geodiversitas

2018 • 40 • 4

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art. 40 (4) — Published on 1 March 2018
www.geodiversitas.com

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NATIONAL D'HISTOIRE NATURELLE
PUBLICATIONS SCIENTIFIQUES

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diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

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ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

Lower Jurassic (Pliensbachian-Toarcian) belemnites from Fresney-le-Puceux (Calvados, France): taxonomy, chronostratigraphy and diversity

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Submitted on 12 May 2017 | accepted on 3 October 2017 | published on 1 March 2018

urn:lsid:zoobank.org:pub:1B9774F9-1B39-446A-BD3C-2DEC49993C83

Weis R., Neige P., Dugué O., Di Cencio A., Thuy B., Numberger-Thuy L. & Mariotti N. 2018. — Lower Jurassic (Pliensbachian-Toarcian) belemnites from Fresney-le-Puceux (Calvados, France): taxonomy, chronostratigraphy and diversity. *Geodiversitas* 40 (4): 87-113. https://doi.org/10.5252/geodiversitas2018v40a4. http://geodiversitas.com/40/4

KEY WORDS
Belemnites,
ammonites,
cephalopods,
stratigraphy,
Pliensbachian,
Toarcian,
la Roche Blain quarry,
Normandy.

ABSTRACT
The present paper deals with the systematic description of the belemnite assemblages from the Lower Jurassic, collected at the *Roche Blain* quarry, Fresney-le-Puceux. In spite of the reduced thickness of the succession at Fresney-le-Puceux, 13 successive ammonite chronozones could be documented in this rather unique outcrop situation in mainland Europe. Twelve genera and 26 species of belemnites belonging to the Passaloteuthididae, Hastitidae, Megateuthididae, Salpingoteuthididae, and family

incertae sedis are described and illustrated herein. The stratigraphical range of the belemnites is correlated with the standard ammonite zonation, using the chronozone concept: the described specimens range from the lower Pliensbachian (Davoei Chronozone) to the uppermost Toarcian (Aalensis Chronozone) while ammonites indicate the Aalenian (Murchisonae Chronozone) to be present too, but these beds delivered no identifiable belemnites so far. The belemnite diversity from Normandy is compared to data from coeval outcrops in Western and Central Europe.

RÉSUMÉ
Bélemnites du Jurassique inférieur (Pliensbachien-Toarcien) de Fresney-le-Puceux (Calvados, France): taxonomie, chronostratigraphie et diversité.
Cet article traite de la systématique des bélemnites du Jurassique inférieur récoltées dans la carrière de la Roche Blain à Fresney-le-Puceux. Malgré l'épaisseur réduite de la succession de Fresney-le-Puceux, 13 chronozones successives d'ammonites ont été documentées dans cet affleurement assez unique en Europe continentale. Douze genres et 26 espèces de bélemnites appartenant aux Passaloteuthididae, aux Hastitidae, aux Megateuthididae et aux Salpingoteuthididae, ainsi qu'à une famille *incertae sedis*, sont décrits et illustrés ici. L'extension stratigraphique des bélemnites est corrélée avec la zonation standard des ammonites en utilisant le concept de chronozone : les spécimens décrits s'étendent du Pliensbachien (Chronozone à Davoei) au Toarcien supérieur (Chronozone à Aalensis), tandis que les ammonites indiquent que l'Aalénien (Chronozone à Murchisonae) pourrait être présent, mais ces niveaux n'ont pas livré de bélemnites identifiables jusqu'ici. La diversité des bélemnites de Normandie est comparée à celle d'affleurements équivalents en Europe occidentale et centrale.

MOTS CLÉS
Bélemnites,
ammonites,
céphalopodes,
stratigraphie,
Pliensbachien,
Toarcien,
carrière la Roche Blain,
Normandie.

INTRODUCTION

The Jurassic outcrops of Normandy have been considered as reference sections for many palaeontological studies since the earliest 19th century, mainly for the abundance and good preservation of their fossils. Especially the Middle Jurassic outcrops have received worldwide attention classically encompassing the stratotype of the Bajocian stage, located nowadays along the coast of Bayeux, at Sainte Honorine-des-Pertes (Rioult 1964, 1971; Dugué *et al.* 1998). The Lower Jurassic outcrops have been intensively studied mostly during the 19th century, especially for their rich and well-preserved invertebrate faunas (*e.g.* Eudes-Deslongchamps 1865; Caumont 1849, d'Orbigny 1842-1851). Cephalopods are generally abundant in the fossil assemblages; thus, it is not surprising to note that belemnites from Normandy are present in most historical collections in France. However, despite their abundance, they gained little attention but for Eudes-Deslongchamps (1865), d'Orbigny (1842-1851), and Lissajous (1927). Only recently, Weis *et al.* (2015a) described a new belemnite genus, *Lissajousibelus* Weis *in* Weis, Dzyuba, Mariotti & Chesnier, 2015 from the Toarcian of Feuguerolles-sur-Orne. However, a more comprehensive study of the Lower Jurassic belemnites of Normandy lacked so far. It is the purpose of our work to report the diversity of the Pliensbachian-Toarcian belemnites and document their stratigraphical ranges.

GEOLOGICAL, PALAEOBIOGEOGRAPHIC AND LITHOSTRATIGRAPHICAL SETTING

Herein we study the section of the *Roche Blain* quarry near Fresney-le-Puceux, south of Caen (Normandy, France), where Jurassic outcrops are exposed (Fig. 1), visible as a Jurassic marine transgression event on the Brioverian basement (Upper Proterozoic). Here, Jurassic rocks range from the Pliensbachian to the Aalenian. The section has been studied previously by several authors (Rioult 1968; Dugué *et al.* 1998; Vernhet *et al.* 2002) and a detailed study of Pliensbachian ammonites, including a precise biostratigraphic framework, has been published recently by Dommergues *et al.* (2008).

Recent field work in the quarry allowed the authors of this study to collect bed-by-bed Pliensbachian, Toarcian, and Aalenian ammonites and belemnites. Cephalopods are among the most abundant macrofossils in the marly and calcareous beds of the section, other taxa occur more rarely (echinoderms, other molluscs, brachiopods, etc). Although our focus is on the Toarcian and Aalenian stages, some newly collected Pliensbachian ammonites are also figured, adding to the chronostratigraphic framework of Dommergues *et al.* (2008). During the Early Jurassic, the Normandy area corresponded to a complex marine system where local reliefs were abundant, sometimes acting as reefs (Fig. 2). However, the succession at the *Roche Blain* quarry does not show any of these reefs. Here its base consists of transgressive sandstones (erosion of the Armorican exposed land), dated as early Pliensbachian, discordantly overlying the Brioverian basement, succeeded by fossil-rich marly and calcareous sediments. The latter sediments were deposited in slightly deeper and less turbulent marine settings between the Palaeozoic synclines of May in the north and Urville in the south (see Dommergues *et al.* 2008: fig. 2). Here, the Jurassic succession is approximately 9 m thick.

The Pliensbachian to Toarcian succession of the *Roche Blain* quarry is divided into four geological formations (Fm) comprising seven members (Mb) (Table 1).

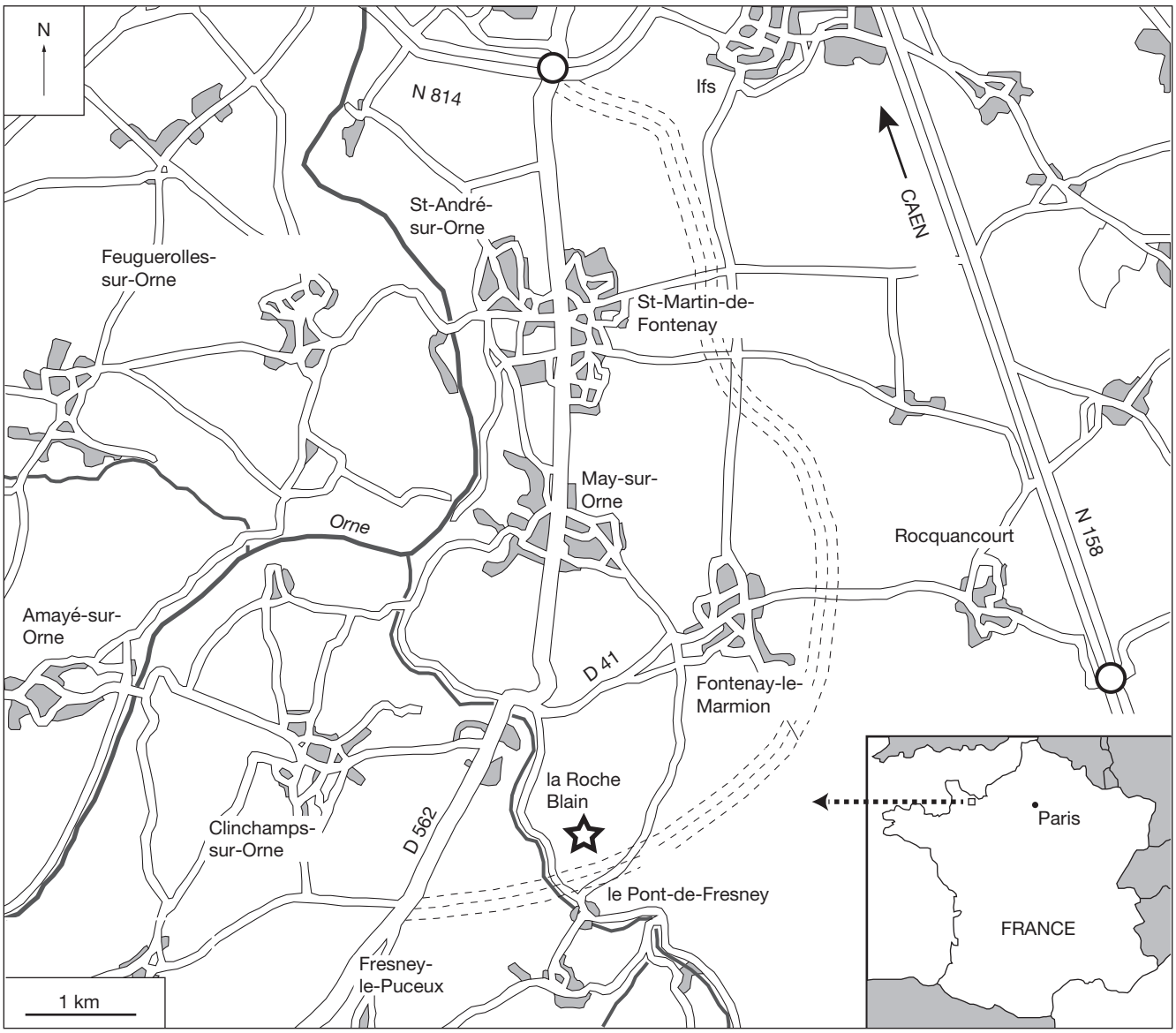

Fig. 1. — Geographical setting of the *Roche Blain* quarry (Normandy, France); modified after Dommergues *et al.* 2008.

Table 1. — Lithostratigraphical subdivision of the studied outcrop.

Formations (Fm)		**Members (Mb)**		**Age**
Calcaire à ammonites	±2.7 m	Calcaire à grains ferrugineux	0.8 m	Upper Toarcian
		Calcaire à *Grammoceras*	1.6 m	Upper Toarcian
		Marnes à *Haugia*	0.3 m	Upper Toarcian
		Calcaires et marnes à *Hildoceras*	0.8 m	Lower Toarcian
Argiles à poissons	0.3 m	–	–	Lower Toarcian
Couche à Tenuicostatum	0.2 m	–	–	Lower Toarcian
Calcaire à bélemnites	±6.8 m	Banc de Roc	1.7 m	Upper Pliensbachian
		Marnes à bélemnites	0.5 m	Lower-upper Pliensbachian
		Calcaire à *Cincta numismalis*	4.6 m	Lower Pliensbachian

THE "*CALCAIRE À BÉLEMNITES*" FM

*The "*Calcaire à *Cincta numismalis" Mb*

At the contact with the Brioverian basement, the first Jurassic deposits are detrital, with fining upward sequences of conglomerates to sandstones (mainly consisting of rworked Triassic sediments), gradually passing upwards into clayey sandstones with belemnites and bivalves, passing upwards into densely bioturbated, bioclastic marl-limestone alternations, with ferruginous pelletoids. The thickness of the marly interbeds decreases upwards in favour of the calcareous banks. In the Bessin area west of the Fresney-le-Puceux section, this member thickens towards the west (Bessin), with more marl-limestone alternations (8 to 10 m). However, to the SW of Caen, and beyond the Palaeozoic paleorelief, these alternations reach a thickness of 2.5 to 4.5 m and are more calcareous and bioclastic, while in the vicinity of the Palaeozoic palaeorelief, they become a crinoidal limestone.

*The "*Marnes à bélemnites*" Mb*

This member consists of blackish pyrite-rich and bioclastic marls, with abundant belemnites and bioturbation, upwards becoming richer in small ferruginous peloids. These marls are intersected by beds of flattened clayey calcareous nodules bioturbated by *Chondrites* and *Planolites* ichnofossils. This member is thick around Bayeux, but decreases in thickness towards the SW of Caen where it was deposited between the Palaeozoic paleoreliefs (e.g. at the *Roche Blain* quarry), and laterally grades into bioclastic limestones with belemnites above the Palaeozoic palaeorelief of the May's syncline, eventually disappearing towards the south.

*The "*banc de Roc*" Mb*

This member is a key regional lithological unit, which has been used as marker bed in the field. In the Fresney-le-Puceux quarry, at the base stacked decimetric bioturbated biomicrites occur, rich in belemnites and ferruginous oolites. These calcareous beds are separated by thin marly layers and become amalgamated upwards, with irregular and partly stylolithic boundary surfaces. To the SW and S of Caen, and beyond the Palaeozoic palaeorelief, the limestones are intensely bioturbated and rich in ferruginous peloids. Over the palaeorelief, the marly interbeds disappear. The upper erosional surface of the "*banc de Roc*" Mb is overlain by a thin marly interbed that grades upwards into a bioturbated micritic limestone (biopelmicrite), with rare belemnites and ammonites ("*Couche à Tenuicostatum*" Fm).

THE "*COUCHE À TENUICOSTATUM*" FM

Consists of condensed carbonates, with ferrugineous peloids, deposited in vertical continuity with the "*banc de Roc*", beyond the palaeoreliefs. The facies of the "*Couche à Tenuicostatum*" Fm is quite similar both in terms of lithology and sedimentology with the underlying "*banc de Roc*" Mb. On the contrary, above this Formation, a significant sedimentary change appears ("*Argiles à poissons*" Fm, see below).

THE "*ARGILES À POISSONS*" FM

Consists of grey, bioturbated marls, with ferruginous oolites, rich in belemnites and ammonites, and including centimetre-scale bioturbated nodular micritic limestone beds. In the vicinity of Caen, the "*Argiles à poissons*" Fm is only recognised beyond the Palaeozoic palaeorelief. To the SW of Caen (Bessin), it is represented by the typical laminated (bituminous) facies, with calcareous nodules. These bituminous facies are absent in the *Roche Blain* section. Near the Palaeozoic palaeorelief, the thickness of this formation decreases and includes abundant ferruginous peloids.

THE "*CALCAIRE À AMMONITES*" FM

*The "*Calcaires et marnes à *Hildoceras" Mb*

This member is a clayey limestone with a very irregular lower surface, surmounted by a stromatolitic pavement. The uppermost part is characterised by amalgamated, decimetric thick bioclastic calcareous beds, with scattered ferruginous oolites and small ferruginous oncoliths. This member is thick in the Cotentin and Bessin area (6-8 m), but thins towards the Caen district, even disappearing above some Palaeozoic palaeorelief and towards Falaise (Rioult 1980). On the Palaeozoic palaeorelief of the May syncline (Feuguerolles) and in the nearby *Roche Blain* quarry, the first beds are encrusted with calcareous stromatolites.

*The "*Marnes à *Haugia" Mb*

This member is characterised by bioturbated grey marls with ferruginous oolites, and clayey calcareous nodules. Now the terrigenous facies appears both on the Palaeozoic palaeorelief and beyond, corresponding to a new transgressive incursion, expressed as bioturbated marls, containing abundant phosphatised ammonites.

*The "*Calcaire à *Grammoceras" Mb*

This member consists of an alternation of marls and micritic limestones, with ferruginous oolites.

*The "*Calcaire à grains ferrugineux*" Mb*

This member is a condensed limestone with phosphatised ammonites and ferruginous oolites. It is overlain by an erosional surface and covered by the "*Marnes à ammonites*" Mb which has a lateral lenticular form. The "Calcaire à ammonites" Fm is locally truncated by the Aalenian "*Oolithe ferrugineuse*" Fm, a condensed lenticular deposit (0.2 to 0.8 m), including small ferruginous oolites. It is exposed from Cotentin to Bessin, in the Caen district, and at Falaise, but it is absent around Le Havre and to the south of the Falaise massif (Rioult 1980).

CHRONOSTRATIGRAPHY

The investigated section yielded several stratigraphically important ammonites (cf. Dommergues *et al.* 1997; Elmi *et al.* 1997; Page 2003), of which some were not previously mentioned by Dommergues *et al.* (2008), substantiating and

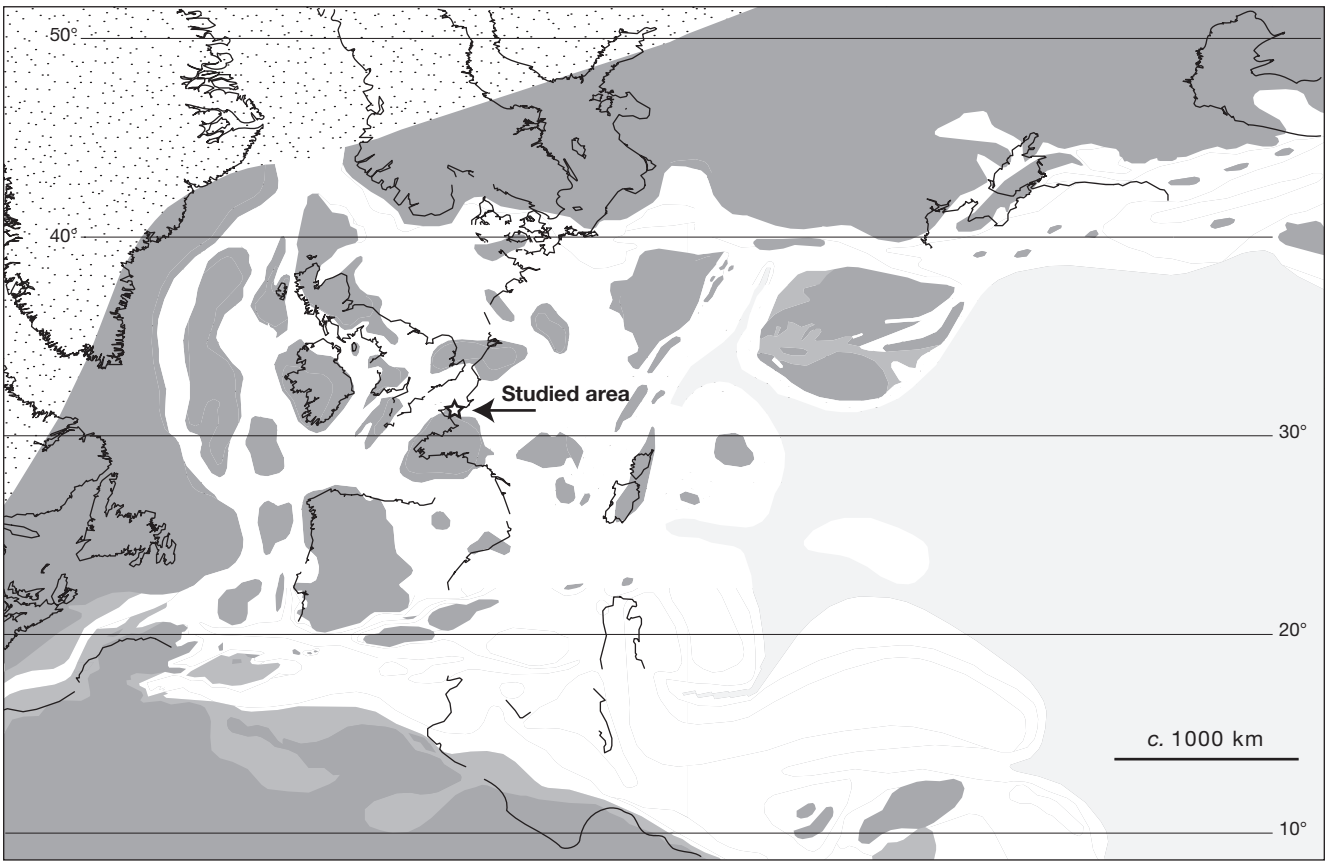

FIG. 2. — Paleogeographical map and location of the *Roche Blain* quarry during the Toarcian (modified after Thierry & Barrier 2000). **Light grey**, deep oceanic basins; **white**, shallow marine to deep marine; **mid-grey**, shallow environments with fluctuating salinities; **dark grey**, exposed land.

adding to their chronostratigraphical scheme for this section (Figs 3, 4). This scheme, as elaborated by Page (2003), corresponds to a standard zonation scheme where chronozones (and subchronozones) are defined by their base only. It gives us the opportunity to establish a framework which will serve as a reference to document the temporal distribution of the belemnite species (Figs 5, 6).

The systematic description of the ammonite faunas exceeds the scope of the present paper, but the section yields taxa well-known from the north-west European paleobiogeographical province (Howarth 1992; Dommergues *et al.* 1997; Page 2003). Therefore, we figured only some stratigraphically important species (Figs 7-9).

MATERIAL AND METHODS

The fossils were collected in 2015 and 2017 during joint field work by collaborators from the Luxembourg Natural History Museum, and the universities of Caen and of Burgundy (Dijon). All the specimens were collected in situ (unless otherwise specified), including numerous ammonites, and some 200 belemnite specimens, of which 164 were identified at species level. The studied belemnite material is housed at the Musée national d'Histoire naturelle de Luxembourg (MNHNL); the illustrated ammonite specimens are housed partially at the geological collections of Université de Bourgogne (UBGD) and in part at the MNHNL. Additional belemnites from the Feuguerolles-sur-Orne section, used herein as a control for belemnite diversity in Normandy (Table 1), are housed in the private collection of Marc Chesnier (Cresserons, Calvados, France).

In general, the preservation of the belemnite rostra is good, although phragmocones are rarely preserved. Most specimens show traces of endo- and/or epibionts. The collected rostra were cleaned from the matrix using a sandblaster with iron powder at 6-8 bar pressure. Illustrated ammonites and belemnites were coated with magnesium oxide prior to photographing.

SYSTEMATIC DESCRIPTIONS

The systematic employed herein follows the proposals and revisions of Doyle (1994, 2003, 2010), Riegraf *et al.* (1998), Riegraf (2000), and Weis *et al.* (2015b). Synonymy lists and geographic occurrences are confined to papers with detailed descriptions and/or proper illustrations, eventual additional synonyms may be found consulting the indicated literature,

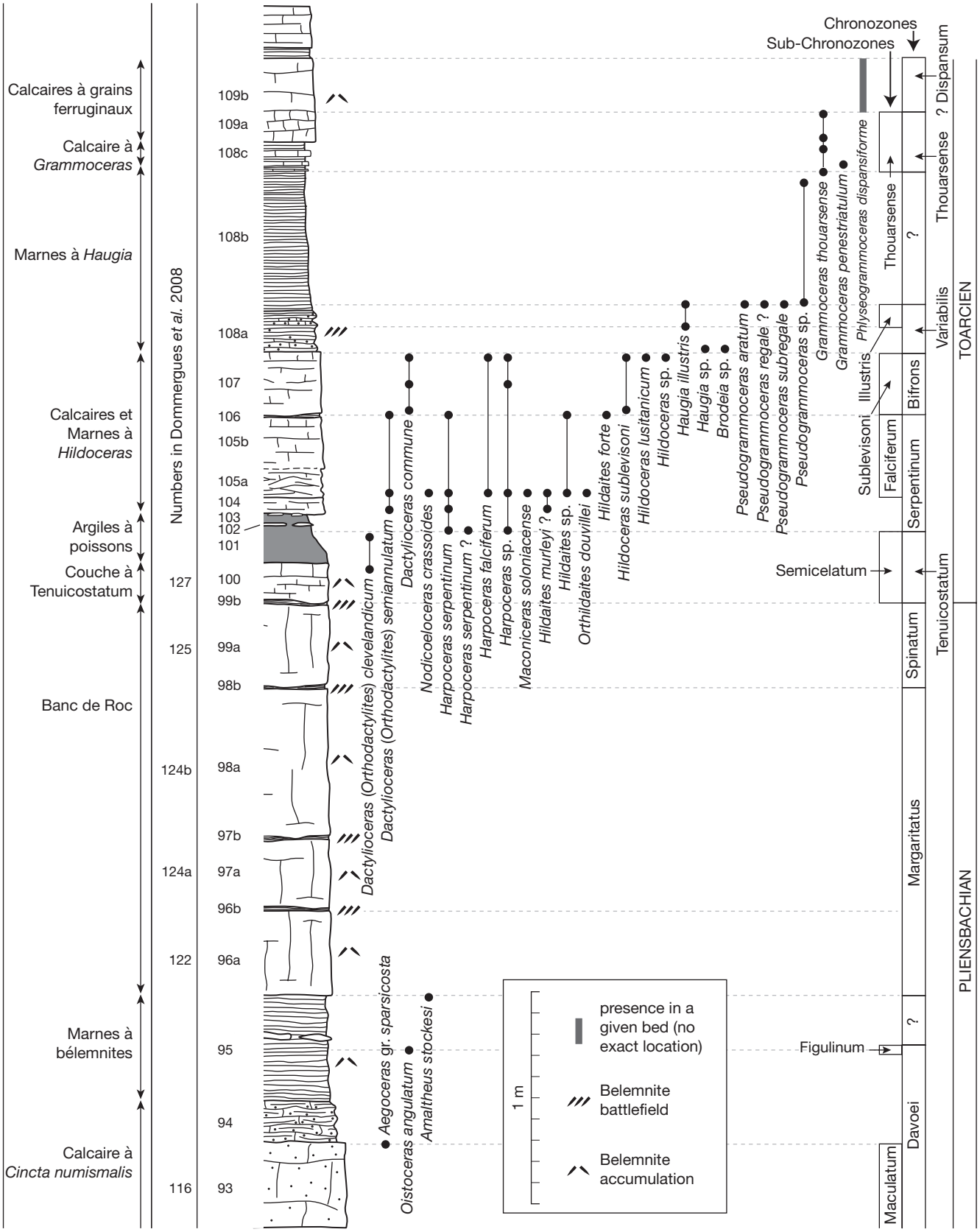

FIG. 3. — Stratigraphic occurence of collected ammonites and chronostratigraphic scheme of the section (Part 1, bottom). Left: main lithostratigraphic units recognised in the literature (Formations or Members, see text), following Dugué *et al.* 1998.

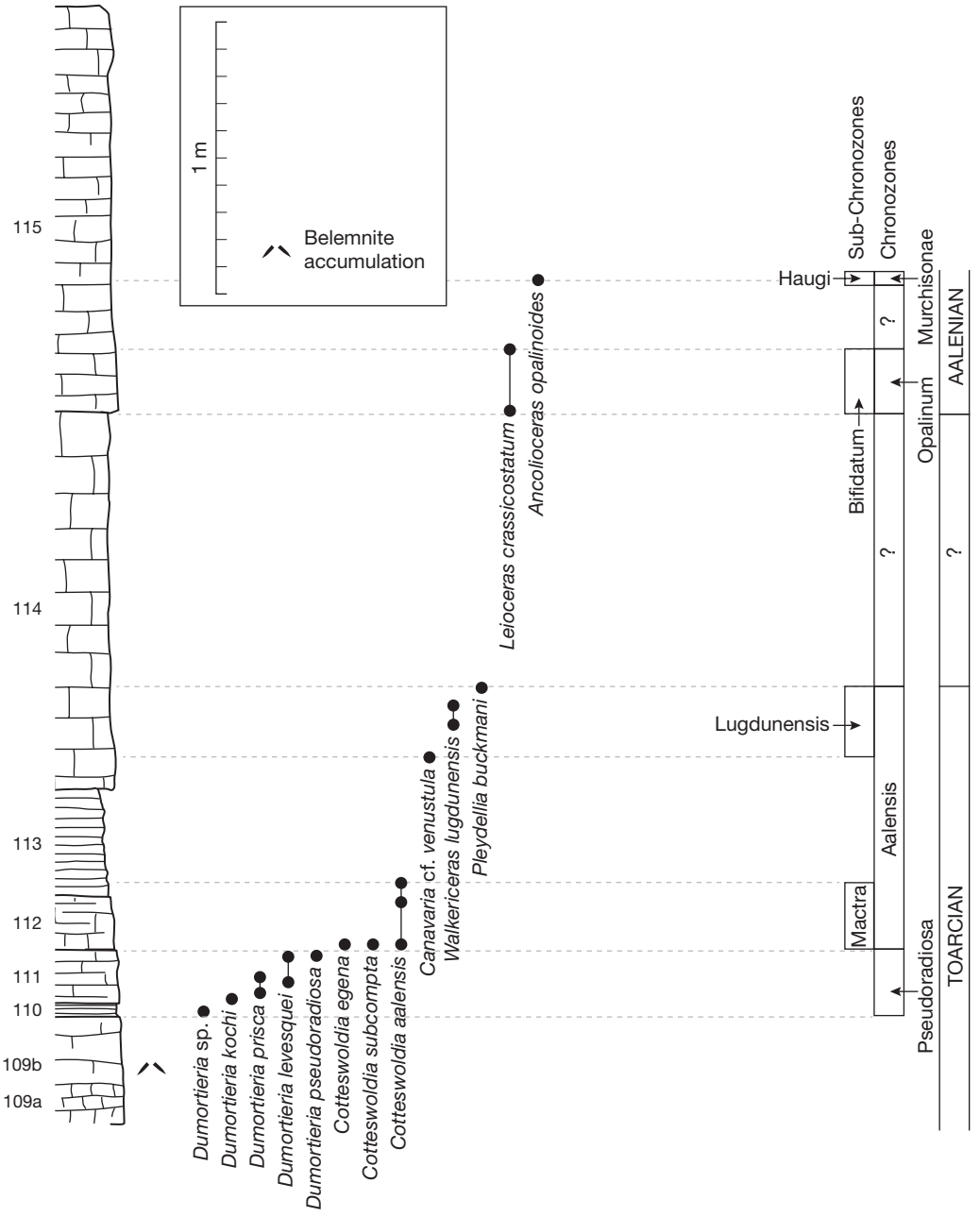

FIG. 4. — Stratigraphic occurence of collected ammonites and chronostratigraphic scheme of the section (Part 2, top).

especially the references marked by "*cum syn.*". Descriptive terms are used according to Doyle & Kelly (1988) and Doyle (1990), while size categories are as follows: "very small" (< 30 mm), "small" 30-60 mm, "medium" (61-100 mm), "large" (101-150 mm), and "very large" (> 150 mm). The used compression index (I_c) is the ratio between the dorso-ventral diameter and the lateral diameter; values of > 1 indicate a (laterally) compressed rostrum, values of < 1 indicate a (dorsoventrally) depressed rostrum. Further measurements were not retained useful for the purpose of the present paper, as most taxa are represented by only a few, often fragmentary, specimens.

Order BELEMNITIDA Zittel, 1895
Suborder BELEMNITINA Zittel, 1895
Family HASTITIDAE Naef, 1922

Genus *Hastites* Mayer-Eymar, 1883

TYPE SPECIES. — *Belemnites clavatus* Schlotheim, 1820, by subsequent designation (Naef 1922) (= *Belemnites neumarktensis* Oppel, 1856; subj. syn.) from the uppermost Toarcian (? Opalinuston Fm) of Franconia, south-east Germany (see revision by Riegraf 2000).

DISTRIBUTION. — Upper Toarcian to lowermost Bajocian of Europe and northern Russia.

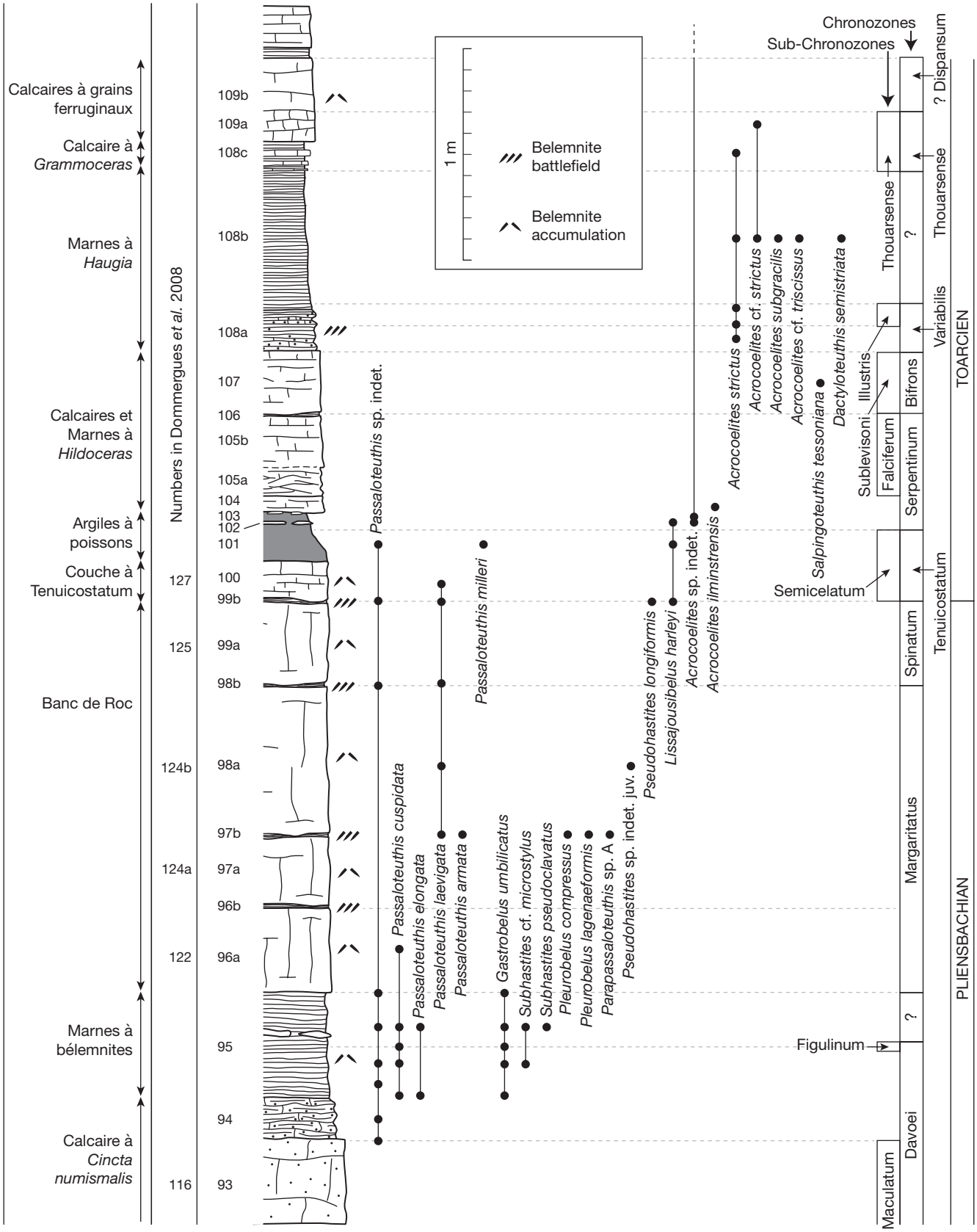

FIG. 5. — Stratigraphic occurence of collected belemnites (Part 1, bottom). Chronostratigraphic and lithostratigraphic scheme following Figure 3.

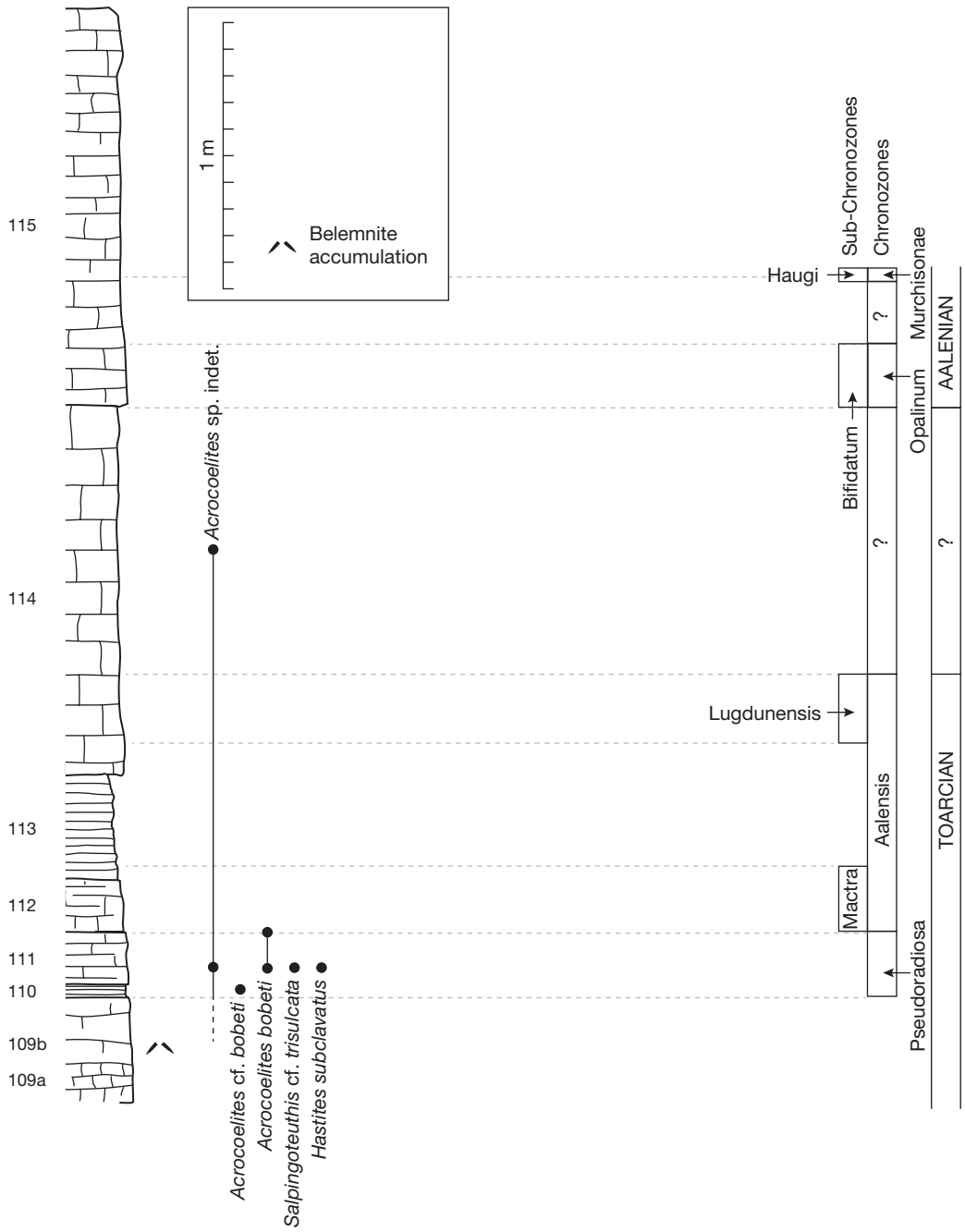

FIG. 6. — Stratigraphic occurence of collected belemnites (Part 1, bottom). Chronostratigraphic scheme following Figure 4.

Hastites subclavatus (Voltz, 1830) (Fig. 10A)

Belemnites subclavatus Voltz, 1830: 38, pl. 1, fig. 11.

Rhabdobelus subclavatus – Sturz-Köwing 1960: 9, pl. 1, figs 5, 6, 11.

Hastites toarcensis – Činčurová 1975: 49, pl. 1, fig. 4.

Rhopalobelus subclavatus – Činčurová 1983: 10, 55, text-fig. 5; pl. 1, figs 5a,b.

Rhopalobelus toarcensis – Činčurová 1983: 11, 55, text-fig. 6; pl. 1, figs 6a, b.

Neoclavibelus subclavatus – Schlegelmilch 1998: 73, pl. 12, figs 4-7.

Parahastites subclavatus – Weis 1999: 226, fig. 22.

Hastites subclavatus – Riegraf 2000: 285.

Neoclavibelus toarcensis – Arp 2010: pl. 4, figs 21-22.

Neoclavibelus bergensis – Arp 2010: pl. 4, figs 23-24.

MATERIAL. — One specimen (MNHNL BEL489).

STRATIGRAPHICAL DISTRIBUTION. — Upper Toarcian, Pseudoradiosa Chronozone up to Aalensis Chronozone. Fresney-le-Puceux: "*Calcaire à grains ferrugineux*" Mb, bed 111.

GEOGRAPHIC DISTRIBUTION. — North-west Germany (Sturz-Köwing 1960); south Germany, Swabia and Franconia (Kolb 1942; Schwegler 1971; Schlegelmilch 1998; Arp 2010); Slovakia (Činčurová 1975, 1983); north-east France and Luxembourg (Voltz 1830; Weis 1999); north-west France, Normandy (this work).

DESCRIPTION
This small-sized, slender rostrum shows a slightly subclavate profile and outline. The apical region is short andsharply pointed. Lateral lines are indistinct. Cross sections are elliptical compressed in the stem region, and subquadrate compressed in the alveolar region; I_c =1.08 (measured at half of the rostrum length). The alveolus occupies approximately ¼ of the total rostrum length.

REMARKS
The taxonomic status of the genus *Hastites* and its type species *Hastites clavatus* (Schlotheim, 1820) have been revised by Riegraf (2000), confining thereby the genus *Hastites* to hastate rostra occurring in the upper Toarcian, in opposition to the better known hastate forms of the Pliensbachian, now referred to as *Subhastites* Gustomesov, 1977, with type species *Subhastites pseudoclavatus* Gustomesov, 1977 (see below). Statistical analysis by Sturz-Köwing (1960), based on material from the north-west of Germany, and including data from Kolb (1942), demonstrated that the taxa established by Kolb (*Hastites forthensis* Kolb, 1942; *Hastites bergensis* Kolb, 1942; *Hastites compactus* Kolb, 1942) and Oppel (*Belemnites toarcensis* Oppel, 1857) might be variants of one single, highly variable species. Riegraf (2000: 285) on the other hand considered the possibility to include *Hastites forthensis* Kolb, 1942 and *Hastites bergensis* Kolb, 1942 in the specific variation of *Hastites clavatus*. According to both above mentioned opinions, only two valid species are currently retained: *Hastites clavatus*, senior subjective synonym of *Hastites neumarktensis* (Oppel, 1857) and *Hastites subclavatus*.

Genus *Subhastites* Gustomesov, 1977

TYPE SPECIES. — *Subhastites pseudoclavatus* Gustomesov, 1977 (by original designation) from the Pliensbachian of Côte d'Or, Burgundy, France.

DISTRIBUTION. — Sinemurian to Pliensbachian of mainland Europe and possibly Greenland.

Subhastites pseudoclavatus Gustomesov, 1977
(Fig. 10C)

Subhastites pseudoclavatus Gustomesov, 1977: 106, pl. 1, fig. 8, pl. 2, fig. 1. — Riegraf *et al.* 1998: 203. — Weis *et al.* 2015b: 735, fig. 2c.

Belemnites clavatus Stahl, 1824: 31, pl. 2, fig. 2.

Hastites fustiformis Lang, 1928: 218, pl. 15, fig. 6 (*fide* Doyle 2010).

Hastites clavatus clavatus – Schumann 1974: 30, pl. 6, figs 1-7.

Hastites clavatus – Schlegelmilch 1998: 57, pl. 4, figs 13-17. — Doyle 2010: 273, pl. 47, figs 13, 14.

Hastites clavatus – Combémorel 1997: pl. 27, fig. 4. — Rulleau 2007: 75, pl. 41, fig. 8.

MATERIAL. — One specimen (MNHNL BEL503).

STRATIGRAPHICAL DISTRIBUTION. — Lower Pliensbachian, Ibex and Davoei chronozones. Fresney-le-Puceux: "*Marnes à bélemnites*" Mb, bed 95 (upper part).

GEOGRAPHIC DISTRIBUTION. — North-west Germany (Schumann 1974); south-west Germany (Schwegler 1962; Schlegelmilch 1998); England, Dorset and Yorkshire (Phillips 1865; Lang 1928; Doyle 2003, 2010); north-east France and Luxembourg (R. Weis unpublished field data); north-west France, Normandy (this work); central France, Mont d'Or Lyonnais (Rulleau 2007); south France, Lozère (Combémorel 1997); central Italy (Weis *et al.* 2015b).

DESCRIPTION
The very small sized rostrum is strongly hastate ("club-shaped") and shows no grooves or other imprints. The anterior end shows typical exfoliated rostral layers. The alveolar region is not preserved.

REMARKS
The shape of the rostrum and the exfoliated anterior part are typical for the species *Subhastites pseudoclavatus* (= *Hastites clavatus Auctorum* [pars]; see Riegraf 2000).

Subhastites cf. ***microstylus*** (Phillips, 1867)
(Fig. 10B)

Belemnites microstylus Phillips, 1867: 66, pl. 13, fig. 31.

cf. *Belemnites microstylus* – Dumortier 1869, pl. 4, figs 16-19.

cf. *Hastites microstylus microstylus* – Schumann 1974: 34: pl. 7, figs 11-21; pl. 8, figs 1, 2.

cf. *Hastites clavatus* – Combémorel *et al.* 1994: 15, pl. 3, fig. 2.

cf. *Hastites microstylus* – Schlegelmilch 1998: 57, pl. 5, fig. 1. — Rulleau 2007: 42, figs 16-19.

MATERIAL. — Two specimen (MNHNL BEL526a, b).

STRATIGRAPHICAL DISTRIBUTION. — Lower Pliensbachian, Jamesoni up to Davoei chronozones. Fresney-le-Puceux: "*Marnes à bélemnites*" Mb, bed 95 (upper part).

GEOGRAPHIC DISTRIBUTION. — England (Phillips 1867); north-east France (Combémorel *et al.* 1994); Luxembourg (R. Weis unpublished field data); central France, Mont d'Or Lyonnais (Dumortier 1869; Rulleau 2007); north-west Germany (Schumann 1974); south Germany (Schlegelmilch 1998); Bulgaria (Stoyanova-Vergilova 1993).

DESCRIPTION
The preserved apical fragments belong to a cylindrical or subhastate, presumably small-sized rostrum. The elongated apical region narrows more or less regularly. Lateral lines are present as two closely-spaced imprints ("Doppellinien"). Cross sections at the broken ends are rounded.

REMARKS
Only two small-sized apical fragments were recovered from the "*Marnes à bélemnites*". Their rather cylindrical

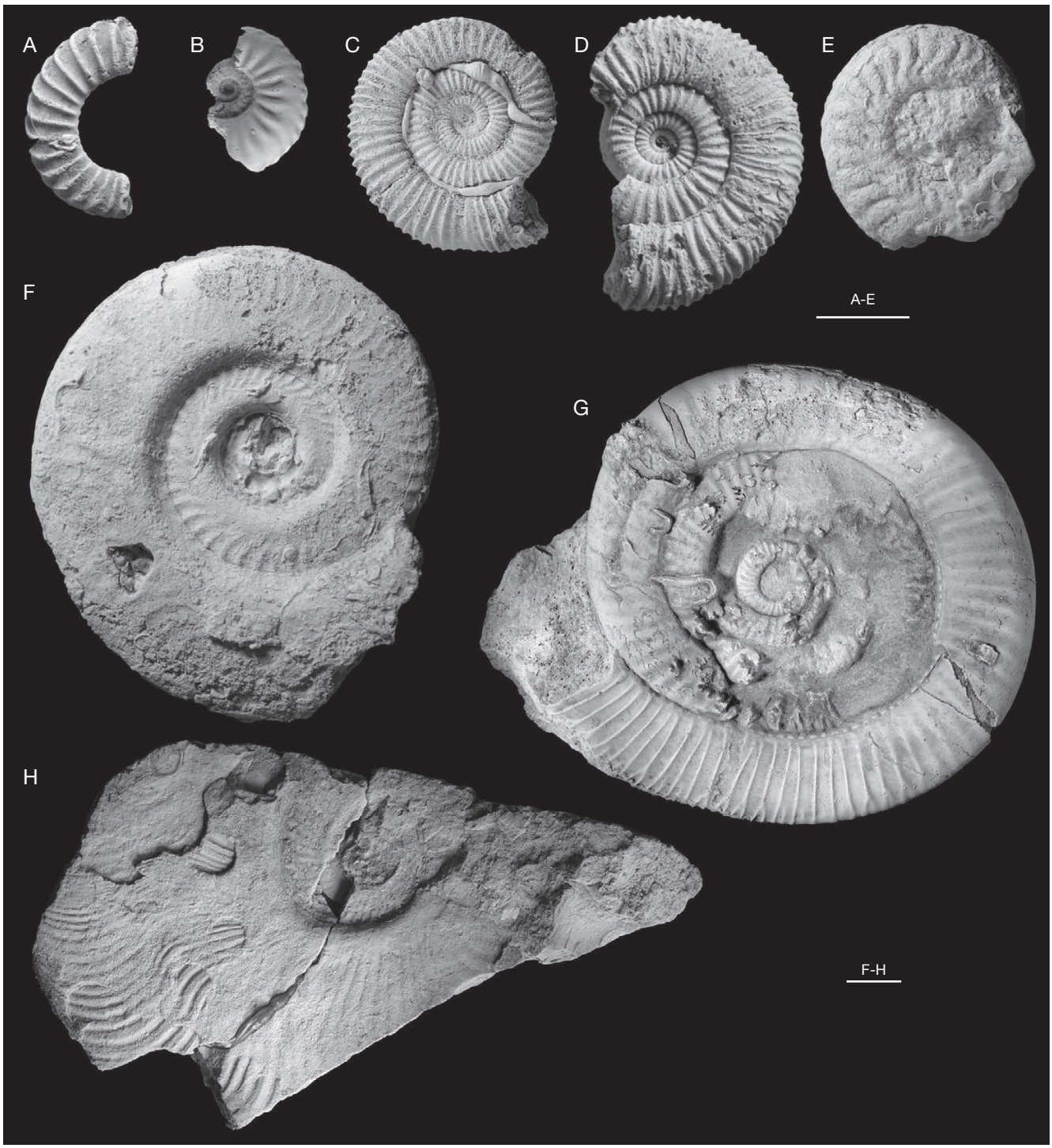

Fig. 7. — Pliensbachian and lower Toarcian ammonites from Fresney-le-Puceux: **A**, *Oistoceras angulatum* (Quenstedt, 1858), specimen no. UBGD 30599, "*Marnes à bélemnites*", bed 95 (middle part); **B**, *Amaltheus stockesi* (Sowerby, 1818), specimen no. MNHNL QH644, "*Marnes à bélemnites*", bed 95 (top); **C**, **D**, *Dactylioceras* (*Orthodactylites*) *annulatum* (Sowerby, 1819), "*Calcaires et marnes à* Hildoceras", bed 105a; **C**, specimen no. UBGD 30600; **D**, specimen no. UBGD 30601; **E**, *Hildaites forte* (Buckman, 1921), specimen no. UBGD 30602, "*Calcaires et marnes à* Hildoceras", bed 106; **F**, *Hildoceras lusitanicum* Meister, 1913, specimen no. UBGD 30603, "*Calcaires et marnes à* Hildoceras", bed 107 (top); **G**, *Dactylioceras* (*Orthodactylites*) *clevelandicum* Howarth, 1973, specimen no. UBGD 30604, "*banc de Roc*" s.l., bed 100 (top); **H**, *Harpoceras serpentinum* (Schlotheim, 1813), specimen no. UBGD 30605, "*Argiles à poissons*", bed 101 (nodular level). Scale bar: 1 cm.

and elongate apical region allows comparing them with *Subhastites microstylus*, a thin, needle-like hastitid species. A similar species, *Subhastites stonebarroensis* (Lang, 1928) has been described from England (Lang 1928; Doyle 2010). This species was first considered as a synonym of *Subhastites spadixari* (Simpson, 1855) by Doyle (2003); later, the same author (Doyle 2010) reported it as a synonym of *S. microstylus*.

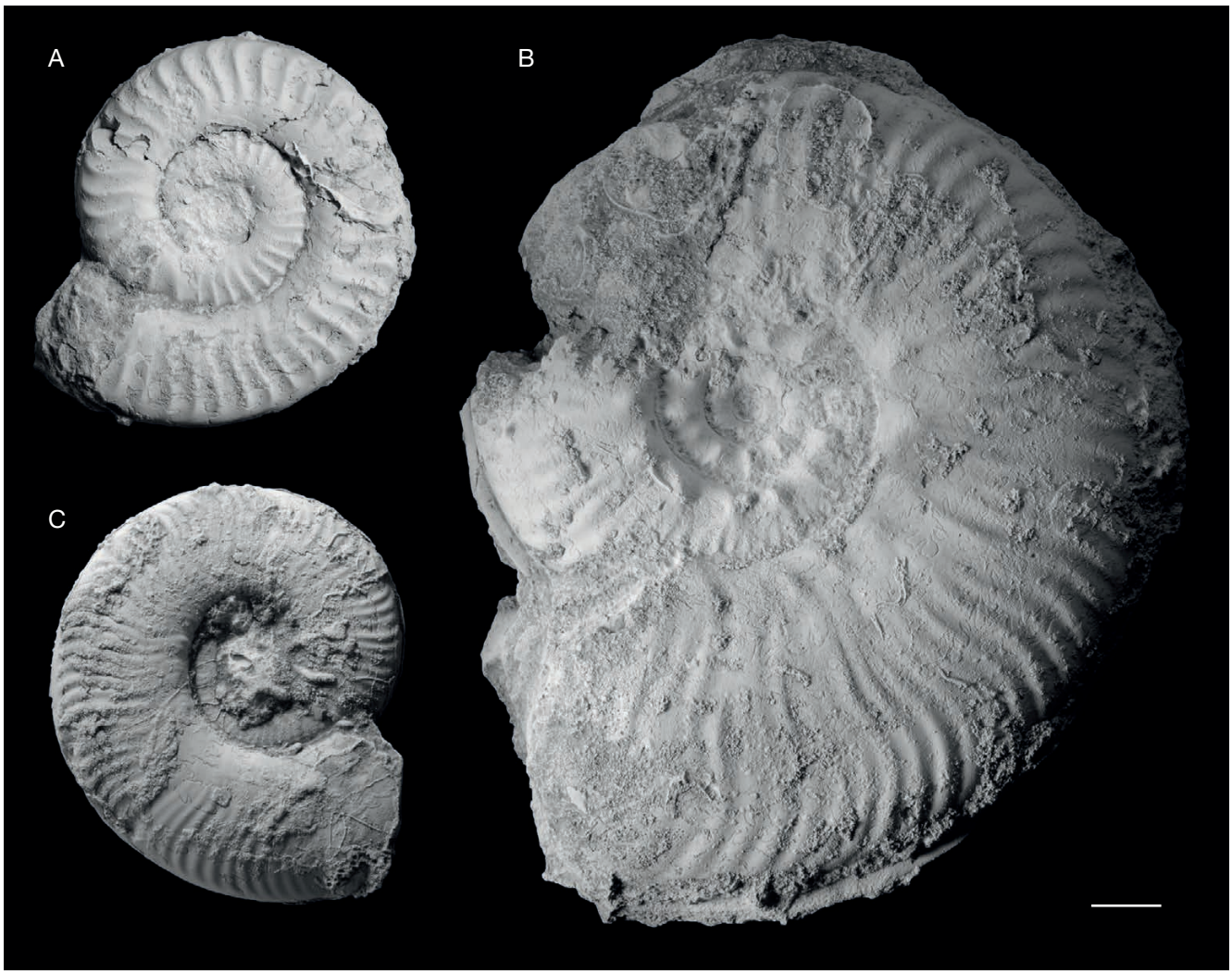

Fig. 8. — Upper Toarcian ammonites (part 1) from Fresney-le-Puceux: **A**, *Grammoceras penestriatulum* (Schirardin, 1914), specimen no. UBGD 30606, "*Calcaire à* Grammoceras", bed 108c; **B**, *Haugia illustris* (Denckmann, 1887), specimen no. UBGD 30607, "*Marnes à* Haugia", bed 108a; **C**, *Pseudogrammoceras subregale* Pinna, 1968, specimen no. UBGD 30608, "*Marnes à* Haugia", bed 108b (base). Scale bar: 1 cm.

Family Megateuthididae Sachs & Nalnjaeva, 1967

Genus *Acrocoelites* Lissajous, 1915

Type species. — *Belemnites oxyconus* Hehl *in* Zieten, 1831 (by original designation) from the lower Toarcian, Posidonienschiefer Fm of South-West Germany.

Distribution. — Uppermost Pliensbachian to lower Aalenian of Europe, Siberia, and probably North and South America and Japan.

Acrocoelites bobeti Lissajous, 1927
(Fig. 10D-F)

Acrocoelites bobeti Lissajous, 1927: 19. — Combémorel 1971: 63, pl. 1, figs 1, 2; 1997: pl. 27, fig. 16. — Doyle 1990: 33, pl. 7, figs 9-11, 13-15. — Pinard *et al.* 2014: 165, fig. 6C.

material. — Six specimens (MNHNL BEL486a, b; BEL487a, b; BEL488; BEL529).

Stratigraphical distribution. — Upper Toarcian, Pseudoradiosa and Aalensis chronozones. Fresney-le-Puceux: "*Calcaire à grains ferrugineux*" Mb, beds 110 and 111.

Geographic distribution. — England, Dorset (Doyle 1990); north-west France, Normandy (this work); south France, Aveyron and Lozère (Lissajous 1927; Combémorel 1971, 1997; Pinard *et al.* 2014).

Description

The small to medium-sized, slender rostra show a cylindriconical profile and a cylindrical to subhastate outline. The acute apex is relatively short in most specimens and bears a short, well-incised ventral groove and two less developed dorsolateral grooves. Lateral lines are indistinct. The cross section is elliptical compressed, compression is not very marked in the stem region (I_c varying between 1.04 and 1.09), but the alveolar region is strongly compressed (I_c between 1.16 and 1.25). The alveolus occupies approximately ⅓ to ⅙ of the rostrum.

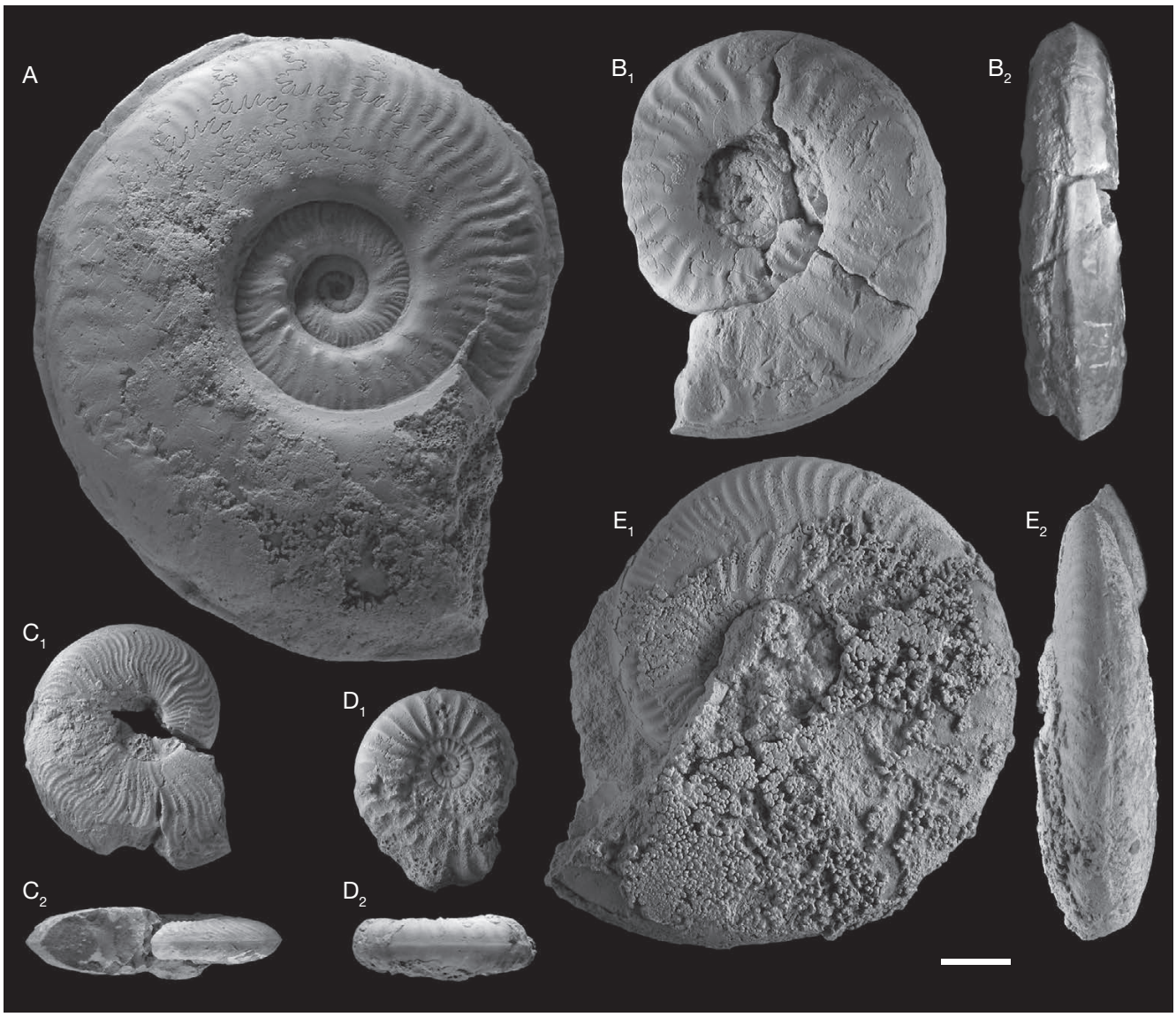

FIG. 9. — Upper Toarcian ammonites (part 2) and Aalenian ammonites from Fresney-le-Puceux: **A**, *Phlyseogrammoceras dispansiforme* (Wunstorf, 1904), specimen no. MNHNL QH622, "*Calcaire à grains ferrugineux*", bed 109b; **B**, *Grammoceras thouarsense* (d'Orbigny, 1843), specimen no. MNHNL QH627, "*Calcaire à* Grammoceras", bed 108c; **C**, *Pleydellia buckmani* (Maubeuge, 1947), specimen no. MNHNL QH628, bed 114; **D**, *Dumortieria prisca* Buckman, 1891, specimen no. MNHNL QH632, "*Calcaire à grains ferrugineux*", bed 111; **E**, *Ancolioceras opalinoides* (Mayer, 1864), specimen MNHNL QH625, bed 115. Scale bar: 1 cm.

REMARKS

The rostra herein referred to *A. bobeti* are morphologically comparable to the stratigraphically older *Acrocoelites strictus* Lissajous, 1927 (see also below for morphological differences). Some individuals with a more pronounced subhastate outline (Fig. 10D) approach the genus *Simpsonibelus*, but lack the subquadrate cross section, the strongly asymmetrical profile and the pronounced double lateral lines of the latter (Doyle 1992).

Acrocoelites ilminstrensis (Phillips, 1867) (Fig. 10G)

Belemnites ilminstrensis Phillips, 1867: 64, pl. 12, fig. 30.

Acrocoelites ilminstrensis – Riegraf *et al.* 1984: 155, pl. 10, figs 2, 3, 5, 9 (*cum syn.*). — Schlegelmilch 1998: 59, pl. 5, figs 11, 12. — Pinard *et al.* 2014: 165, fig. 6C.

Acrocoelites (*Toarcibelus*) *ilminsterensis* [sic] – Doyle 1990: 39, pl. 1, figs 1-7 (*cum syn.*).

MATERIAL. — One specimen (MNHNL BEL492).

STRATIGRAPHICAL DISTRIBUTION. — Lower Toarcian, Serpentinum and Bifrons chronozones. Fresney-le-Puceux: "*Calcaires et Marnes à* Hildoceras" Mb, bed 104.

GEOGRAPHIC DISTRIBUTION. — England, Dorset and Yorkshire (Phillips 1867; Doyle 1990); south Germany (Riegraf *et al.* 1984; Schlegelmilch 1998); north-west France (this work); central France, Mâconnais, Monts Lyonnais (Lissajous 1906); Luxembourg (R. Weis unpublished field data); Bulgaria (Stoyanova-Vergilova 1993).

DESCRIPTION
The medium-sized rostrum is reasonably robust and shows a conical profile and a cylindriconical outline. The acute apex bears two short and weakly preserved dorsolateral grooves; a broader and longer ventral groove is stronger developed. The flanks of the rostrum are flattened, due to the presence of broad, indistinct lateral lines. Cross sections are elliptical, moderately compressed (I_c = 1.03, measured at half of the rostrum length). The alveolus occupies approximately ⅓ of the rostrum.

Acrocoelites strictus Lissajous, 1927
(Fig. 10I-L)

Acrocoelites strictus Lissajous, 1927: 16, pl. 2, figs 2-4.

Acrocoelites (*Acrocoelites*) *strictus* – Doyle 1990: 32, pl. 7, figs 7, 8, 12.

MATERIAL. — 63 specimens (MNHNL BEL479a-c, BEL480a-s, BEL482a-s, BEL525a-e, BEL528, BEL531a-c, BEL532a-b, BEL533a-d, BEL537a-g).

STRATIGRAPHICAL DISTRIBUTION. — Toarcian, Bifrons up to Thouarsense chronozones. Fresney-le-Puceux: "*Marnes à* Haugia" and "*Calcaires à* Grammoceras" Mb, beds 108a, b, c, and 109.

GEOGRAPHIC DISTRIBUTION. — England, Northhamptonshire (Lissajous 1927; Doyle 1990); north-west France, Normandy (this work).

DESCRIPTION
The small to medium sized rostra are moderately robust and show a conical profile and a cylindriconical to slightly subhastate outline. The elongated apical region is tapering regularly towards the acute apex, bearing two well-incised but short dorsolateral grooves and a considerably longer ventral groove; the latter fades out anteriorly resulting in a flattened ventral area: as a result, the apical region is characterized by a slightly depressed cross section. Cross sections in the stem region are rounded or subquadrate, in the alveolar region they become slightly compressed. Lateral lines are indistinctly developed as two parallel running shallow depressions. The alveolus occupies approximately ⅓ to ¼ of the rostrum length.

REMARKS
The species resemble the stratigraphically younger *Acrocoelites bobeti* (see above) and morphologically connecting forms exist in the Dispansum chronozone. Typical specimens of *A. strictus* are characterized by the relatively robust rostrum with a conical profile, the long and broad ventral apical groove and the depressed cross sections of the apical region; these features distinguish them from typical *A. bobeti*, characterized by a more slender rostrum, with cylindrical profile and a short ventral apical groove.

Acrocoelites subgracilis Kolb, 1942
(Fig. 10H)

Acrocoelites subgracilis Kolb, 1942: 161, pl. 8, figs 5-7.

Belemnites tripartitus gracilis Quenstedt, 1848: 420, pl. 26, fig. 17a-c.

Acrocoelites (*Acrocoelites*) *subgracilis* – Doyle 1990: 35, pl. 7, fig. 16, pl. 8, figs 1-2 (pars, see remark below). — Schlegelmilch 1998: 60, pl. 6, figs 1-2. — Arp 2010: pl. 4, figs 9-10.

MATERIAL. — One specimen (MNHNL BEL485).

STRATIGRAPHICAL DISTRIBUTION. — Upper Toarcian, Variabilis or Thouarsense Chronozone up to Aalensis Chronozone. Fresney-le-Puceux: "*Marnes à* Haugia" Member, bed 108b.

GEOGRAPHIC DISTRIBUTION. — South Germany, Swabia and Franconia (Quenstedt 1845-1849; Kolb 1942; Schlegelmilch 1998); England, Yorkshire, Northamptonshire (Doyle 1990); north-west France, Normandy (this work).

DESCRIPTION
The estimated medium- to large-sized, slender-elongate rostrum shows a cylindriconical profile and a cylindrical to subhastate outline. A part of the apex is missing, but two weak dorsolateral grooves can be recognized by observing the growth lines in cross section at the broken-off apical end; a long ventral groove extends approximately up to half the length of the rostrum solidum. Lateral lines are developed as broad and shallow lateral depressions, especially well-developed on the alveolar region. Cross sections of the rostrum are elliptical compressed, the compression index (I_c) is varying between 1.08 in the stem region and 1.24 in the alveolar region. The alveolus occupies about ⅓ to ¼ of the total rostrum.

REMARKS
The species is here interpreted in the sense of Kolb (1942) and Schlegelmilch (1998), who limit it to the rostra from the upper Toarcian. The species concept proposed by Doyle (1990) is a broader one, as he includes also stratigraphically older material from the Bifrons/Variabilis chronozones. The latter are currently referred to other species such as *Salpingoteuthis persulcata* (Janensch, 1902) (*in* Riegraf *et al.* 1984: 163, pl. 12, fig. 11; referred to *Salpingoteuthis bauhini* [*nomen novum* established by Schlegelmilch 1998]). In our opinion the latter taxa should be maintained distinct, although their generic attribution remains debatable.

Acrocoelites cf. *triscissus* (Janensch, 1902)
(Fig. 11A)

cf. *Belemnites triscissus* – Janensch 1902: 8, pl. 12, figs 7-7b.

cf. *Acrocoelites triscissus* – Kolb 1942: 157, pl. 9, figs 3, 6.

cf. *Acrocoelites* (*Odontobelus*) *triscissus* – Doyle 1990: 46, pl. 16, figs 1-5. — Rulleau *et al.* 1998 : 19, pl. 1, figs 1-2.

MATERIAL. — One specimen (MNHNL BEL483).

STRATIGRAPHICAL DISTRIBUTION. — Upper Toarcian, Variabilis up to Aalensis chronozones. Fresney-le-Puceux: "*Marnes à* Haugia" Mb, bed 108b.

GEOGRAPHIC DISTRIBUTION. — England, Yorkshire, Gloucestershire (Doyle 1990); north-east France, Alsace (Janensch 1902); Luxembourg (R. Weis unpublished field data); north-west France, Normandy (this work); south Germany, Franconia (Kolb 1942).

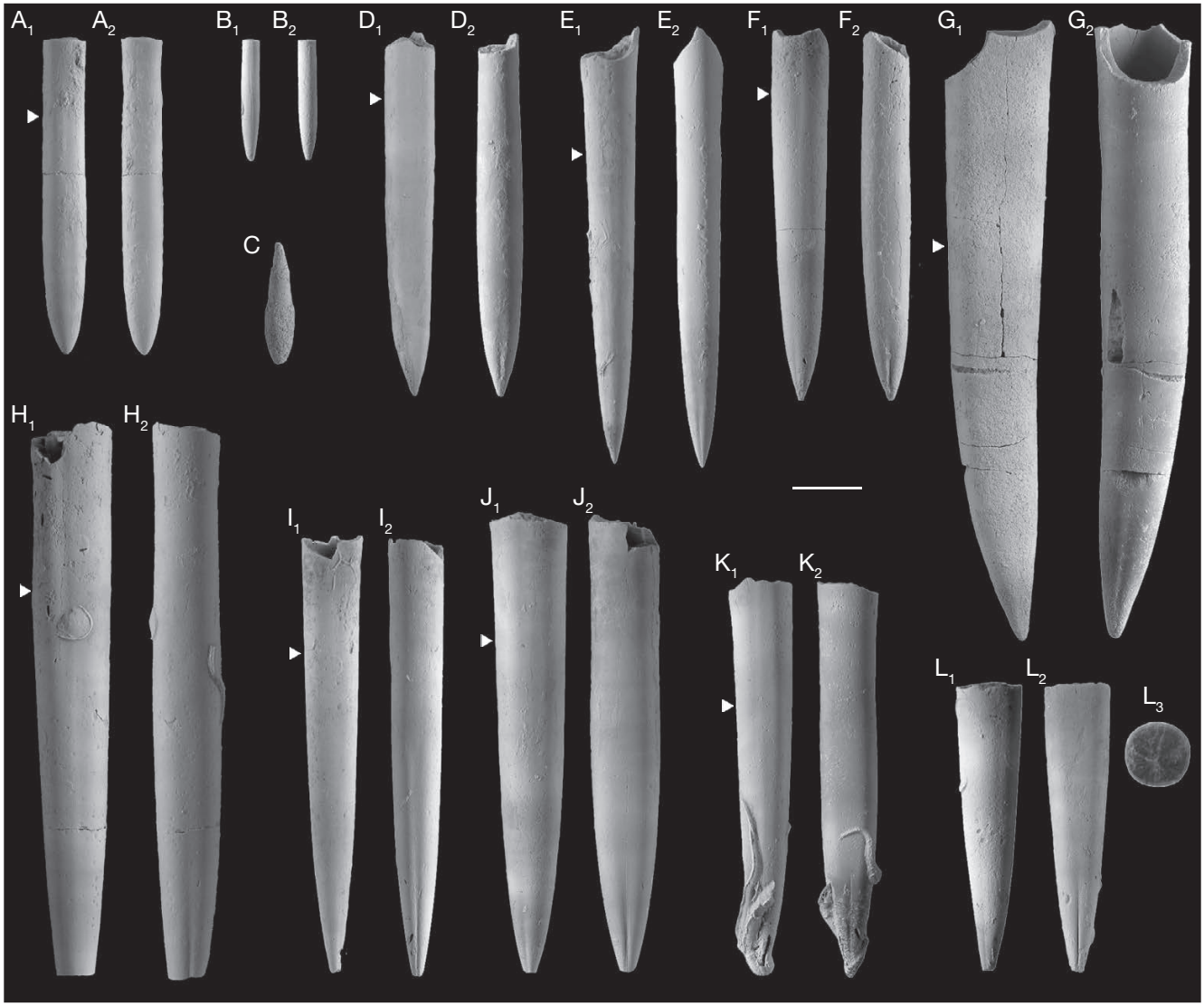

Fig. 10. — Hastitidae and Megateuthididae (part 1), Pliensbachian-Toarcian of Fresney-le-Puceux: **A**, *Hastites subclavatus* (Voltz, 1830), specimen no. MNHNL BEL489, bed 111; **A1**, lateral view; **A2**, ventral or dorsal view; **B**, *Subhastites* cf. *microstylus* (Phillips, 1867), apical fragment, specimen no. MNHNL BEL526a, bed 95; **B1**, lateral view; **B2**, ventral or dorsal view; **C**, *Subhastites pseudoclavatus* Gustomesov, 1977, corroded specimen without alveolar part, no. MNHNL BEL503, bed 95, non-orientated view; **D**-**F**, *Acrocoelites bobeti* Lissajous, 1927; **D**, specimen no. MNHNL BEL487b, bed 111 (top); **D1**, lateral view, venter right; **D2**, ventral view; **E**, specimen no. MNHNL BEL487a, bed 111 (top); **E1**, lateral view, venter right; **E2**, ventral view; **F**, specimen no. MNHNL BEL486a, bed 110; **F1**, lateral view, venter right; **F2**, ventral view; **G**, *Acrocoelites ilminstrensis* (Phillips, 1867), specimen no. MNHNL BEL492, bed 104; **G1**, lateral view, venter left; **G2**, ventral view; **H**, *Acrocoelites subgracilis* Kolb, 1942, apex not preserved, no. MNHNL BEL485, bed 108; **H1**, lateral view, venter right; **H2**, ventral view; **I**-**L**, *Acrocoelites strictus* Lissajous, 1927; **I**, specimen no. MNHNL BEL480a, bed 108 (top); **I1**, lateral view, venter left; **I2**, ventral view; **J**, specimen no. MNHNL BEL482a, bed 108; **J1**, lateral view, venter right; **J2**, ventral view; **K**, specimen with serpulid incrustations, no. MNHNL BEL482b, bed 108; **K1**, lateral view, venter left; **K2**, ventral view; **L**, apical fragment of a large specimen, no. MNHNL BEL480b, bed 108 (top); **L1**, lateral view, venter right; **L2**, ventral view, **L3**, cross section. Scale bar: 1 cm. **White arrows** indicate the estimated position of the protoconch.

Description

The specimen represents a robust, conical to cylindriconical rostrum with the apical and stem region preserved, but missing the alveolar region completely. The conical apical region shows three equally long and well-developed apical grooves; the dorsolateral grooves are slightly curved towards the dorsum. The ventral groove is slightly deeper and broader than the dorsolateral ones. The cross sections are elliptical and slightly compressed (I_c = 1.04 at protoconch level).

Remarks

Despite its incomplete state of preservation, the specimen shows typical characters of the apical region (e.g. the strongly developed apical grooves, with curved dorsolateral grooves) which permit to compare it to *A. triscissus*. This species is included by most authors within the variation range of either *A. quenstedti* (Oppel, 1856) (Werner 1912) or *A. conoideus* (Oppel, 1856) (Schlegelmilch 1998). Based on a statistical approach, Sturz (1958) synonymized *A. triscissus* with both *A. conoideus* and *A. quenstedti*, giving

priority to the latter name. On the other hand, Doyle (1990) considered these three taxa as independent species. In lack of a comprehensive review of *Acrocoelites* and a better understanding of the intraspecific variability, for the time being we consider here *A. triscissus* herein as a distinct taxon.

Genus *Dactyloteuthis* Bayle, 1878

TYPE SPECIES. — *Belemnites irregularis* Schlotheim, 1813 (by subsequent designation of Douvillé 1879), from the upper Toarcian, Jurensismergel Fm of Franconia, South-East Germany.

DISTRIBUTION. — Upper Toarcian of West and Central-East Europe.

Dactyloteuthis semistriata (Münster, 1830) (Fig. 11B)

Belemnites semistriatus Münster, 1830: 15, pl. 2, fig. 4.

Belemnites (*Dactyloteuthis*) *acuarius* – Lissajous 1906: 55, pl. 4, fig. 8.

Dactyloteuthis semistriata – Riegraf *et al.* 1984: 163, pl. 12, figs 4, 12, text-fig. 48u. — Schlegelmilch 1998: 66, pl. 9, figs 8-10. — Delsate & Weis 2010: pl. 5, fig. 2.

Dactyloteuthis irregularis – Combémorel *et al.* 1994: pl. 1, figs 4-5 (non figs 1-3).

MATERIAL. — One specimen (MNHNL BEL484).

STRATIGRAPHICAL DISTRIBUTION. — Upper Toarcian, Variabilis chronozone and Thouarsense chronozone. Fresney-le-Puceux: "*Marnes à* Haugia" Mb, bed 108b.

GEOGRAPHIC DISTRIBUTION. — North-west Germany (Sturz-Köwing 1960); south Germany, Swabia and Bavaria (Riegraf *et al.* 1984; Schlegelmilch 1998); north-west France, Normandy (this work); central France, Mâconnais (Lissajous 1906); north-east France, Lorraine (Combémorel *et al.* 1994); Luxembourg (Delsate & Weis 2010). Probably also south France, Causses (Pinard *et al.* 2014, recorded as *D.* cf. *semistriata*).

DESCRIPTION

The small sized, stout orthorostrum (the epirostrum is not preserved) shows a cylindriconical outline and profile. The obtuse apex is mucronate and bears several fine apical striae; a shallow and weakly developed ventral apical groove is present. Cross sections are elliptical compressed (I_c = 1.21 at half of the rostrum length). The alveolus occupies approximately ⅔ of the rostrum.

Family PASSALOTEUTHIDIDAE Naef, 1922

Genus *Gastrobelus* Naef, 1922

TYPE SPECIES. — *Belemnites ventroplanus* Voltz, 1830 (by original designation), from the Pliensbachian of Alsace, north-east France.

DISTRIBUTION. — Pliensbachian to lowermost Toarcian of Europe and Greenland.

Gastrobelus umbilicatus (Blainville, 1827) (Fig. 11C-G)

Belemnites umbilicatus Blainville, 1827: 97, pl. 3, fig. 11.

Hastites umbilicatus – Combémorel *et al.* 1994: 10, pl. 1, fig. 6.

Gastrobelus umbilicatus – Schlegelmilch 1998: 53, pl. 3, fig. 8. — Rulleau 2007: pl. 41 fig. 12.

Gastrobelus ventroplanus – Doyle 2010: 274, pl. 47, figs 3-4.

MATERIAL. — 36 specimen (MNHNL BEL506, BEL507, BEL508, BEL510, BEL511, BEL517a-j, BEL518a-c, BEL519a-k, BEL535a-b, BEL539a-e).

STRATIGRAPHICAL DISTRIBUTION. — Pliensbachian, Davoei up to Margaritatus Chronozone. Fresney-le-Puceux: "*Marnes à Belemnites*" Mb, bed 95.

GEOGRAPHIC DISTRIBUTION. — North-west France, Normandy (this work); central France, Mont d'Or Lyonnais (Combémorel *et al.* 1994; Rulleau 2007); south Germany (Schlegelmilch 1998); England, Dorset (Doyle 2010: reported as *G. ventroplanus*).

DESCRIPTION

The medium sized, slender-elongate rostra show a cylindrical to subhastate profile and a subhastate outline. The apical region is elongated to short (at later ontogenetic stages), and obtuse; several short and weak apical striae are present in some individuals. Lateral lines are usually well developed, especially in the alveolar region. Cross sections in the apical and stem regions are subtriangular depressed, due to a marked ventral flattening which extends over the whole rostrum solidum. In the alveolar region, cross sections are less depressed and rather subquadrate. The alveolus occupies about ⅕ to ⅙ of the rostrum length.

REMARKS

Larger specimens, such as the specimen illustrated in Figure 11G, develop an obtuse apex and a more robust rostrum, reminding elongated specimens of *G. ventroplanus*. Combémorel *et al.* (1994: 11) and Lissajous (1925: 151) considered *G. umbilicatus* as a senior subjective synonym of *G. ventroplanus*, a species which is short and stout, with a strongly marked ventral depression. Schwegler (1965), Schumann (1974) and Schlegelmilch (1998) kept these taxa separated, but mentioned the presence of numerous morphological transitional forms between them. In absence of a comprehensive review of the genus, the distinction of the two taxa is here maintained.

Genus *Parapassaloteuthis* Riegraf, 1980

TYPE SPECIES. — *Belemnites zieteni* Werner, 1912 (by original designation), from the upper Pliensbachian, Amaltheenton Fm of south-west Germany.

DISTRIBUTION. — Pliensbachian to lower Toarcian of Europe, northern Africa and Greenland.

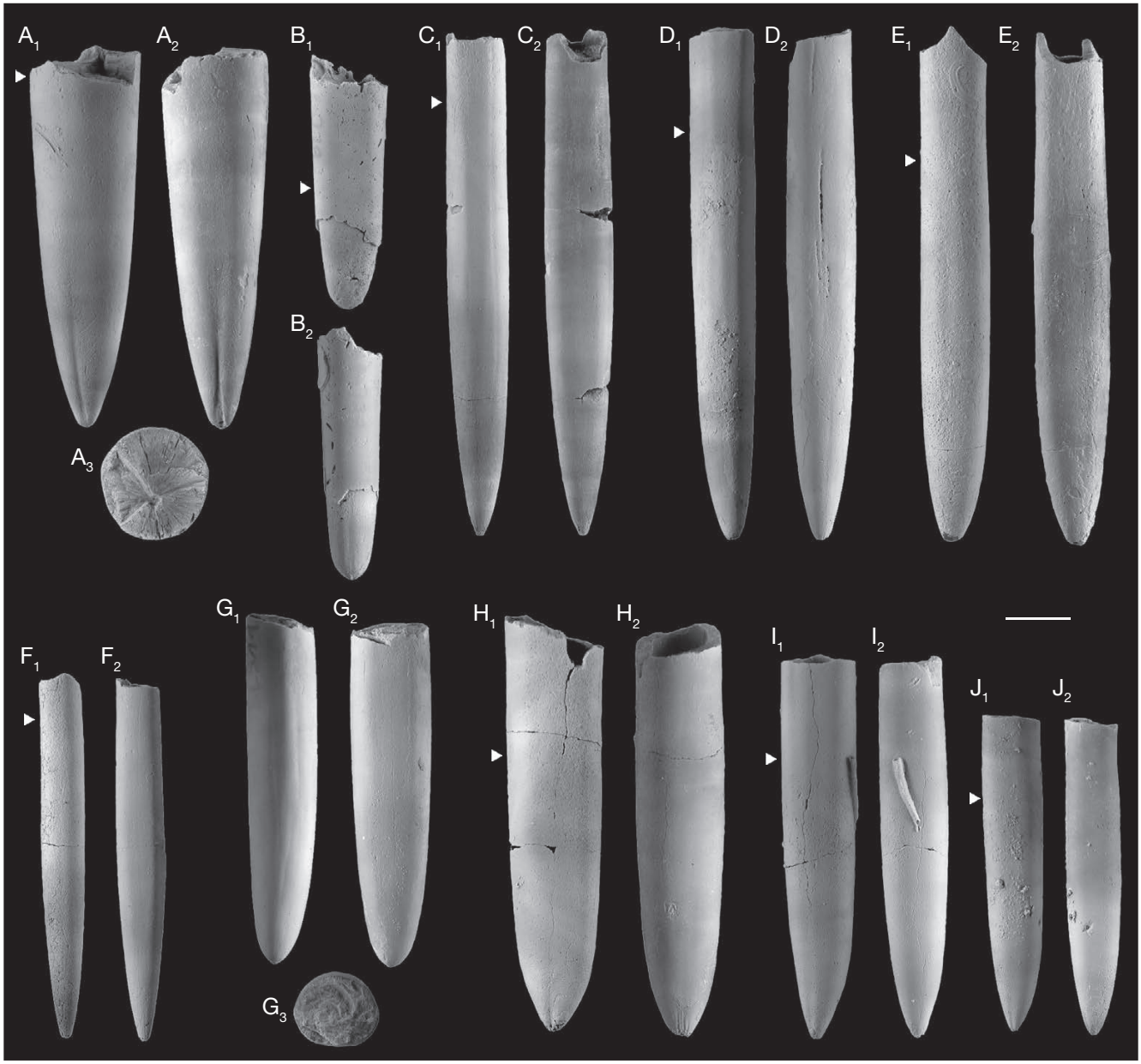

FIG. 11. — Megateuthididae (part 2) and Passaloteuthididae (part 1), Pliensbachian-Toarcian of Fresney-le-Puceux: **A**, *Acrocoelites* cf. *triscissus* (Janensch, 1902), alveolar region not preserved, specimen no. MNHNL BEL483, bed 108; **A1**, lateral view, venter left; **A2**, ventral view; **A3**, cross section, ventral side at bottom; **B**, *Dactyloteuthis semistriata* (Münster, 1830), orthorostrum (epirostrum not preserved), specimen no. MNHNL 484, bed 108; **B1**, lateral view, venter left; **B2**, ventral view; **C**-**G**, *Gastrobelus umbilicatus* (Blainville, 1827); **C**, specimen no. MNHNL BEL508, bed 95; **C1**, lateral view, venter right; **C2**, ventral view; **D**, specimen with a scar (predator attack?) on the ventral side, no. MNHNL BEL509, bed 95 (base); **D1**, lateral view, venter left; **D2**, ventral view; **E**, specimen no. MNHNL BEL507, bed 95; **E1**, lateral view, venter right; **E2**, ventral view; **F**, juvenile/subadult specimen, no. MNHNL BEL506, bed 95; **F1**, lateral view, venter right; **F2**, ventral view; **G**, fragment of a larger specimen, lacking part of the stem and the alveolar region, no. MNHNL BEL511, bed 95; **G1**, lateral view, venter right; **G2**, ventral view; **G3**, cross section of the stem region; **H**-**J**, *Passaloteuthis armata* (Dumortier, 1869); **H**, specimen no. MNHNL BEL513a, bed 97b; **H1**, lateral view, venter right; **H2**, ventral view, showing the apical striae; **I**, specimen with serpulid incrustation, no. MNHNL BEL513b, bed 97b; **I1**, lateral view, venter right; **I2**, ventral view; **J**, probably juvenile specimen, no. MNHNL BEL513c, bed 97b; **J1**, lateral view, venter right; **J2**, ventral view. Scale bar: 1 cm. **White arrows** indicate the estimated position of the protoconch.

Parapassaloteuthis sp. A
(Fig. 12H)

?*Parapassaloteuthis* sp. A – Sanders *et al.* 2015: 57, figs 8a-i.

MATERIAL. — One specimen (MNHNL BEL501).

STRATIGRAPHICAL DISTRIBUTION. — Upper Pliensbachian, Margaritatus Chronozone and possibly lowermost Toarcian, Tenuicostatum Chronozone. Fresney-le-Puceux: "*banc de Roc*" Mb, bed 97b.

GEOGRAPHIC DISTRIBUTION. — North-west France, Normandy (this work); possibly also Rif area, Morocco (Sanders *et al.* 2015).

DESCRIPTION

Medium sized, robust rostrum, with a cylindrical profile and outline. The obtuse apex bears no grooves. Lateral lines are weakly developed as shallow, broad depressions in the alveolar region. Cross sections are elliptical, compressed;

the alveolus is ventrally displaced, and occupies ½ of the total rostrum length; the apical line is goniolineate. Alveolar angle *c.* 24°.

Remarks

This single rostrum can be tentatively compared with the rostra recorded by Sanders *et al.* (2015) from the lowermost Toarcian of northern Morocco and described therein as *Parapassaloteuthis* sp. A.

Genus *Passaloteuthis* Lissajous, 1915

Type species. — *Belemnites bruguierianus* d'Orbigny, 1843 (by original designation) (= *P. laevigata* (Zieten, 1831), senior subjective synonym), from the upper Pliensbachian of Calvados, France (neotype designated in Combémorel *et al.* 1994).

Distribution. — Pliensbachian to lower Toarcian of Europe, northern Africa, Turkey and Greenland.

Remark

Numerous species have been assigned to the genus *Passaloteuthis*, most of them described by earlier workers in the 19th century and the first half of the 20th century. Some of them have been reviewed by Schumann (1974), Schlegelmilch (1998) and Doyle (1990, 2010). Doyle (2003) revised and illustrated for the first time the nominal species described by Martin Simpson (1855, 1884), reinstating them. Other species include the ones by Lissajous (1927) mainly from central France, Činčurová (1974, 1989, 1991), from Slovakia and Sachs & Nalnjaeva (1970) from northern Russia, but these species have not been recently reviewed and may represent, at least in part, subjective synonyms, of the taxa recognized as valid by the aforementioned workers.

Passaloteuthis armata (Dumortier, 1869) (Fig. 11H-J)

Belemnites armatus Dumortier, 1869: 40, pl. 1 figs 13-16.

Belemnites armatus armatus – Schumann 1974: 26, pl. 4, figs 1, 2, 7, 8.

Passaloteuthis armata – Rulleau 2007: pl. 41 fig. 9.

Material. — Three specimen (MNHNL BEL513a-c).

Stratigraphical distribution. — Pliensbachian, Jamesoni up to Margaritatus chronozones. Fresney-le-Puceux: "*banc de Roc*" Mb (lower part), bed 97b.

Geographic distribution. — Central France, Rhône valley, Mont d'Or Lyonnais (Dumortier 1869; Rulleau 2007); north-west France, Normandy (this work); north Germany (Schumann 1974); Bulgaria (Stoyanova-Vergilova 1993); possibly also England, Dorset (see remark below).

Description

Medium sized, stout rostra with a cylindrical profile and a cylindrical to subhastate outline. The short, acute apex is slightly displaced towards the dorsal side, creating an asymmetrical profile; the apex bears tow short dorsolateral grooves, one specimen shows irregular apical striae on the ventral side only. Lateral lines are well-developed as double, shallow depressions, running parallel on the flanks in a dorsolateral position (in continuation of the dorsolateral apical groove) respectively in a dorsoventral position; the latter depression is more widely and deeply expressed. Cross sections are subquadrate, compressed (I_c ranging between 1.04 and 1.09; measurements taken at half of the total rostrum length); in the alveolar region, the ventral part of the section is rounded, meanwhile the dorsal part is flattened. The alveolus occupies approximately ⅓ of the total rostrum length.

Remarks

The species *Passaloteuthis ridgensis* Lang, 1928 from the lower Pliensbachian (Jamesoni-Ibex chronozones) of Dorset strongly resembles *Passaloteuthis armata* and might be a junior subjective synonym of the latter.

Passaloteuthis cuspidata (Simpson, 1884) (Fig. 12A-D)

Belemnites cuspidatus Simpson, 1884: 50, 250.

Passaloteuthis ima Lang, 1928: 199, pl. 13, fig. 5 (*fide* Doyle 2010).

Passaloteuthis stonebarroensis Lang, 1928: 200, pl. 13, fig. 6 [*fide* Doyle 2010].

Belemnites (*Passaloteuthis*) *cuspidatus* – Doyle 2003: 161, figs 2C, D.

Passaloteuthis cuspidata – Doyle 2010: 268, pl. 46, figs 1-2.

Material. — 29 specimens (MNHNL BEL512a-c, BEL514, BEL515a-o, BEL516a-g, BEL527a-c).

Stratigraphical distribution. — Pliensbachian, Jamesoni Chronozone up to Margaritatus chronozone. Fresney-le-Puceux: "*Marnes à bélemnites*" Mb, beds 95-96a.

Geographic distribution. — England, Dorset and Yorkshire (Lang 1928, Doyle 2003, 2010); north-west France, Normandy (this work); possibly also Turkey (Doyle & Mariotti 1991, recorded as *Passaloteuthis* aff. *ima* Lang, 1928).

Description

The medium sized rostra show a cylindriconical profile and a cylindrical to subhastate outline. The apical region is rather elongated, acute (sometimes "spine-like") and bears two well-developed dorsolateral grooves. The lateral lines are especially well-developed in the alveolar region and consist of two parallel running broad depressions. The cross sections are rounded in the stem region, but compressed in the alveolar region. The alveolus occupies approximately ⅓ of the rostrum length.

Remarks

The species erected by Simpson (1884) has been revised by Doyle (2003), who figured the type material for the first time and established a synonym list. *Passaloteuthis cuspidata* differs from *P. laevigata* (Zieten, 1831) by its more compressed cross sections and the more elongated apical region, and the well-developed lateral lines.

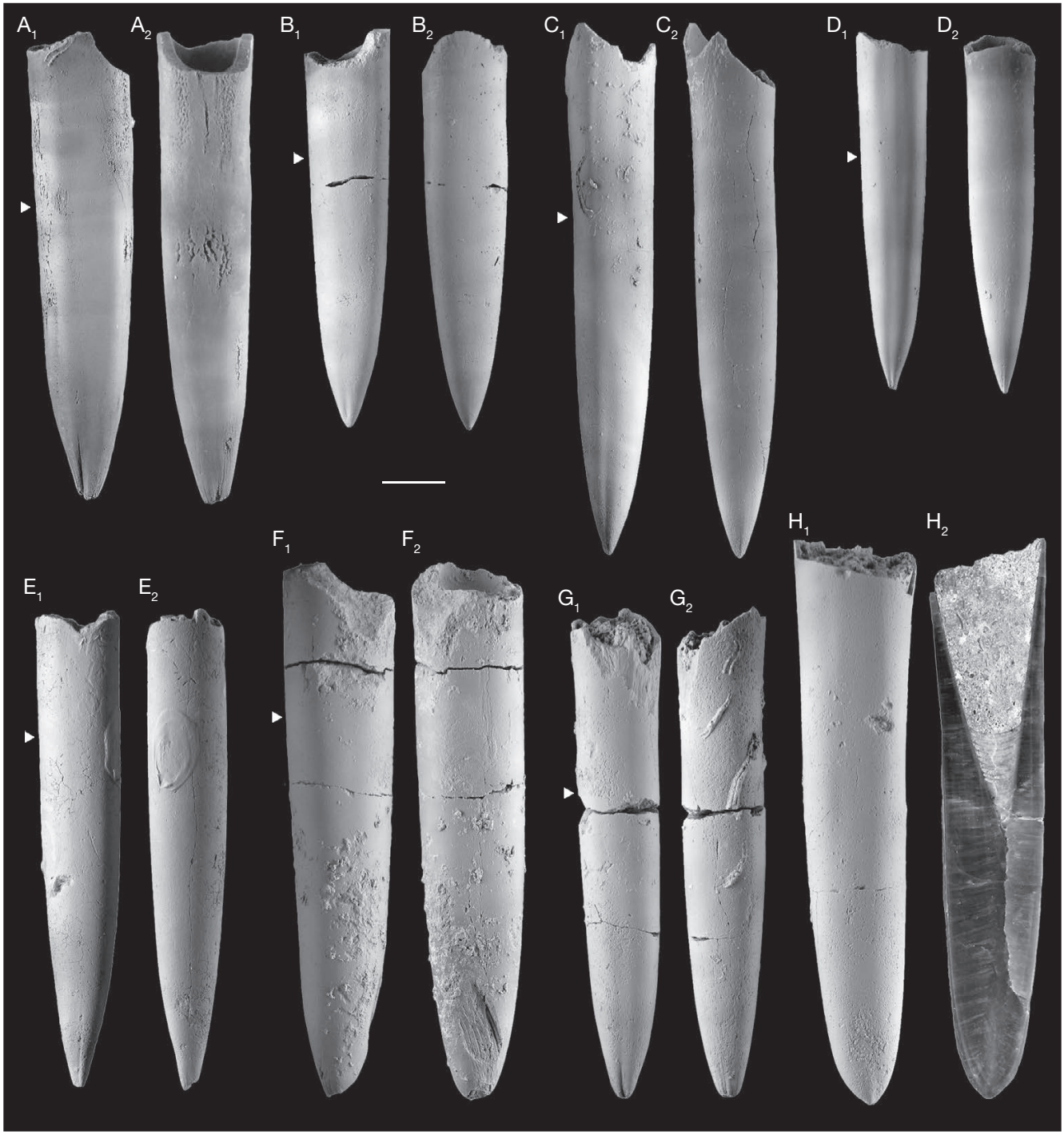

FIG. 12. — Passaloteuthididae (part 3) from the Pliensbachian of Fresney-le-Puceux: **A**-**D**, *Passaloteuthis cuspidata* (Simpson, 1884), **A**, specimen no. MNHNL BEL512a, bed 95; **A1**, lateral view, venter right; **A2**, ventral view, showing an irregular, groove-like incision; **B**, presumably juvenile/subadult specimen, no. MNHNL BEL512b, bed 95; **B1**, lateral view, venter right; **B2**, ventral view; **C**, specimen with well-developed lateral lines, no. MNHNL BEL514, bed 96a; **C1**, lateral view, venter right; **C2**, ventral view; **D**, possibly juvenile specimen, no. MNHNL BEL527a, bed 95 (base); **D1**, lateral view, venter right; **D2**, ventral view; **E**, *Passaloteuthis elongata* (Miller, 1826), specimen no. MNHNL BEL505a, bed 95 (base); **E1**, lateral view, venter right; **E2**, ventral view; **F**, **G**, *Passaloteuthis laevigata* (Zieten, 1831); **F**, large specimen with damaged apex and alveolar region in part preserved, no. MNHNL BEL498, bed 98a; **F1**, lateral view, venter right; **F2**, ventral view; **G**, specimen no. MNHNL BEL538, bed 98a; **G1**, lateral view, venter right; **G2**, ventral view; **H**, *Parapassaloteuthis* sp. A, no. MNHNL BEL501, bed 97b; **H1**, lateral view, venter left; **H2**, longitudinal section, lateral view, venter right. Scale bar: 1 cm. **White arrows** indicate the estimated position of the protoconch.

Passaloteuthis elongata (Miller, 1826) (Fig. 12E)

Belemnites elongatus Miller, 1826: 60, pl. 7, figs 6-8. — Combémorel *et al.* 1994 : 11, pl. 2, fig. 1.

Passaloteuthis argillarum Lang, 1928: 200, pl. 13, fig. 7 (*fide* Doyle 2010).

Belemnites paxillosus elongatus – Schumann 1974: 23, pl. 2, fig. 14 ; pl. 3, figs 3-5.

Passaloteuthis elongata – Lang 1928: 201, pl. 13, fig. 8. — Rulleau 2007: pl. 41 fig. 3. — Doyle 2010 : 268, pl. 45, figs 14-17 (non fig. 13). — Weis & Thuy 2015: 107, figs 3B-C.

MATERIAL. — Three specimen (MNHNL BEL505a-c).

STRATIGRAPHICAL DISTRIBUTION. — Lower Pliensbachian, Jamesoni-Davoei chronozones. Fresney-le-Puceux: "*Marnes à bélemnites*" Mb, bed 95 (base).

GEOGRAPHIC DISTRIBUTION. — England, Dorset (Lang 1928, Doyle 2010); north-west Germany (Schumann 1974); Austria, northern Calcareous Alps (Weis & Thuy 2015); north-west France, Normandy (this work); central France, Mont d'Or Lyonnais (Dumortier 1869 ; Rulleau 2007), Bulgaria (Stoyanova-Vergilova 1993).

DESCRIPTION
The medium-sized, moderately slender rostra show a cylindriconical profile and outline. The apical region is elongated and sharply pointed and bears two weakly developed dorsolateral grooves. Lateral lines are indistinct. The cross sections are rounded to slightly compressed (I_c ranging between 1.00 and 1.03; taken at half of the rostrum length). The alveolus occupies approximately ¼ of the rostrum length.

REMARKS
The species, insufficiently described by its original author (Miller 1826), has been emended since the designation of a neotype by Lang (1928: 201), and re-illustrated in Doyle (2010: pl. 45, figs 16-17). *Passaloteuthis elongata* stands morphologically between the slender-elongate passaloteuthid taxa such as *P. pessula* (Simpson, 1884) and the stouter, cylindrical taxa such as *P. laevigata*.

Passaloteuthis laevigata (Zieten, 1831)
(Fig. 12F-G)

Belemnites laevigatus Zieten, 1831: 29, pl. 21, fig. 12.

Passaloteuthis (*Passaloteuthis*) *paxillosa* (*sensu* Voltz 1830) – Riegraf *et al.* 1984: 147, pl. 9, figs 3-4, text-figs 43f, 45a, 48a, b (*cum syn.*).

Passaloteuthis bisulcata – Doyle 1990: 19, pl. 1 figs 1-8; pl. 2, figs 1-4 ; pl. 3, figs 1-4 (*cum syn.*). — Schlegelmilch 1998: 51, pl. 2, figs 6-7. — Sanders *et al.* 2015: 55, figs 5A-B, 7A-E.

Belemnites paxillosus – Combémorel *et al.* 1994: 9, pl. 1, figs 9, 10.

Passaloteuthis bisulcatus [sic] – Combémorel 1997: pl. 27, fig 9.

Passaloteuthis laevigata – Schlegelmilch 1998: 51, pl. 2, fig. 8. — Pinard *et al.* 2014: 172, fig. 8D. — Weis *et al.* 2015b: 737, fig. 2i, j, k (*cum syn.*).

Passaloteuthis bruguieriana – Pinard *et al.* 2014: 172, fig. 8C.

MATERIAL. — Five specimen (MNHNL BEL498, BEL502, BEL522, BEL523, BEL538).

STRATIGRAPHICAL DISTRIBUTION. — Upper Pliensbachian (Margaritatus Chronozone) up to lowermost Toarcian (Tenuicostatum Chronozone). Fresney-le-Puceux: "*banc de Roc*" Mb, beds 97b, 98a, 98b, 99b, 100.

GEOGRAPHIC DISTRIBUTION. — England, Dorset and Yorkshire (Doyle 1990, 2003); Austria, northern Calcareous Alps (Weis & Thuy 2015); Slovakia (Činčurová 1991); Bulgaria (Stoyanova-Vergilova 1993); south Germany (Riegraf *et al.* 1984, Schlegelmilch 1998); north-west France, Calvados (Combémorel *et al.* 1994; this work); north-east France, Lorraine and Luxembourg (R. Weis unpublished field data); Morocco, Rif (Sanders *et al.* 2015); central France, Mâconnais and Mont d'Or Lyonnais (Combémorel 1997; Rulleau 2007); Italy, Latium and western Sicily (Weis *et al.* 2015b).

DESCRIPTION
The medium- to estimated large-sized, robust rostra shows a cylindrical to cylindriconical profile and a cylindrical or subhastate outline. The apex is rather obtuse and bears two short but well-developed dorsolateral grooves. Especially the ventral side of the apex bears irregular striae. Lateral lines are indistinct. Cross sections are elliptical and only weakly compressed. The alveolus occupies approximately one third to ¼ of the total rostrum length.

REMARK
This variable taxon (Doyle 1990 distinguished three "varieties", "Var. A", "Var. B". and "Var. C") has a particularly complex nomenclatural history (see Riegraf *et al.* 1984 and Doyle 1990). Initially often referred to as "*Belemnites paxillosus*" (name suppressed by ICZN, see Doyle & Riegraf 1986) and later *Passaloteuthis bruguieriana* (d'Orbigny, 1842), respectively *Passaloteuthis bisulcata* (Blainville, 1827), it has been synonymized by Riegraf *et al.* (1984), Doyle (1990) and Weis *et al.* (2015b) with *Passaloteuthis laevigata* (Zieten, 1831). Other authors (Schlegelmilch 1998; Pinard *et al.* 2014) consider the latter taxon as a distinct species, a view which is not followed herein. The name given by Blainville (*Belemnites bisulcatus* Blainville, 1827) would have the priority according to the ICZN, but the type series of *Belemnites bisulcatus*, partially lost and recently re-investigated by Sanders *et al.* (2015) presents some nomenclatural issues (Sanders *et al.* 2015: 55). Pending the nomenclatural status of *Belemnites bisulcatus* Blainville, 1827, we use here the first valid name, *Belemnites laevigatus* Zieten, 1831.

Passaloteuthis milleri (Phillips, 1867)
(Fig. 13A)

Belemnites milleri Phillips, 1867: 54, pl. 8, fig. 19. — Dumortier 1869: 30, pl. 1, figs 1-6.

Passaloteuthis milleri – Doyle 1990: 22, pl. 2, figs 5-9. — Stoyanova-Vergilova 1993: pl. 22, figs 8-10. — Schlegelmilch 1998: 52, pl. 3, fig. 4; 7, fig. 6. — Pinard *et al.* 2014: 172, fig. 8E.

MATERIAL. — One specimen (MNHNL BEL493).

STRATIGRAPHICAL DISTRIBUTION. — Upper Pliensbachian up to lowermost Toarcian (Tenuicostatum Chronozone). Fresney-le-Puceux: "*Argiles à poissons*" Mb, bed 101.

GEOGRAPHIC DISTRIBUTION. — England, Yorkshire, Northampton, Dorset (Phillips 1867; Doyle 1990); north-west France, Normandy (this work); central France, Rhône Valley (Dumortier 1869); south France, Causses (Pinard *et al.* 2014); south Germany, Swabia (Schlegelmilch 1998); Bulgaria (Stoyanova-Vergilova 1993); Luxembourg (R. Weis unpublished field data).

DESCRIPTION
A single fragmentary rostrum is described, in which the apical and part of the stem regions are preserved. The estimated medium sized rostrum shows a cylindrical or cylindriconical outline and profile. The smooth apex bears only traces of weak and short dorsolateral grooves. The cross section is rounded-subquadrate.

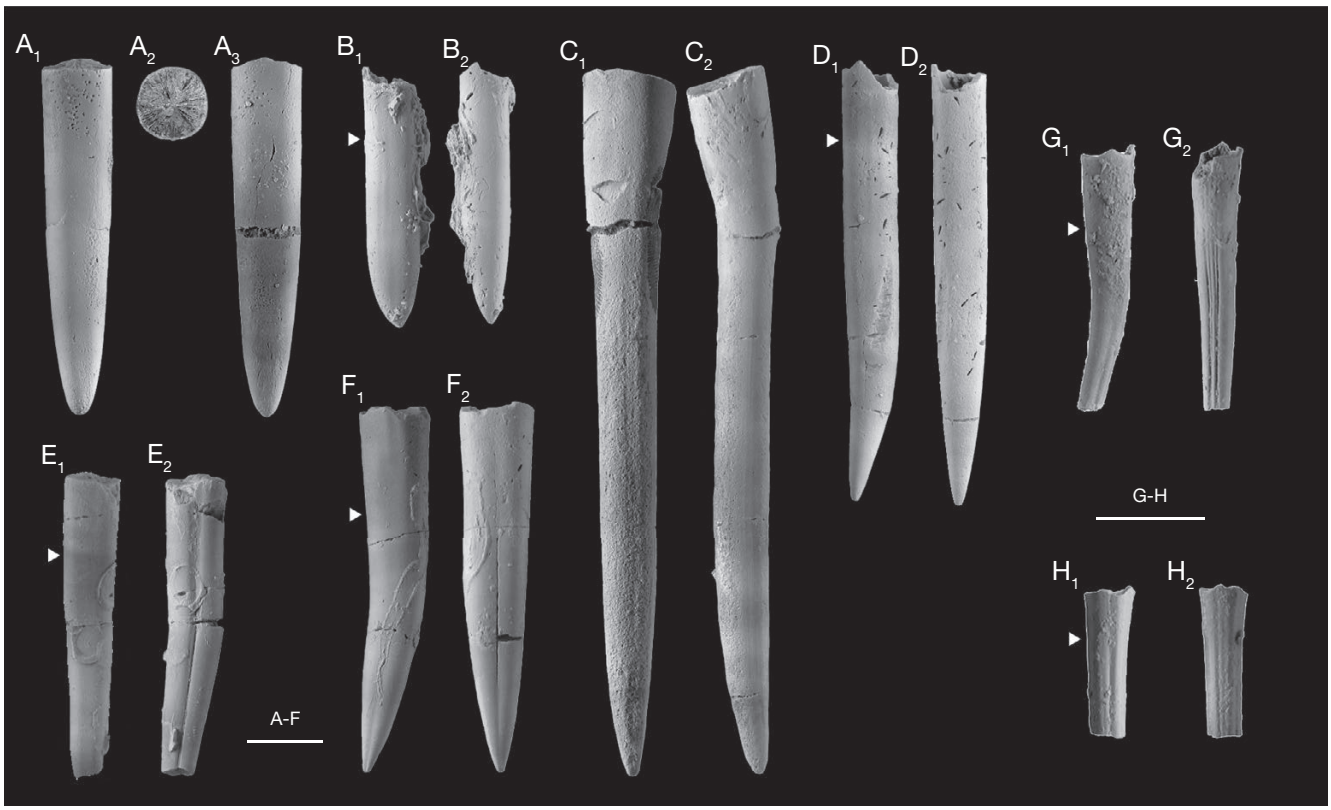

FIG. 13. — Passaloteuthididae (part 4), Salpingoteuthididae and incertae sedis, from the Pliensbachian-Toarcian of Fresney-le-Puceux: **A**, *Passaloteuthis milleri* (Phillips, 1867), alveolar part not preserved, specimen no. MNHNL BEL493, bed 101; **A1**, lateral view, non-orientated; **A2**, cross section in the stem region; **A3**, ventral or dorsal view; **B**, *Pleurobelus compressus* (Stahl, 1824), specimen with serpulid incrustations, no. MNHNL BEL499, bed 97b; **B1**, lateral view, venter left; **B2**, ventral view; **C**, *Pleurobelus lagenaeformis* (Hartmann *in* Zieten, 1832), epirostrum and initial part of orthostrum of a larger specimen, no. MNHNL BEL500, bed 97b; **C1**, lateral view, non-orientated; **C2**, ventral or dorsal view; **D**, *Pseudohastites longiformis* (Blake in Tate & Blake, 1876), specimen with numerous borings, no. MNHNL BEL481, bed 99b; **D1**, lateral view, venter right; **D2**, ventral view; **E**, **F**, *Lissajousibelus harleyi* (Mayer, 1866); **E**, specimen with missing apex, no. MNHNL BEL495, bed 102; **E1**, lateral view, venter right; **E2**, ventral view; **F**, specimen no. MNHNL BEL496, bed 99b; **F1**, lateral view, venter left; **F2**, ventral view; **G**, *Salpingoteuthis tessoniana* (d'Orbigny, 1842), apical part of epirostrum missing, specimen no. MNHNL BEL491a, bed 107; **G1**, lateral view, venter left; **G2**, ventral view; **H**, *Salpingoteuthis* cf. *trisulcata* (Blainville, 1827), fragmentary specimen, major part of epirostrum missing, no. MNHNL BEL490, bed 111; **H1**, lateral view, venter right; **H2**, ventral view. Scale bars: 1 cm. **White arrows** indicate the estimated position of the protoconch.

Genus *Pleurobelus* Naef, 1922

TYPE SPECIES. — *Belemnites compressus* Stahl, 1824 (by original designation), from the upper Pliensbachian of south-west Germany.

DISTRIBUTION. — Upper Pliensbachian from Europe.

Pleurobelus compressus (Stahl, 1824) (Fig. 13B)

Belemnites compressus Stahl, 1824: 33.

Pleurobelus compressus – Combémorel *et al.* 1994: 13, pl. 2, fig. 3. — Schlegelmilch 1998: 54, pl. 4, fig. 3. — Pinard *et al.* 2014: 161, fig. 5A, B.

MATERIAL. — One specimen (MNHNL BEL499).

STRATIGRAPHICAL DISTRIBUTION. — Upper Pliensbachian, Margaritatus chronozone. Fresney-le-Puceux: "*banc de Roc*" Mb, bed 97b.

GEOGRAPHIC DISTRIBUTION. — South Germany (Schlegelmilch 1998); north-west France, Normandy (Combémorel *et al.* 1994; this work); south France, Causses (Pinard *et al.* 2014); north-east France, Lorraine (R. Weis unpublished field work); England (Phillips 1866).

DESCRIPTION

The small sized rostrum possesses a cylindrical outline and profile. The short apex is acute and asymmetrical. A lateral depression is present in the apical region. Triple lateral lines are present. The cross section is compressed (I_c = 1.1, taken at half of the rostrum length). The alveolus occupies approximately ⅓ to ¼ of the total rostrum length.

Pleurobelus lagenaeformis (Hartmann *in* Zieten, 1832) (Fig. 13C)

Belemnites lagenaeformis Hartmann *in* Zieten, 1832: 33, pl. 25, fig. 1.

Pleurobelus lagenaeformis – Schlegelmilch 1998: 54, pl. 4, figs 4-6. — Pinard *et al.* 2014: 162, fig 5E-G.

MATERIAL. — One specimen (MNHNL BEL500).

STRATIGRAPHICAL DISTRIBUTION. — Upper Pliensbachian, Margaritatus chronozone. Fresney-le-Puceux: "*banc de Roc*" Mb, bed 97b.

GEOGRAPHIC DISTRIBUTION. — South Germany (Schlegelmilch 1998); north-west France, Normandy (this work); south France, Causses (Pinard *et al.* 2014).

Description
Only the epirostral part and a fragment of the orthorostrum are preserved. Large sized rostrum (epirostral length *c.* 75 mm). The epirostrum bears two long, lateral depressions and further striae. The cross section of the orthorostrum is subquadrate, compressed (I_c = 1.15).

Remarks
The epirostral development and the peculiar subquadrate and compressed cross section of the orthorostrum are typical for *P. lagenaeformis*, as described by Müller-Stoll (1936).

Genus *Pseudohastites* Naef, 1922

Type species. — *Belemnites scabrosus* Simpson, 1866, from the lower Pliensbachian of Robin Hood's Bay, North Yorkshire, England.

Distribution. — Pliensbachian to lowermost Toarcian of Europe, Northern Africa, and Greenland.

Pseudohastites longiformis (Blake *in* Tate & Blake, 1876) (Fig. 13D)

Belemnites longiformis Blake *in* Tate & Blake, 1876: 320, pl. 4, figs 8a-b.

Belemnites virgatus – Dumortier 1869 (pars): 41, pl. 4, figs 4-6 (*fide* Doyle 1990: 24).

Pseudohastites longiformis – Doyle 1990: 24, pl. 3 figs 5-9. — Sanders *et al.* 2015: 57, fig. 7F-G. — Weis *et al.* 2015b: 738, figs 2h, m.

Material. — One specimen (MNHNL BEL481).

Stratigraphical distribution. — Uppermost Pliensbachian (Spinatum Chronozone) to lowermost Toarcian (Tenuicostatum Chronozone). Fresney-le-Puceux: "*banc de Roc*" Mb, bed 99b.

Geographic distribution. — England, Cleveland, Yorkshire (Doyle 1990); north-west France (this work); Mont d'Or Lyonnais (Dumortier 1869); Morocco, Rif (Sanders *et al.* 2015); Italy, central Apennines (Weis *et al.* 2015b).

Description
The small sized, slender rostrum shows a cylindriconical outline and profile. The acute and elongate apical region shows only weak imprints of dorsolateral grooves. Lateral lines are well developed as double shallow depressions. The cross sections are rounded or slightly compressed (in the alveolar region). The alveolus occupies approximately ⅙ of the rostrum length.

Family Salpingoteuthididae Doyle, 1992

Genus *Salpingoteuthis* Lissajous, 1915

Type species. — *Belemnites trisulcatus* Blainville, 1827 (by original designation), from the Toarcian of Calvados department, Normandy, north-west France.

Distribution. — Lower Toarcian to lower Aalenian of Europe.

Salpingoteuthis tessoniana (d'Orbigny, 1843) (Fig. 13G)

Belemnites tessonianus d'Orbigny, 1843: 102, pl. 11, figs 13-18.

Salpingoteuthis tessoniana – Doyle 1992: 70, pl. 28, figs 7-9, 11. — Combémorel *et al.* 1994: 14, pl. 1, figs 11, 12. — Schlegelmilch 1998: 71, pl. 10, figs 9-10.

Material. — Two specimen (MNHNL BEL491a, b).

Stratigraphical distribution. — Lower Toarcian, Bifrons chronozone. Fresney-le-Puceux: "*Calcaires et Marnes à* Hildoceras" Mbr, bed 107.

Geographic distribution. — North-west France (d'Orbigny 1843; and this work); England (Doyle 1992); less typical records also from south Germany (see remark in Schlegelmilch [1998: 71]).

Description
The very small sized rostra are conical and have a strongly asymmetrical profile. The rostrum largely consists of a striated epirostrum; striation is strong along the whole ventral side, with four distinct striae which merge into two distinct striae towards the apical end. Striation is present also on the dorsal side, but less strongly developed. Two incised dorsolateral grooves are developed on the epirostrum. Cross sections are subtriangular, compressed in the alveolar region.

Salpingoteuthis cf. ***trisulcata*** (Blainville, 1827) (Fig. 13H)

cf. *Belemnites trisulcatus* – Blainville 1827: 83, pl. 5, fig. 13.

cf. *Salpingoteuthis trisulcata* – Doyle 1992: 71, pl. 28, figs. 2-5, 10. — Combémorel *et al.* 1994: 13, pl. 2, figs 12-13. — Schlegelmilch 1998: 70, pl. 10, fig. 1. — Arp 2010: pl. 4, figs 5-6. — Pinard *et al.* 2014: 173, fig. 8H.

Material. — One specimen (MNHNL BEL490).

Stratigraphical distribution. — Upper Toarcian, Pseudoradiosa Chronozone. Fresney-le-Puceux: "*Calcaire à grains ferrugineux*" Mb, bed 111.

Geographic distribution. — South Germany (Schlegelmilch 1998; Arp 2010); England, Dorset (Doyle 1992); central-east France, Monts Lyonnais and Isère (Rulleau *et al.* 1998; Rulleau 2007); south France, Hérault and Aveyron (Rulleau *et al.* 1998; Pinard *et al.* 2014); north-west France, Normandy (Blainville 1827; this work).

Description
Presumably small sized rostrum, with a "trumpet"-like alveolar widening. The well-developed epirostrum bears two long and well-incised dorsolateral grooves and several dorsal and ventral striae.

Remark
Despite its fragmentary state of preservation, the studied specimen is tentatively referred to *S. trisulcata*, a well-known and widespread species, whose type material originates from the upper Toarcian of Normandy.

	PLIENSBACHIAN			TOARCIAN							
	Davoei	Margaritatus	Spinatum	Tenuicostatum	Serpentinum	Bifrons	Variabilis	Thouarsense	Dispansum	Pseudoradiosa	Aalensis
Salpingoteuthis cf. *trisulcata* (Blainville, 1827)										●?○	●?○
Acrocoelites bobeti Lissajous, 1927										● ○	● ○
Hastites subclavatus (Voltz, 1830)										●	
Acrocoelites strictus Lissajous, 1927							● ○	● ○			
Acrocoelites subgracilis Kolb, 1942							●	●			
Acrocoelites cf. *triscissus* (Janensch, 1902)							●?○	●?○			
Dactyloteuthis semistriata (Münster, 1830)							● ○	● ○			
Acrocoelites subtenuis (Simpson, 1855)						○					
Acrocoelites riegrafi Doyle, 1992						○					
Odontobelus subpyramidalis (Lissajous, 1927)						○					
Salpingoteuthis tessoniana (d'Orbigny, 1843)						● ○					
Acrocoelites ilminstrensis (Phillips, 1867)					● ○						
Lissajousibelus harleyi (Mayer, 1866)				● ○	●?○?						
Parapassaloteuthis zieteni (Werner, 1912)				○							
Passaloteuthis milleri (Phillips, 1867)				● ○							
Pseudohastites longiformis (Blake *in* Tate & Blake, 1876)			●	●							
Passaloteuthis laevigata (Zieten, 1831)		● ○	●	● ○							
Pleurobelus compressus (Stahl, 1824)		● ○									
Pleurobelus lagenaeformis (Hartmann *in* Zieten, 1832)		●									
Parapassaloteuthis sp. A		●									
Passaloteuthis armata (Dumortier, 1869)		● ○									
Passaloteuthis cuspidata (Simpson, 1884)	●	●									
Passaloteuthis elongata (Miller, 1826)	●										
Subhastites pseudoclavatus Gustomesov, 1977	● ○										
Subhastites cf. *microstylus* (Phillips, 1867)	●										
Gastrobelus umbilicatus (Blainville, 1827)	●										

FIG. 14. — Stratigraphical distribution of the species studied in Normandy. Species from Fresney-le-Puceux are marked by **black dots**. Species from Feuguerolles-sur-Orne (unpublished collection data) are marked by **white dots**. Question marks refer to uncertain stratigraphic attribution.

Suborder ?BELEMNOPSEINA
Family indet.

Genus *Lissajousibelus* Weis *in* Weis *et al.*, 2015

TYPE SPECIES. — *Belemnites harleyi* Mayer, 1866 (by original designation), from the Toarcian of Calvados department, Normandy, north-west France.

DISTRIBUTION. — ?Uppermost Pliensbachian to lowermost Toarcian of western France and north-east Spain.

Lissajousibelus harleyi (Mayer, 1866)
(Fig. 13E, F)

Belemnites harleyi Mayer, 1866: 362.

Lissajousibelus harleyi – Weis *et al.* 2015a: 292, figs 2a-k, 3a-i (*cum syn.*).

STUDIED MATERIAL. — Three specimen (MNHNL BEL494, BEL495, BEL496).

STRATIGRAPHICAL DISTRIBUTION. — ?Uppermost Pliensbachian to lower Toarcian (Tenuicostatum and ?Serpentinum chronozones): Fresney-le-Puceux: "*banc de Roc*" Mb, bed 99b, and "*Argiles à poissons*" Fm, beds 101 and 102.

GEOGRAPHIC DISTRIBUTION. — North Spain, Asturias (Mouterde 1971); north-west France, Vendée, Sarthe and Calvados (Lissajous 1927; Weis *et al.* 2015a).

DESCRIPTION

The small sized rostra show a conical profile and a cylindriconical outline. The acute apex bears two weakly incised dorsolateral grooves. A long and deeply incised ventral groove is present; it displays an intermediate position, fading out both on the apical and the alveolar region without reaching neither the apex nor the alveolar border. Lateral lines are present as broad, shallow depressions on the flanks. The dorsal side of

the alveolar region is flattened. Cross sections of the rostrum are overall depressed (I_c taken at half of the rostrum length corresponding to 0.87 and 0.91 respectively). The alveolus occupies approximately ⅓ of the total rostrum length.

Remarks

The species has recently been described in detail by Weis *et al.* (2015a), based on abundant material from Feuguerolles-sur-Orne, a section near Fresney-le-Puceux. The material collected in Fresney is complementary to this study and confirms the stratigraphic range of *L. harleyi* (Weis *et al.* 2015a).

LOWER JURASSIC BELEMNITE DIVERSITY IN NORMANDY COMPARED TO WESTERN AND CENTRAL EUROPEAN BELEMNITE FAUNAS

The studied outcrop in Fresney-le-Puceux allows a rather unique insight into the diversity of the belemnite assemblages of a single locality with belemnites recorded from 10 out of the 13 identified chronozones. Together with a largely unpublished collection (reported herein as preliminary results; Figs 14, 15) from the nearby locality of Feuguerolles-sur-Orne (Weis *et al.* 2015a), we consider these data as a representative taxonomic record for the Pliensbachian-Toarcian interval in the western part of the Paris Basin. The data from Normandy will be included in a comprehensive work on the paleobiogeography and taxonomic diversity of European Lower Jurassic belemnites.

Lower Pliensbachian (Davoei Chronozone)

The "*Marnes à bélemnites*" Member yields large quantities of belemnites of which most rostra belong to the Passaloteuthididae, especially *Passaloteuthis*, well represented by rather robust and conical morphologies. Numerous specimens are also attributed to *Gastrobelus umbilicatus*. Only rare specimens, mostly preserved as fragments owing to their thin and small rostrum, can be attributed to the hastitid genus *Subhastites*.

The most diversified faunas from the lower Pliensbachian have been described from England (Dorset: Lang 1928, revised in Doyle 2010), from north Germany (Schumann 1974) and from south Germany (Swabia: summarized in Riegraf 1980 and Schlegelmilch 1998). Other, more scattereds and often less-well stratigraphically constrained faunas are known from central France (Dumortier 1869), from Turkey (Doyle & Mariotti 1991), from the northern Calcareous Alps (Weis & Thuy 2015) and the Pienniny Klippenbelt (Činčurová 1974, 1975) and Bulgaria (summarized in Stoyanova-Vergilova 1993). They all present a similar composition, at least at generic level (Doyle 1994; Weis & Thuy 2015).

Upper Pliensbachian (Margaritatus and Spinatum chronozones)

The "*banc de Roc*" Member yields numerous belemnites, but the carbonaceous nature of the embedding rock strongly hampers collecting them in greater numbers. Passaloteuthidids of the genera *Passaloteuthis*, *Pleurobelus,* and *Pseudohastites* are dominant.

At a European scale, the belemnite faunas of the upper Pliensbachian, in contrast to the better known and more diverse faunas from lower Pliensbachian and Toarcian (see also Dera *et al.* 2016), are not very well known, as there is no monographic treatment of them, so far. Under these circumstances, the most significant data in this respect are from the south of Germany (Swabia: Riegraf 1980; Schlegelmilch 1998). Other occurrences comprise Central Italy (Weis *et al.* 2015b), Bulgaria (summarized in Stoyanova-Vergilova 1993), and the south of France (Pinard *et al.* 2014). They all show strong similarities in taxonomic composition, comprising several species assigned to *Passaloteuthis* and other passaloteuthid genera (*Pleurobelus*, *Gastrobelus*). Only the upper Pliensbachian of central Italy yields some rare, peculiar forms with alveolar grooves (Weis *et al.* 2015b), that have not yet been found elsewhere.

Lower Toarcian (Tenuicostatum-Bifrons chronozones)

The lower Toarcian belemnite record in Fresney-le-Puceux is rather meagre, due to the calcareous nature of the "*Couche à Tenuicostatum*" Fm and the strongly reduced thickness of the "*Argiles à poissons*" Fm. The latter units contain numerous, but poorly diversified passaloteuthids and acrocoelitids. The presence of *Lissajousibelus harleyi*, a peculiar belemnite with an intermediate ventral canal is a remarkable feature of the lowermost Toarcian (Tenuicostatum Chronozone) assemblages in Normandy (Weis *et al.* 2015a). This taxon has not been found yet in coeval and well-studied assemblages of England and the south of Germany.

The "*Calcaires et Marnes à* Hildoceras" Member (Bifrons Zone) yielded relatively few belemnite rostra, indicating low diversity (*Acrocoelites* spp. and the dwarfed *Salpingoteuthis tessoniana,* which is known also from England (Doyle 1992) and Swabia (Schlegelmilch 1998)). Belemnite faunas from the Bifrons Zone are more diverse in England (Doyle 1990, 1992) and south Germany (Riegraf 1980). The relatively low species diversity in Fresney-le-Puceux needs further investigation as it might be caused by collection bias, given the apparent absence of sediment from the upper part of the Bifrons zone (Bifrons subzone).

The second-order crisis of the Pliensbachian-Toarcian (i.e. the early Toarcian crisis) affects many marine taxa (see Neige *et al.* 2013), and has been shown to be a two-pulses phenomenon (Dera *et al.* 2010, 2011): one at the Pliensbachian-Toarcian boundary (i.e. Spinatum-Tenuicostatum chronozones boundary), and the other in the Early Toarcian, at the Tenuicostatum-Serpentinum chronozones boundary. However, apparently belemnite data from Fresney-le-Puceux, or complementary data from Feuguerolles-sur Orne, do not exactly follow this scheme (Fig. 15): whereas the Tenuicostatum-Serpentinum boundary clearly shows a decrease of species numbers, the Pliensbachian-Toarcian boundary is apparently marked by an increase of belemnites species. Further date are needed to substantiate this seemingly paradoxical trend.

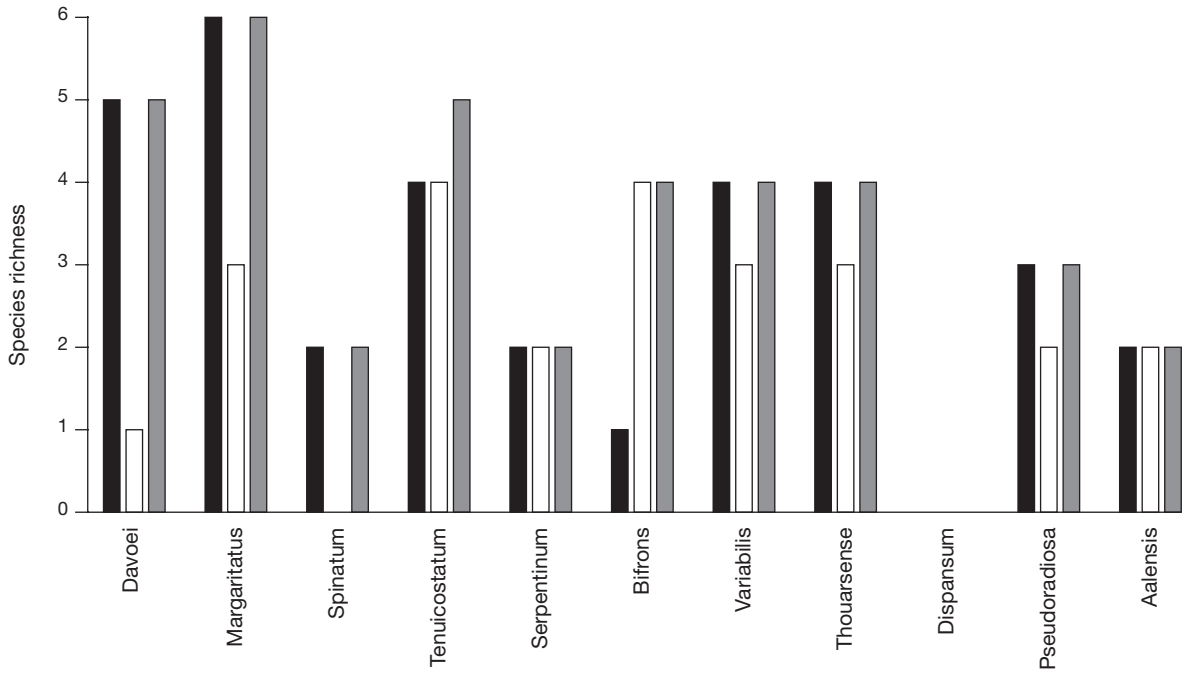

Fig. 15. — Species richness throughout the studied period. **Black bars**, Fresney-le-Puceux; **white bars**, Feuguerolles-sur Orne (unpublished collection data); **grey bars**, total number of species from Normandy (Fresney-le-Puceux and Feuguerolles-sur-Orne).

Upper Toarcian (Variabilis-Aalensis chronozones)

The "*Marnes à* Haugia" Member and the subsequent "*Calcaires à* Grammoceras" and "*Calcaires à grains ferrugineux*" members are particularly rich in belemnite specimens, although most specimens belong to *Acrocoelites strictus* and *Acrocoelites bobeti*. Other species of *Acrocoelites* and other genera (*Dactyloteuthis*, *Hastites*, *Salpingoteuthis*) are far less represented in absolute numbers.

Belemnite faunas from the upper Toarcian have also been described from many areas of western and central Europe including England (revised by Doyle 1990, 1992), south Germany (summarized in Schlegelmilch 1998), south France (Causses: Pinard *et al.* 2014), Luxembourg (Weis 1999), central-east France (Monts Lyonnais and Isère: revision in Rulleau 2007), Slovakia (e.g. Činčurová 1983), Bulgaria (summarized in Stoyanova-Vergilova 1993). In the south of Germany, belemnites reach a diversity peak during the uppermost Toarcian (Pseudoradiosa-Aalensis chronozones: Dera *et al.* 2016). However, in the south France, diversity is relatively low in the uppermost Toarcian with a poorly diversified acrocoelitid fauna and apparently "Tethyan" elements (*Salpingoteuthis* and *Rhabdobelus*) (Doyle 1994). Based on our data from Fresney-le-Puceux and Feuguerolles-sur-Orne (Fig. 15), a low diversity for the uppermost Toarcian can be recognized also in Normandy, with the presence of *Acrocoelites bobeti*, *Acrocoelites* spp., *Hastites subclavatus*, and *Salpingoteuthis trisulcata*.

Acknowledgements

Marc Chesnier (Cresserons, Calvados) allowed the study of his remarkable belemnite collection from Feuguerolles-sur-Orne (Calvados, France), used herein as comparative material. Paul Braun (MNHNL) assisted with the processing of the photographs. Jo Simon, Guy Kronz and Paul Braun (all MNHNL) are acknowledged for technical support during the cleaning process of the specimens. The management of the "*Société des carrières de la Roche Blain*" is thanked for their permission to take samples for study at the Fresney quarry. We are particularly grateful to Peter Doyle and a second anonymous reviewer for their constructive remarks. This work was carried out as part of the project "The Pliensbachian-Toarcian perturbations and their legacy in marine biodiversity of the Western Tethys" by the Natural History Museum Luxembourg. This publication was supported by INSU Intervie (PN), and is a contribution by the SAMBA team of the Biogeosciences laboratory (Dijon, France).

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Submitted on 12 May 2017;
accepted on 3 October 2017;
published on 1 March 2018.