Outliers are represented as dots.

Lehmann (1968) for *D. athleticum* and *D. ernsti*. In addition, microconchs bear more slender ribs than macroconchs.

Subgenus *Eodactylites* Schmidt-Effing, 1972

Type species. *Dactylioceras pseudocommune* Fucini, 1935.

Occurrence. Lower Toarcian.

Description. Quadratic and compressed whorls, ventral ribs more prorsiradiate than primary ones. Rib branching occurs close to the ventrolateral edge.

Remarks. This subgenus was created for particular morphologies occurring in the latest Pliensbachian. Most of the species included in *Eodactylites* were established by Fucini (1935) on the basis of material collected in Lower Jurassic strata cropping out near Taormina (Sicily), whose precise stratigraphical provenance is unknown. Furthermore, Fucini figured very few adult specimens showing their complete ontogeny. In the Tethyan domain, most of the studied and figured specimens have been ascribed to the subgenus *Eodactylites* for stratigraphical more than morphological reasons.

Dactylioceras (Eodactylites) simplex Fucini, 1935 (Fig. 4E, F)

1935 *Coeloceras* ? cfr. *sellae* Gemmellaro; Fucini: pl. 8, figs 11, 12.

1935 *Dactylioceras simplex* Fucini: 86, pl. 9, figs 4, 5.

- 1935 *Dactyloceras polymorphum?* Fucini: 88, pl. 9, fig. 13.
 1972 *Dactyloceras simplex* Fucini; Ferretti: 108, pl. 18, fig. 1.
 1973 '*Catacoeloceras simplex*' (Fucini); Guex: 509, pl. 12, fig. 11.
 ?1978 *Dactyloceras simplex* Fucini; Farinacci *et al.*, pl. 2, fig. 7.
 non 1980 *Dactyloceras simplex* Fucini; Wiedenmayer: 80, pl. 9, figs 11, 12 [= *Reynesoceras* sp.].
 1990 *Dactyloceras (Eodactylites) simplex* Fucini; Goy & Martinez: pl. 1 fig. 1.
 1991 *Dactyloceras (Eodactylites) simplex* Fucini; Jiménez & Rivas: 164, pl. 2, figs 5–7.
 1994 *Eodactylites pseudocommunis* (Fucini); Faraoni *et al.*: pl. 3, fig. 4, pl. 5, figs 1, 3, 7.
 1995 *Dactyloceras (Eodactylites) simplex* Fucini; Rakús: 167, pl. 1, fig. 4.
 ?1996 *Dactyloceras (Eodactylites) simplex* Fucini; Garcia: 32, pl. 2, figs 1–5.
 2004 *Dactyloceras (Eodactylites) polymorphum-simplex* Fucini; Morard: pl. 5, fig. 1.
 2004 *Dactyloceras (Eodactylites) cf. simplex* Fucini; Morard: pl. 5, figs 4, 6, 8, 9.
 2004 *Dactyloceras (Eodactylites) simplex* Fucini; Morard: 253, pl. 5, figs 7, 12, 13.

Types. The specimen figured by Fucini (1935, p. 86, pl. 9, fig. 4) was selected as the lectotype by Pinna & Levi-Setti (1971).

Material. 14-IIa: macroconchs: UPMC-281; microconchs: UPMC-282; undetermined dimorph: UPMC-275.

Occurrence. Lower Toarcian (Mirabile Subchronozone), Spain, Portugal, Morocco, Italy, France (?), Germany, Chile, Canada and Russia. Lower Toarcian (Mirabile Subchronozone, Simplex Zonule) in our succession.

Description. The crushing of the lectotype hampers observation of whorl shape. Rib density is relatively low. Ribs are rectiradiate and on the ventrolateral edge each primary rib bears a tubercle at the point of branching, from which spring two to four secondary ribs. Our specimen is a microconch.

Subgenus *Orthodactylites* Buckman, 1926

Type species. *Dactyloceras directus* Buckman, 1926 by original designation.

Occurrence. Lower Toarcian (Semicelatum Subchronozone to the Serpentinus Chronozone).

Description. Whorls rounded. Primary and secondary ribs are straight.

Dactyloceras (Orthodactylites) semicelatum (Simpson, 1843) (Fig. 6A–J)

Macroconch:

- 1943 *Ammonites semicelatus* Simpson: 20.
 ?1955 *Dactyloceras* aff. *semicelatum* (Simpson); Imlay: 87, pl. 10, figs 6, 13.
 1957 *Dactyloceras semicelatum* (Simpson); Maubeuge: 191, figs 1, 2, 8.
 1957 *Dactyloceras* cf. *semicelatum* (Simpson); Maubeuge: 194, figs 10, 17.
 1957 *Dactyloceras* aff. *semicelatum* (Simpson); Maubeuge: 192, fig. 16.
 1957 *Dactyloceras semicelatoides* Maubeuge: 200, fig. 27.
 non 1966 *Dactyloceras semicelatum* (Simpson); Pinna: 93, pl. 7 fig. 19 [= *Dactyloceras* aff. *clevelandicum*].
 1971 *Dactyloceras (Orthodactylites) cf. semicelatum* (Simpson); Pinna & Levi-Setti: 90, pl. 2, figs 3, 4.
 1971 *Dactyloceras (Orthodactylites) anguinum* (Reinecke); Pinna & Levi-Setti: 90, pl. 2, figs 1, 2, 5.
 1972 *Dactyloceras (Orthodactylites) semicelatum* (Simpson); Schmidt-Effing, pl. 4, figs 1–4.
 1972 *Dactyloceras (Orthodactylites) semicelatoides* Maubeuge; Schmidt-Effing: 95, pl. 6, figs 1, 2.
 V 1973 *Dactyloceras (Orthodactylites) crosbeyi* (Simpson); Howarth: 255, pl. 1, figs 2–4, pl. 2, fig. 2.
 V 1973 *Dactyloceras (Orthodactylites) semicelatum* (Simpson); Howarth: 262, pl. 6, fig. 1, pl. 7, figs 1, 2, pl. 8, figs 1, 2, pl. 9, figs 2, 3.
 1976 *Dactyloceras semicelatum* (Simpson); Schlegelmilch: 87, pl. 38, fig. 3.
 pars V 1980 *Dactyloceras (Orthodactylites) semicelatum* (Simpson); Howarth: 646, pl. 80, figs 1, 2, 5–10, pl. 81, figs 1–11 [non pl. 82, figs 11, 12 = *Dactyloceras (Dactyloceras) sp.*].
 V 1980 *Dactyloceras (Orthodactylites) clevelandicum* (Simpson); Howarth: 652, pl. 82, figs 15, 16.
 V ?1980 *Dactyloceras (Orthodactylites) crosbeyi* (Simpson); Howarth: 654, pl. 82, figs 17, 18.
 1990 *Dactyloceras (Eodactylites) mirabile* (Fucini); Goy & Martinez: pl. 1, fig. 2.
 1990 *Dactyloceras (Orthodactylites) crosbeyi* (Simpson); Goy & Martinez, pl. 1, fig. 3.
 1990 *Dactyloceras (Orthodactylites) tenuicostatum* (Young & Bird); Goy & Martinez, pl. 1, fig. 4.
 1990 *Dactyloceras (Orthodactylites) semicelatum* (Simpson); Goy & Martinez: pl. 1, fig. 5.
 1996 *Dactyloceras (Orthodactylites) mite* (Buckman); Garcia: pl. 46, pl. 3, figs 1–6.
 1996 *Dactyloceras (Orthodactylites) semicelatum* (Simpson); Garcia: 37, pl. 3, figs 7, 8, pl. 9, figs 2–5.
 1997 *Dactyloceras (Orthodactylites) gr. semicelatum* (Simpson); Rulleau: pl. 1, figs 1–4.

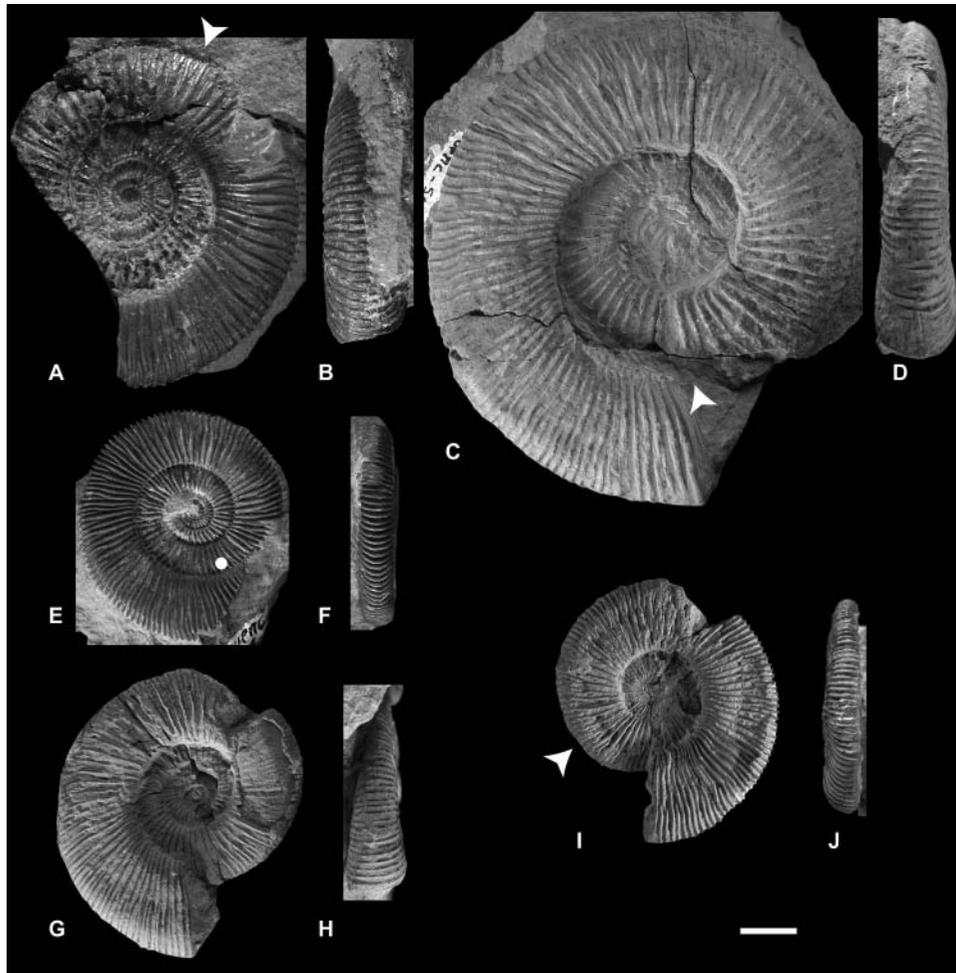


Figure 6. *Dactylioceras (Orthodactylites) semicelatum* (Simpson, 1843). **A–D**, macroconchs; **A, B**, UPMC-404, 14-IIIc; **C, D**, UPMC-510, 7-1a. **E–J**, microconchs; **E, F**, UPMC-401, 14-IIIc; **G, H**, UPMC-661, 6-1a; **I, J**, UPMC-696, 6-1a. Arrows indicate the beginning of the body chamber, except in E where the arrow is replaced by a white dot. Scale bar = 1 cm.

2008 *Dactylioceras (Orthodactylites) semicelatum* (Simpson); Metodiev: fig. 3c.

2008 *Dactylioceras (Orthodactylites) semicelatum* (Simpson); Seyed-Emami *et al.*: 247, fig. 4i, m.

Microconch:

?1957 *Dactylioceras microdactyliformis* Maubeuge: fig. 38.

1973 *Dactylioceras mirabile* Fucini; Guex: pl. 13, fig. 8.

1973 *Dactylioceras polymorphum* Fucini; Guex: pl. 13, figs 9, 10.

?1980 *Dactylioceras polymorphum* Fucini; Wiedenmayer: pl. 9, figs 3, 4.

pars 1981 *Dactylioceras (Orthodactylites) kanense* McLearn; Imlay: pl. 11, figs 4, 5, 9.

1991 *Dactylioceras (Eodactylites) polymorphum* Fucini; Jiménez & Rivas: pl. 3, figs 1–3.

pars 2004 *Dactylioceras (Eodactylites) polymorphum* Fucini; Morard: pl. 5, figs 14–16 [*non* pl. 5, fig. 3 = *Dactylioceras triangulum* Fischer].

Types. The holotype was designated by Buckman (1911, p. 31, pl. 31).

Material. 6-1a: Macroconchs: UPMC-660, 672, 674, 694, 707. Microconchs: UPMC-661, 663, 664, 665, 666, 667, 669, 670, 673, 676, 677, 680, 682, 683, 686, 690, 691, 692, 693, 696, 697, 705, 706.

7-1a: Macroconchs: UPMC-501, 502, 503, 504, 505, 508, 510, 511, 514, 515, 518, 519, 522, 523, 524, 526, 529, 531, 533, 535, 537, 542, 544, 545, 547, 548, 554, 560, 562, 564, 565, 569, 571, 578, 579, 581, 585, 587, 589, 590, 592, 593, 598, 599, 601, 603, 604, 607, 610, 611, 616c. Microconchs: UPMC-509, 520, 521, 525, 527, 530, 534, 536, 540, 556, 557, 558, 597, 609, 613, 614, 616a.

7-IIa: Macroconchs: UPMC-619, 622, 623, 625, 642, 643, 647, 647b, 649, 654. Microconchs: UPMC-617, 620, 621, 640.

13-1a: Macroconchs: UPMC-231, 238, 239, 249, 252, 254.

13-IIIa: Macroconchs: UPMC-745, 746.

14-IIIc: Macroconchs: UPMC-391, 394, 398, 404, 407.
Microconchs: UPMC-390, 401, 402.

14-IVa: Macroconchs: UPMC-424, 425, 428, 430, 434, 437, 438, 440. Microconchs: UPMC-427, 429, 431, 432, 436.

14-VIa: Macroconchs: UPMC-445, 446. Microconchs: UPMC-443.

14-XIa: Macroconchs: UPMC-473, 474, 475. Microconchs: UPMC-476.

From the rubble: 451, 708.

Occurrence. Lower Toarcian (Polymorphum Chronozone to Serpentinum Chronozone), Spain, Morocco, Algeria, France, England, Germany and Bulgaria. Lower Toarcian (Mirabile Subchronozone to Semicelatum Subchronozone) in our succession.

Description. Moderately evolute forms (M: $U_w/D = 0.42 \pm 0.05$; m: $U_w/D = 0.43 \pm 0.03$), whorl shape sub-circular with slightly flattened ventrolateral margins and rounded venter. Venter width is almost two times the height of the flanks. Ribs are thin, single or bifurcating, usually prorsiradiate. Adult body chamber becomes more compressed with a higher rib density on approximately half a whorl. On the last 20° of the whorl before the adult mouth, the rib density strongly increases while the *Rdi* decreases drastically. This species is dimorphic. Macroconchs reached a diameter of almost 70 to 90 mm, whereas the diameter of adult microconch specimens is almost 40 to 55 mm. Microconch ribbing is slender with the mid-flank part of the ribs usually projected forward.

Remarks. Above-mentioned specimens have been ascribed to *D. (O.) semicelatum* because they are morphologically very close to the holotype and to several specimens published by Howarth (1973, e.g. pl. 6, fig. 1). They differ from species of the genus *Eodactylites* in having a rounded whorl section and a more dorsal point of division. They cannot be confounded with *D. (O.) clevelandicum* because they bear thinner ribs and have more evolute whorls. *D. (O.) crosbeyi* has more depressed whorls, especially in the early ontogeny.

The dimorphism of this species has never been discussed because morphological differences of the dimorphs are not detectable when specimens are not adult and complete. The microconch forms of *Dactylioceras* species are very similar to each other. They all share the characteristic slender ribbing and the definite decrease of *Dpr*, *Dvr* and *Rdi* at the end of ontogeny. The main differences between microconchs of different species are observed in the inner whorls. *Dactylioceras (Eodactylites) polymorphum* (see for example, holotype and paratypes, Fucini 1935, pl. 9, figs 9–13), which is considered the microconch form of *Dactylioceras (Eodactylites) mirabile*, develops strong, straight and spaced ribbing in the inner whorls, whereas

the end of the growth is similar to any *Dactylioceras* microconch.

Subgenus *Dactylioceras* Hyatt, 1867

Type species. *Ammonites communis* Sowerby, 1815.

Occurrence. Base of the Levisoni Chronozone to the base of the Bifrons Chronozone.

Description. Evolute shell with subcircular whorls and flat flanks. The ornamentation is made of rectiradiate ribs. Primary ribs are strong and largely spaced. They branch on a barely marked ventrolateral edge. Secondary ribs can be slightly prorsiradiate.

Remarks. This subgenus is morphologically very similar to the subgenus *Eodactylites*. Primary ribs of *Dactylioceras* s.s. have a high relief on the middle of the flank, whereas rib relief is uniform on *Eodactylites*, or is higher on both ventrolateral and dorsolateral edges of the whorl.

Dactylioceras (Dactylioceras) laticostatum sp. nov.
(Figs 7A–H, 8A, B, E–K)

Types. Holotype: UPMC-776, a complete macroconch (Fig. 7A–D). Paratypes: Macroconchs: UPMC-757, 734, 733, 741, 775 (Figs 7E–J, 8A–D); microconchs: UPMC-449, 450, 719, 763, 780 (Fig. 8E–K).

Diagnosis. *Dactylioceras laticostatum* is diagnosed by the low density of primary ribbing and high density of secondary ribbing. Macroconchs show thickening of the last few ribs preceding the adult mouth.

Derivation of name. The name refers to the relatively wide interspaces between the primary ribs.

Material. 4-Ia: Macroconchs: UPMC-753, 755, 756, 762. Microconchs: 758.

5-Ia: Macroconchs: UPMC-768. Microconchs: UPMC-763, 766, 780.

12-Ia: Macroconchs: UPMC-717, 718, 724, 730, 733, 734, 741, 757, 759, 760, 761, 773, 775, 776, 777, 778, 779. Microconchs: 719, 722, 725, 732, 740.

14-XIIa: Macroconchs: UPMC-448, 453, 454, 455, 456, 457, 458, 459, 460, 461, 462, 465, 466, 467, 468, 469, 470, 471, 486, 490, 492, 495, 496, 499. Microconchs: UPMC-449, 450, 463, 464.

Occurrence. Top of the Semicelatum Subchronozone.

Type locality. Vicinity of the old jail, Moulay Idriss, South Riffian ridges, Morocco.

Type horizon. 14-XIIa.

Description. Evolute to subevolute forms (Fig. 9). Whorls subcircular with a ventral area flattened on ventral margins. There is no ribbing up to 4–5 mm, then a more

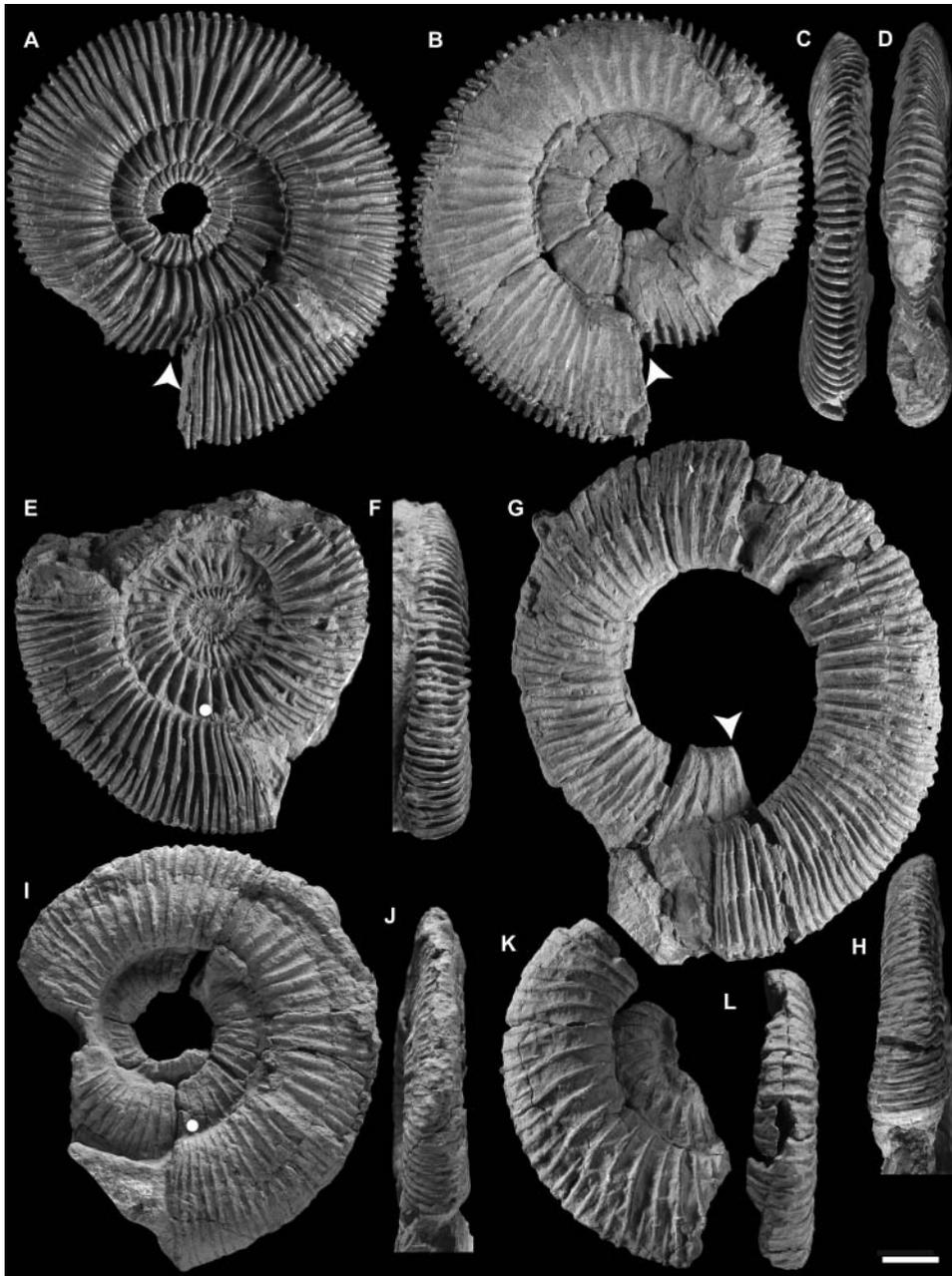


Figure 7. *Dactylioceras (Dactylioceras) laticostatum* sp. nov., macroconchs. A–D, UPMC-776, 12-Ia; E, F, UPMC-757, 12-Ia; G, H, UPMC-734, 12-Ia; I, J, UPMC-733, 12-Ia; K, L, UPMC-718, 12-Ia. Arrows indicate the beginning of the body chamber, except in E and I where arrows are replaced by white dots. Scale bar = 1 cm.

or less uniform ornamentation develops. Primary ribs are strong, with the maximum relief on the middle of the flanks. Rib density is relatively low but higher for secondary ribs that give an *Rdi* of about 2.1. Several changes occur into the adult body chamber (Figs 10, 11, see measurements in Supplemental Appendices 2, 3). The species is dimorphic (Figs 5, 10F, G).

Macroconchs: adult diameter ranges from 65 to 80 mm. Rib density continuously increases up to the end of the phragmocone. In the adult body chamber, five successive ornamental stages can be distinguished (Fig. 10A). Stage A

begins after the last septum and marks the stop of rib density increasing. The boundary between stages A and B coincides with the end of inner shell secretion (Fig. 10B). Stage C begins with a new increase in rib density (Fig. 10A). Because this increase is similar for both primaries and secondaries, *Rdi* does not change, so we conclude that this is due to the deceleration of shell accretion. Stage D starts with a reduction in the relief of primary ribs on the middle of the flank (Fig. 10C). In some specimens, there is no stage C because the increase of rib density occurs at the beginning of stage D. The final stage, E,

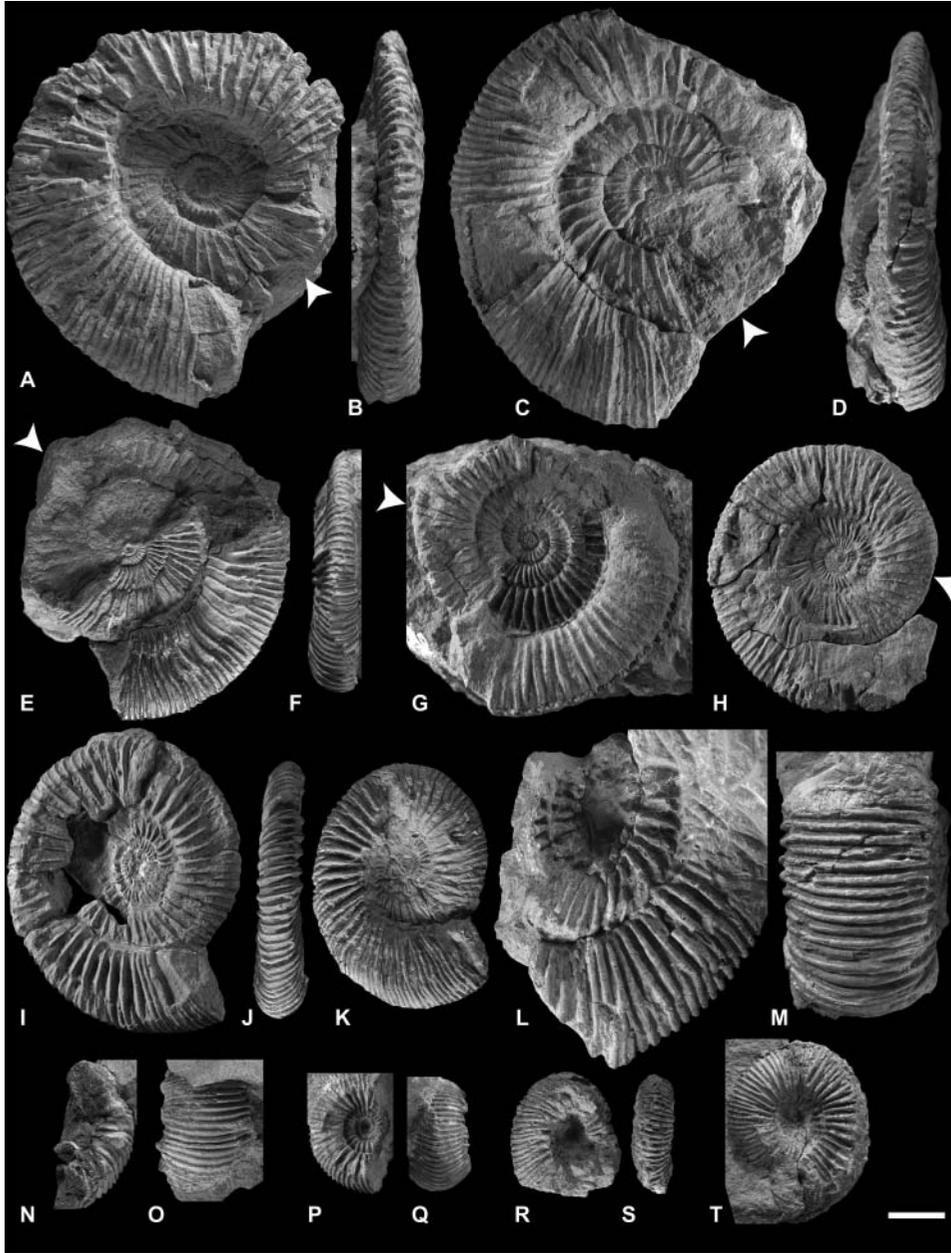


Figure 8. A–K, *Dactylioceras* (*Dactylioceras*) *laticostatum* sp. nov. A–D, macroconchs; A, B, UPMC-741, 12-Ia; C, D, UPMC-775. E–K, microconchs; E, F, UPMC-449, 14-XIIa; G, UPMC-450, 14-XIIa; H, UPMC-719, 12-Ia; I, J, UPMC-763, 5-Ia; K, UPMC-780, 5-Ia. L, M, *?Nodicoeloceras*/*?Orthodactylites* sp. indet. A, UPMC-233, 13-Ia. N–T, *?Nodicoeloceras*/*?Orthodactylites* sp. indet. B; N, O, UPMC-406, 14-IIIa; P, Q, UPMC-230, 13-Ia; R, S, UPMC-441, 14-IVa; T, UPMC-433, 14-IVa (entirely septate specimen). Arrows indicate the beginning of the body chamber. Scale bar = 1 cm.

is defined by an increase in rib density of primaries whereas rib density of secondaries remains constant or slightly decreases (Fig. 10D). This results in a decrease of *Rdi* (i.e. simple ribs are the most numerous in stage E). A thickening of the nacreous layer of the shell also occurs at this stage in both the inner (Fig. 10D) and outer sides of the shell, but it is particularly marked in the inner side to form the mouth border pseudoconstriction (as in most *Dactylioceratidae*).

Microconchs: adult diameter ranges from 45 to 55 mm. Compared to macroconchs, ontogenetic changes in microconchs are simpler. Stages B to D do not exist, whereas the increase of rib density occurs with the thickening of the shell both for primaries and secondaries, allowing stage E to be recognized (Fig. 10E).

Remarks. This species is close to some species of the subgenus *Dactylioceras* but its whorls are more rounded.

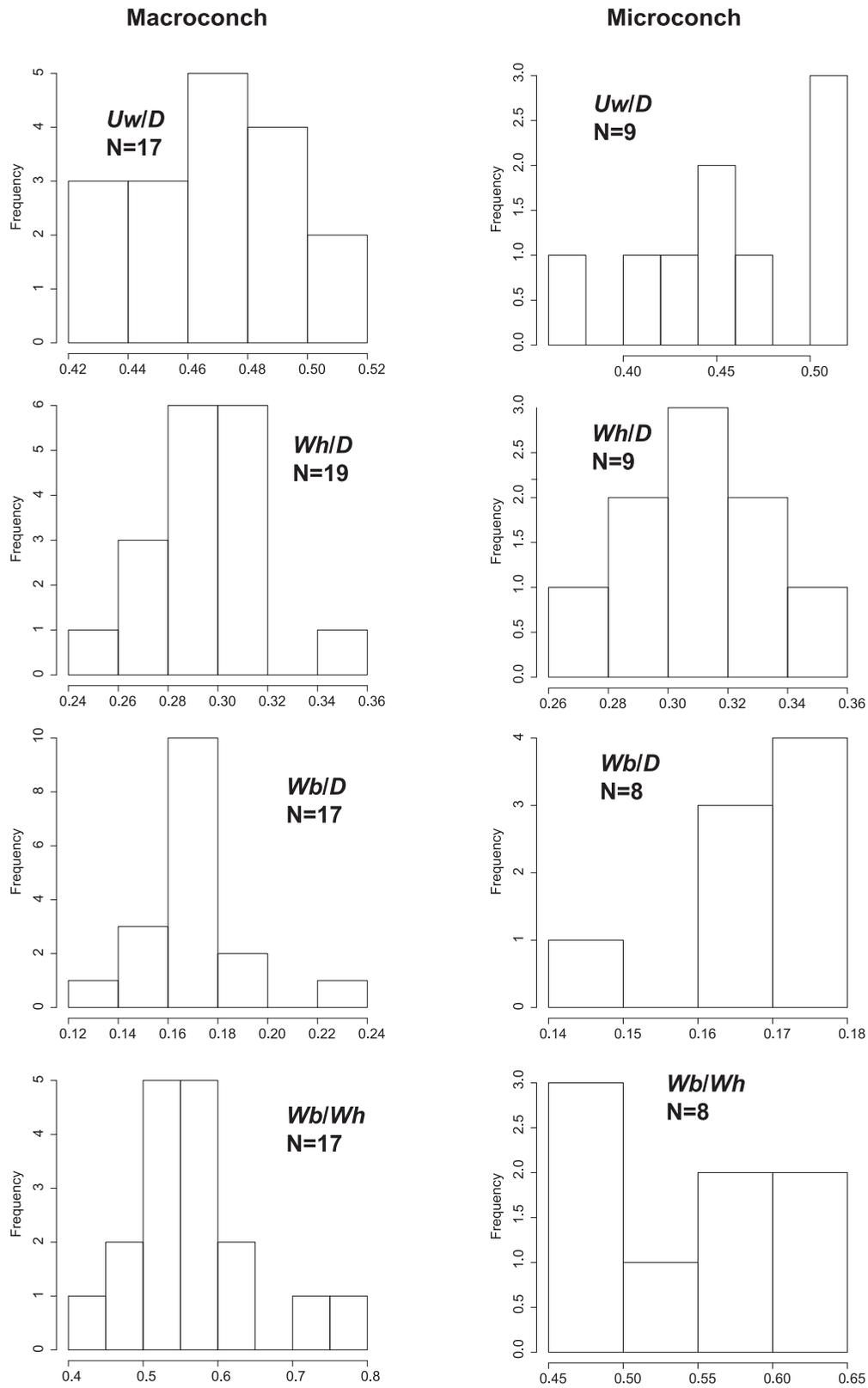


Figure 9. Shell shape parameters in the population of *Dactyloceras (Dactyloceras) laticostatum* sp. nov. for both macroconchs and microconchs.

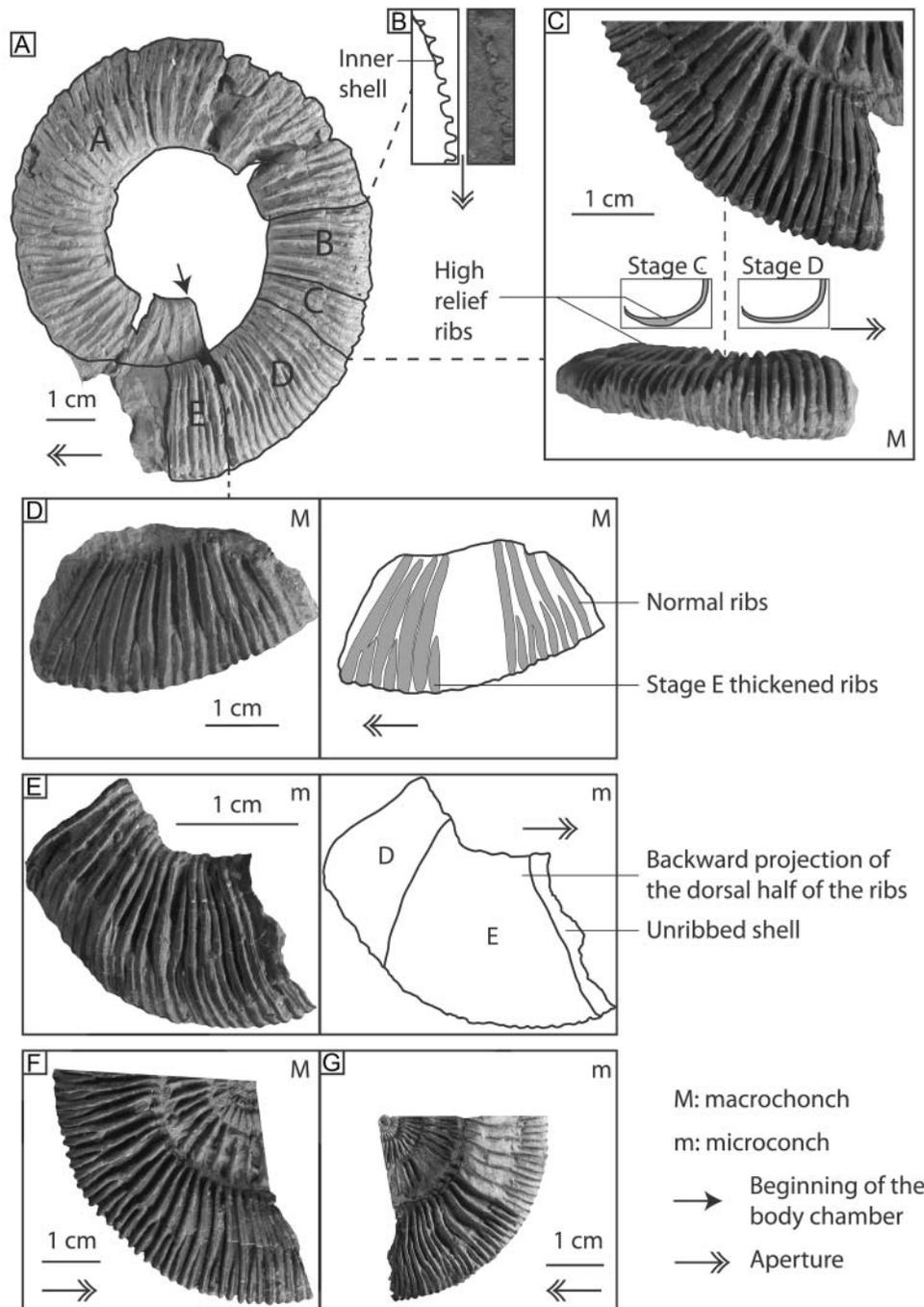


Figure 10. Drawings and photographs of *Dactylioceras (Dactylioceras) laticostatum* sp. nov. **A**, UPMC-734, specimen showing the five ornamental stages (A to E) in the adult macroconch body chamber. **B**, UPMC-450, sketch of the transition between stages A and B marked by the end of secretion of the inner shell layer. **C**, UPMC-757, transition from stages C to D showing the end of the ribbing with high relief on the middle of the flank. **D**, UPMC-468: transition from stages D to E showing the thickening of the ribs in macroconch specimens. **E**, end of stage D and stage E showing the backward directed dorsal half of the ribs and the unribbed shell at the end of growth in microconch specimens. **F**, **G**, comparison of fully grown macroconch (UPMC-757) and microconch (UPMC-449) specimens showing ontogenetic ornamental differences.

Diameter mean (mm)	45 ⁽⁷⁾ 37 ⁽²⁾	58 ⁽¹¹⁾	65 ⁽⁴⁾	67 ⁽⁵⁾	72.2 ⁽⁶⁾ 49.4 ⁽³⁾
Angle mean (°)		254 ⁽²⁴⁾	348 ⁽¹⁹⁾ 236 ⁽⁴⁸⁾	83 ⁽¹⁷⁾	33 ⁽¹⁷⁾ 15 ⁽⁴⁾ 14.5 ^(1,5)
Stages		A	B	C	D E
Inner shell	=====	—————			
Thickening of the inside of the shell forming the mouth border constriction					—————
Primary ribs with high relief on the middle of the flank	=====	—————			
Ribbing Division Index	2.1 ^(.12) 1.2 ^(.13)	2.05 ^(.2) 1.2 ^(.08)			
Rib density (rib/degree)	secondary .37 ^(.06) primary .4 ^(.1)	.53 ^(.13) /	.32 ^(.06) /	.4 ^(.1) /	
	.29 ^(.03) /	.3 ^(.06) /	.14 ^(.01) /	.15 ^(.03) /	
Legend	<p>— both dimorphs</p> <p>— macroconchs (values in bold)</p> <p>— microconchs (values in italics)</p> <p>beginning of the adult body chamber</p> <p>adult mouth border</p>				

Figure 11. Characteristics of different features of *Dactylioceras* (*Dactylioceras*) *laticostatium* sp. nov. subdivided into five different ornamental stages (A to E). Bold characters and thick grey lines correspond to macroconchs, italic characters and thick white lines to microconchs. For each couple of values (e.g. 45(7)), the unbracketed value is the average, whereas the bracketed value corresponds to the standard deviation.

Confusion can also be made with *D. (O.) semicelatum* but primary rib density is much lower in the new species. It also shows similarities with *D. (O.) hispanum* (Schmidt-Effing, 1972) but differs because of its more evolute shell (Uw/D (*laticostatium*) = 0.46 > Uw/D (*hispanum*) = 0.49), higher whorls (Wh/D (*laticostatium*) = 0.30 > Wh/D (*hispanum*) = 0.28) and lower rib density. This species has already been recognized by several authors but never described because of the lack of well-preserved material (e.g. bed 13, outcrop of Saragosse; Mouterde 1971).

?Nodicoeloceras/?Orthodactylites sp. indet. A
(Fig. 8L–O)

Material. 13-Ia: UPMC-233, 243. 14-IIIa: UPMC-406. 14-IVa: UPMC-442.

Occurrence. Lower Toarcian (Mirabile Subchronozone to Semicelatum Subchronozone) in our succession.

Description. This species is characterized by evolute and very depressed cadicone shells. Inner whorls bear tubercles which are nearly as numerous as the primary ribs.

?Nodicoeloceras/?Orthodactylites sp. indet. B
(Fig. 8P–T)

Material. 13-Ia: UPMC-230. 14-IVa: UPMC-433, 441.

Occurrence. Semicelatum Subchronozone.

Description. The shell is moderately evolute with depressed whorls. Changes in the ornamentation allow the definition of four ontogenetic stages. The first stage is characterized by the absence of ribbing up to a diameter of 5 mm. In the second stage, ribs appear and each primary bears a small spine. In the third stage, which starts from a diameter of around 12 mm, spines are not inserted on every primary rib. The recurrent pattern is three spines on three consecutive primary ribs followed by one or

rarely two ribs lacking spines. In the fourth and last stage, spines disappear. No definite characters showing the end of growth have been observed. None of the three specimens found bear all ontogenetic stages preserved, thus we leave this new species in open nomenclature.

Remarks. Unlike most of the *Nodicoeloceras*, there is no significant change in the shape of the whorl during ontogeny.

Superfamily **Hildoceratoidea** Hyatt, 1867
 Family **Hildoceratidae** Hyatt, 1867
 Subfamily **Harpoceratinae** Neumayr, 1875
 Genus ***Lioceratoides*** Spath, 1919

Type species. *Leioceras? grecoi* Fucini, 1901, by original designation = *Prealeioceras grecoi* in Fucini, 1931, p. 94.

Occurrence. Middle Domerian to Lower Toarcian.

Description. The shell is involute with a discoidal whorl section and a narrow ventral area. The diameter of most specimens is less than 40 mm. Ornamentation is composed of very weak and numerous falcoid ribs. In early whorls, rib relief is more pronounced at the mid-lateral inflection point; secondary ribs are thinner and weaker. Some large specimens show that ribs in mature whorls are similar to the above-described ones but the relief at the mid-lateral inflection point is very weak. Each species bears a thin keel.

Remarks. This genus has a complicated taxonomic and nomenclatural history (see Braga 1983; Macchioni & Meister 2003; Ferretti 2008). According to Ferretti (2008), dimorphism can be recognized by plotting rib density against diameter: one dimorph has narrowly spaced and thin ribs (*Lioceratoides*), the other has widely spaced and large ribs (*Neolioceratoides*). There are three reasons for maintaining a traditional view of the genus in contrast to Ferretti's interpretation. First, his figure 15 of *Lioceratoides* species does not show the above-mentioned pattern (Ferretti 2008). Secondly, Ferretti did not take into account the discontinuous pattern of rib relief, which represents an important part of the morphological variability and the basis for the distinction of *Lioceratoides* species. Thirdly, most of the specimens are poorly preserved and do not allow observation of the three successive ribbing stages.

Lioceratoides serotinus (Bettoni, 1900)
 (Fig. 12A–F)

1900 *Hildoceras* (?) *serotinum* Bettoni: 65, pl. 6, figs 7, 8.
 1923 *Praelioceras naumachense* Fucini: 74, pl. 14, fig. 11.
 1923 *Praelioceras scuderi* Fucini: 74, pl. 14, fig. 14.

1969 *Harpoceratoides* aff. *serotinum* (Bettoni); Gallitelli-Wendt: 21, pl. 7, figs 5, 6.

?1972 *Lioceratoides serotinus* (Bettoni); Ferretti: p. 113, fig. 5.

1983 *Lioceratoides serotinus* (Bettoni); Braga: 191, pl. 8, figs 1–3 (*cum syn.*).

?1992 *Lioceratoides serotinus* (Bettoni); Howarth: 68, pl. 5, fig. 1.

non 2002 *Lioceratoides* aff. *serotinum* (Bettoni); Bécaud: pl. 1, fig. 6. [= *Harpoceratoides* sp.].

2004 *Lioceratoides serotinus* (Bettoni); Morard: 304, pl. 11, fig. 5.

2007 *Lioceratoides* gr. *serotinum* (Bettoni); Fauré *et al.*: 494, fig. 7d–h.

Types. The specimen figured by Bettoni (1900: pl. 6, fig. 7) was lectotypified by Kottek (1966, p. 107).

Material. 14-IIa: UPMC-268, 269, 270, 271, 284, 285. 14-IIIa: UPMC-403, 410, 411, 418, 420, 423. From rubble: UPMC-234.

Occurrence. Upper Pliensbachian (Emaciatum Chronozone) to Lower Toarcian (Polymorphum Chronozone), Italy, Spain, Morocco, France (?), Tunisia and Russia (?). Lower Toarcian (Mirabile Subchronozone) in our succession.

Description. Evolute shells whose umbilicus width can decrease in the last whorl. The ornamentation in the early whorls consists of thickening of the ribs from their mid-lateral inflection point up to the ventrolateral margin. In the following whorls, ribs bifurcate or trifurcate from the mid-lateral inflection point, whose relief decreases. In the last whorl, rib relief is very weak in the upper half of the flank.

Remarks. This species is similar to *Lioceratoides lorioli* (Bettoni, 1900). However, the relief of the ribs in *L. serotinus* shows very thin ribs sometimes comparable to striae on the ventral sides, whereas *L. lorioli* shows large ribs of low relief, most of the time barely visible.

Genus ***Neolioceratoides*** Cantaluppi, 1970

1994 *Petranoceras* Venturi in Faraoni *et al.*: 256.

Type species. *Hildoceras (Lillia) hoffmanni* Gemmelaro, 1886a by original designation.

Occurrence. Upper Pliensbachian to Lower Toarcian.

Description. This genus groups evolute shells with a sub-rectangular whorl section. The ornamentation is made of strong sinuous ribs whose relief strongly increases from the mid-lateral inflection point to the ventrolateral edge. The ventral area is tricarinate.



Figure 12. A–F, *Lioceratoides serotinus* (Bettoni, 1900); A, UPMC-418, 14-IIIa; B, UPMC-270, 14-IIa; C, UPMC-271, 14-IIa; D, UPMC-285, 14-IIa; E, UPMC-403, 14-IIIa; F, UPMC-268, 14-IIa. G–K, *Neolioceratoides schopeni* (Gemmellaro, 1886a); G, UPMC-283, 14-IIa; H, UPMC-273, 14-IIa; I, UPMC-274, 14-IIa; J, UPMC-286, 14-IIa; K, UPMC-417, 14-IIIa. L–M, *Protogrammoceras palatum* (Buckman, 1922), UPMC-236, 13-Ia. Scale bar = 1 cm.

Remarks. The main characteristics of *Neolioceratoides* (i.e. specific ribs relief) can be observed in other genera (e.g. *Petranoceras* and *Mercaticeras*). We also find strong morphological similarities with the inner whorls of *Protogrammoceras bassanii* Fucini, 1900. A thorough revision of the morphological variation of these genera is needed, which would lead to a better taxonomic arrangement for these ammonites.

Neolioceratoides schopeni (Gemmellaro, 1886a)
(Fig. 12G–K)

- 1886a *Hildoceras* (*Lillia*?) *schopeni* Gemmellaro: 121, pl. 1, fig. 23, pl. 2, figs 5–7.
1972 *Bassaniceras bassanii* (Fucini); Ferretti: 116, pl. 17, figs 3, 4.
1982 *Neolioceratoides schopeni* (Gemmellaro); Braga *et al.*: 137, pl. 2, figs 3–5.
1983 *Neolioceratoides schopeni* (Gemmellaro); Braga: 209, pl. 9, figs 5–8 (*cum syn.*).
1992 *Neolioceratoides schopeni* (Gemmellaro); Jiménez & Rivas: 57, pl. 4, figs 8–10.
1992 *Hildaites serpentinus* (Reinecke); Jiménez & Rivas: 61, pl. 4, fig. 4.
1992 *Hildaites levisoni* (Simpson); Jiménez & Rivas: 60, pl. 4, figs 3, 5.
2004 *Neolioceratoides schopeni* (Gemmellaro); Morard: 304, pl. 11, figs 3, 4.

Types. The specimen figured by Gemmellaro (1886a, p. 121, pl. 2, fig. 6) was lectotypified by Braga (1983).

Material. 14-IIa: UPMC- 273, 274, 283, 285, 286. 14-IIIa: UPMC-412, 417.

Occurrence. Upper Pliensbachian (Emaciatum Chronozone) to Lower Toarcian (Polymorphum Chronozone), Spain, Italy and Morocco. Lower Toarcian (Mirabile Subchronozone) in our succession.

Description. This species is characterized by the strongest ribs of the genus.

Genus *Protogrammoceras* Spath, 1913

- 1886b *Wrightia* Gemmellaro: 190.
1922 *Paltarpites* Buckman: pl. 362A.
1923 *Argutarpites* Buckman: pl. 363.
1929 *Bassaniceras* Fucini: 63.
1970 *Eoprotogrammoceras* Cantaluppi: 42.
1970 *Neoprotogrammoceras* Cantaluppi: 42.

Type species. *Protogrammoceras bassanii* Fucini, 1901, designated by Spath (1919, p.174).

Occurrence. Lower Pliensbachian (upper part of the Jamesoni Subchronozone) to Lower Toarcian (Polymorphum Chronozone).

Description. Harpoceratinae with planulate shell, flat sides and uncarinate or carinate bisulcate venter. The keel is hollow. The ornamentation consists of gently falcooid ribs.

Protogrammoceras paltum (Buckman, 1922)
(Figs 12L, M, 13A, C, D)

- 1922 *Paltarpites paltus* Buckman: pl. 362A.
1976 *Paltarpites* aff. *paltus* Buckman; Gabilly: 75, pl. 2, figs 4–7.
1976 *Paltarpites paltus* Buckman; Gabilly: 72, pl. 3, figs 1–6.
1976 *Protogrammoceras paltum* (Buckman); Schlegelmilch: 94, pl. 56, fig. 4.
?1981 *Protogrammoceras* cf. *paltum* (Buckman); Imlay: 41, pl. 12, figs 11, 12.
V 1992 *Protogrammoceras* (*Protogrammoceras*) *paltum* (Buckman); Howarth: 57, text-fig. 11, pl. 1, figs 1–3, pl. 2, figs 1, 2 (*cum syn.*).
?2002 *Protogrammoceras paltum* (Buckman); Macchioni: fig. 4.2.
2006 *Protogrammoceras* (*Paltarpites*) aff. *madagascariense* Thévenin; Bécaud: 46, pl. 3, fig. 1.
2009 *Paltarpites toyoranus* Matsumoto; Nakada & Matsuoka: pl. 1, fig. 8.
2009 *Paltarpites paltus* Buckman; Nakada & Matsuoka: pl. 1, fig. 9.

Types. Buckman (1922) selected the specimen figured as pl. 362a as the holotype. It has been refigured by several authors (e.g. Howarth 1992, p. 57, pl. 2, fig. 2; Schlegelmilch 1976, pl. 56, fig. 4).

Material. 7-Ia: UPMC-541. 7-IIa: UPMC-634. 13-Ia: UPMC-236. 14-IVa: UPMC-439. From rubble: UPMC-781.

Occurrence. Upper Pliensbachian (upper part of the Margaritatus Chronozone) to Lower Toarcian (Polymorphum Chronozone), Spain, Morocco, England, Germany, France and Italy. Lower Toarcian (Semicelatum Subchronozone) in our succession.

Description. This species is moderately evolute (adult $U_w/D \approx 0.33$). The umbilical wall is vertical and the umbilical edge rounded. Flanks are slightly convex. The strong hollow keel is bordered by two narrow and flat areas. Up to a diameter of almost 3 cm, ribs are sinuous, blunt and marked only on the ventrolateral area. Then, ribs become falcooid and their relief develops on the entire flank. Rib density generally increases in the adult body chamber but in one of our specimens (UPMC-781,



Figure 13. A, C, D, *Protogrammoceras paltum* (Buckman, 1922); A, UPMC-439, 14-IVa; C, D, UPMC-781, from rubble. B, E, F, *Maconiceras soloniacense* (Lissajous, 1906); B, UPMC-644, 7-IIIa; E, F, UPMC-452, 14-XIIa. G, H, *Cleviceras* aff. *exaratum* Young & Bird, 1828; G, UPMC-662, 7-1a; H, UPMC-588, 7-1a. Arrows indicate the beginning of the body chamber. Scale bar = 1 cm.

Fig. 13D) the observed increase is followed by a decrease. We should note that the body chamber is incomplete, its trace on the preceding whorl suggests that a 1/7 whorl has not been preserved.

Genus *Maconiceras* Buckman, 1926

1928 *Phaularpites* Buckman (type species *Phaularpites exiguus* Buckman, 1928).

Type species. *Maconiceras vigoense* Buckman, 1926.

Description. Moderately evolute shell reaching a diameter between 40 and 50 mm. The ornamentation develops in three stages. The first stage is characterized by strong, blunt, distant, sinuous ribs; simple and intercalatory ribs alternate. The second stage starts at the beginning of the last whorl (D between 32 and 40 mm): the rib density increases, ribs are stronger from the venter up to mid flank. The final stage, starting from a D between 35 and

45 mm, shows a ribbing similar to the one of the first stage and the relief of the mid-lateral inflection point is strong. Some specimens show the mouth with a long rostrum at the end of the growth.

Occurrence. Lower to Middle Toarcian.

Remarks. *Maconiceras* is considered to be the microconch of the genus *Harpoceras* (Gabilly 1976). It is worth noting that this genus is morphologically very close to *Lioceratoides*.

Maconiceras soloniacense (Lissajous, 1906)
(Fig. 13B, E, F)

1976 *Harpoceras* (*Maconiceras*) aff. *soloniacense* (Lissajous); Gabilly: 111, pl. 10, figs 3–7, pl. 11, figs 4–6.

1992 *Harpoceras falciferum* (Sowerby); Howarth: 119, pl. 20, figs 3, 4, 6–11.

1992 *Harpoceras soloniacense* (Lissajous); Howarth: 133, pl. 21, figs 4, 6–8, pl. 22, figs 1–3.

2002 *Maconiceras soloniacense* (Lissajous); Neige & Rouget: 770, fig. 3D.

Types. Buckman (1926, pl. 684) designated as the lectotype the specimen figured by Lissajous (1906, pl. 1, fig. 5).

Material. 7-IIa: UPMC-656. 7-IIIa: UPMC-644, 653b. 7-Va: UPMC-713. 13-IIa: UPMC-743. 14-XIIa: UPMC-452.

Occurrence. Lower Toarcian (Serpentinum Chronozone) to Middle Toarcian (Bifrons Chronozone), England and France. Lower Toarcian (Mirabile Subchronozone) in our succession.

Description. Evolute shell with slightly rounded flanks. The keel is bordered by sulci.

Genus *Cleviceras* Howarth, 1992

Type species. *Ammonites exaratus* Young & Bird, 1828, p. 266.

Occurrence. Toarcian.

Description. Moderately evolute to involute (adult $U_w/D \approx 0.25$) compressed shells with flat flanks. Umbilical walls are sloping, vertical or undercut depending on the species. The hollow keel is bordered by narrow and smooth areas. The ornamentation is made of falcoid ribs. Two ornamental stages have been recognized. The first stage can be compared to the ‘maconiceras stage’ (Gabilly 1976) of *Harpoceras* and consists of bifurcating ribs and striae, whereas the second stage is composed of simple, flat-topped and well-defined ribs. Howarth (1992) published a complete study of the mature characters of both dimorphs.

Cleviceras aff. *exaratus* (Young & Bird, 1828)
(Fig. 13G, H)

1828 *Ammonites exaratus* Young & Bird: 266.

1992 *Cleviceras exaratus* (Young & Bird); Howarth: 90, pl. 9, figs 2–6, pl. 10, figs 1–8, pl. 11, figs 1–5, pl. 13, figs 1, 2, text-figs 10, 16, 18C, 19C, 20, 21 (*cum syn.*).

Types. The holotype is the specimen figured by Buckman (1909, pl. 5).

Material. 7-Ia: UPMC-588. 7-IIIa: UPMC-662.

Occurrence. Lower Toarcian (Exaratum Subchronozone), England, Germany, Switzerland, Siberia and Canada. Lower Toarcian (Semicelatum Subchronozone) in our succession.

Description. Involute, compressed shell with a very narrow ventral area bearing a strong hollow keel. The ornamentation consists of simple falcoid ribs.

Remarks. Our specimens show a very narrow ventral area which is infrequent in *C. exaratus* but the well-defined simple ribbing is very similar. The shell shape of the two specimens could be confused with the morphologies of some *Lioceratoides* macroconchs such as *L. serotinus* or *L. aradasi*. However, the lack of preservation in the internal whorls does not allow us to observe the typical *Lioceratoides* characters.

Discussion

The Early Toarcian episode of biological extinction has been related to important biological disturbance provoked worldwide by the oceanic anoxic event (OAE) (Hallam 1987; Cecca & Macchioni 2004; Aberhan & Fürsich 1997, 2000; Harries & Little 1999; Fürsich *et al.* 2001; Dera *et al.* 2011). The OAE is commonly distinguished by black shales and a strong negative carbon isotope excursion interpreted as a response to abnormally high burial rates of organic carbon (Jenkyns 2010). Macchioni & Cecca (2002) dated the onset of the OAE within the Semicelatum Chronozone in both the Mediterranean and north-west Europe, and showed a longer duration (up to the base of the Bifrons Chronozone) of anoxia in the latter. Other authors have stressed problems in correlating biostratigraphical schemes defined in different areas with different ammonite faunas and have suggested that the OAE occurred at the end of the Semicelatum Subchronozone (Jenkyns 2010) or in an interval overlapping the boundary between the Polymorphum and the Levisoni chronozones (Kemp *et al.* 2005).

In the Moulay Idriss area, no organic-rich bed has been detected (Bassoullet *et al.* 1991) and no chemostratigraphical studies have been carried out. Furthermore, the low

rate of total organic carbon recorded in the Lower Toarcian and also in sections of the Moyen Atlas of Morocco indicates a continental influence (Bassoullet *et al.* 1991), which is also demonstrated by the occurrence of wood remains in our outcrops. The Early Toarcian OAE did not produce sedimentary and geochemical evidence in this area.

Non-ammonoid benthic mollusc faunas are relatively common in the studied succession. They indicate well-oxygenated conditions during the entire Polymorphum Chronozone, supporting the idea that anoxia did not occur in the South Riffian basin.

Very few ammonites have been found from 14-VIIIb to 14-Xb and very small-sized specimens occur in bed 14-XIa (Fig. 5). This could correspond to a Lilliput effect due to stressed conditions (Urbanek 1993). Some studies (Elmi & Benschili 1987; Mignot *et al.* 1993) have suggested that reduction in ammonite size could be due to small isolated basins with poor nutrient supply. However, this does not apply in the South Riffian area because Elmi & Faugères (1974) stressed that the South Riffian basin was not isolated. A similar size reduction has been reported by Morten & Twichett (2009) in molluscan faunas during the Semicelatum Subchronozone of England. Although black shales are not developed in our area, it is worth noting that deterioration of environmental conditions could have been caused by oxygen depletion in the marine environment.

The exact timing of both the onset of the extinction and the succession of disappearances of each species within the Semicelatum Subchronozone is unclear (Cecca & Macchioni 2004). The unfossiliferous beds lying above 14-XIIa could suggest the extinction event. From beds overlying bed 14-XIIa to those containing the first faunas typical of the Levisoni Chronozone there is a lithological transition (Elmi & Faugères 1974; Bassoullet *et al.* 1991). The lack of fossils at the base of the yellow-brown marls hampers the identification of the transition from the Polymorphum to the Serpentinum/Levisoni chronozone.

Conclusions

Faunas of the South Riffian Ridges span the chronostratigraphical interval of the Polymorphum Chronozone and allow biostratigraphical subdivisions of the Mirabile Subchronozone to be recognized. The occurrence in the South Riffian basin of North-West European taxa (e.g. *Dactylioceras* (*Orthodactylites*) *semicelatum*, *Protogrammoceras paltum*) and Mediterranean taxa (e.g. *Lioceratoides serotinus*, *Neolioceratoides schopeni*) allows correlation of the Lower Toarcian successions of these areas. The biostratigraphical ranges of the species *Cleviceras* aff. *exaratum* and *Maconiceras soloniacense*, which according to the literature appear in the Levisoni Zone, seem to start earlier

in the study area, that is in the Semicelatum Subchronozone. *Dactylioceras* (*Orthodactylites*) *semicelatum*, the index species of the latter Subchronozone, is here interpreted as dimorphic.

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Supplemental material

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