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Lissajousibelus nov. gen., an Early Jurassic canaliculate belemnite from Normandy, France

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Abstract *Belemnites harleyi* Mayer, 1866, originally described from the Jurassic of Normandy, has encountered diverging interpretations during the last 150 years of scientific research. It has subsequently been assigned to four different genera (*Belemnopsis*, *Aulacoteuthis*, *Acrocoelites* and *Holcobelus*). The detailed study of the rostrum morphology and its inner structure allows us to attribute it to a new genus, *Lissajousibelus* Weis gen. nov., in honour of the French geologist Marcel Lissajous (1863–1921). Key features of the new genus are the overall depressed rostrum, short dorsolateral apical grooves, a long intermediate ventral groove with splitting surface, and a shallow dorsoalveolar depression. Bed-by-bed sampling at the classic locality Feuguerolles-sur-Orne (Calvados) enables us to revise the stratigraphic position of *Lissajousibelus harleyi* (Mayer, in J de Conchyl 3:358–369, 1866) as lowermost Toarcian Tenuicostatum Chronozone. *Lissajousibelus* Weis gen. nov. is therefore amongst the earliest belemnites with belemnopseine morphology. However, its phylogenetic relationships with younger Belemnopseina from the Aalenian–Bajocian (Middle Jurassic) remain unclear.

Keywords Systematics · Belemnitida · Belemnopseina · Toarcian · Anglo-Paris Basin · Calvados

Introduction

In 1853, Harlé reported a canaliculate belemnite (“*Belemnites canaliculatus* Schlotheim, 1820”) from marl beds intercalated between the “Banc de roc” (upper Pliensbachian) and the “Argiles à poissons” (lower Toarcian) of the French Calvados department (Normandy). Mayer (1866) recognized it as a distinct taxon and described it as *Belemnites harleyi* n. sp. Later, in his monumental monograph on the Jurassic fossils of Normandy, Eudes-Deslongchamps (1878) reported the same form under the name *Belemnites canaliculatus*, stating that it had been encountered exclusively in the “Couches à Ammonites Murchisonae” (upper Aalenian according to modern stratigraphic standards). Lissajous (1915) referred it first to the genus *Belemnopsis* and later (Lissajous 1927) to *Aulacoteuthis*, and indicated a stratigraphic distribution ranging from upper Pliensbachian to Toarcian. Later, Doyle (1994) considered it as the earliest representative of *Acrocoelites*. More recently, Riegraf (1995), Riegraf et al. (1998), and Weis et al. (2012) tentatively attributed it to the Aalenian–Bajocian genus *Holcobelus*, expressing some doubt on its stratigraphic position and emphasizing also the characteristic depression of the rostrum (Weis et al. 2012, p. 23). As the aforementioned authors based their study on

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the limited available material from historical collections of the nineteenth century, with poor stratigraphic and geographic information, the systematic status of the species remained with some doubts. The present paper benefits from recent bed-by-bed sampling by one of us (MC) at the former Guérin quarry of Feuguerolles-sur-Orne (Calvados), a locality already mentioned by Eudes-Deslongchamps (1878). It is now possible to give precise information on the stratigraphic position of "*Belemnites harleyi*" and to provide a more detailed study of its peculiar morphological features, allowing us to establish a new, monospecific genus *Lissajousibelus* Weis gen. nov. for this taxon. The systematic results constitute the basis for discussing the palaeobiogeographical distribution and the morphological affinities of *Lissajousibelus harleyi* (Mayer 1866).

Material and Geological setting

The studied material is composed of 69 belemnite rostra sampled bed-by-bed in the Guérin quarry at Feuguerolles-sur-Orne. All figured and measured specimens from this set are stored at the Musée d'histoire naturelle, Le Mans, France (MHNLM), additional specimens are stored in the private collection of M. Chesnier. Further material was studied from the historical "École des Mines de Paris" collection, now stored at University Claude Bernard, Lyon-Villeurbanne, France (UCBL), the collection of the Musée d'histoire naturelle, Le Mans, France (MHNLM) and the "Pellat" collection, stored at the National Museum for Natural History, Luxembourg (MNHNL). Scanning Electron Microscope (Jeol-Neoscope JCM-5000) has been used to observe phragmocone details. Illustrated rostra are all in natural size (unless otherwise indicated by scale bars) and have been coated with magnesium oxide before photographing.

The section at Feuguerolles-sur-Orne (Calvados, France)

The Guérin quarry is situated at 500 m north of the village of Feuguerolles-sur-Orne, ca. 6 km south of the town of Caen (Fig. 1b). It has been exploited for Palaeozoic limestone, underlying the Jurassic covering. The Silurian basement in the study area consists of a palaeo-escarpment ("Synclinal de May-sur-Orne") with numerous small-scaled depressions that have been filled up by Jurassic deposits. The palaeogeographical position of the synclinal de May-sur-Orne during the Early Jurassic was close to the northeastern margin of the Armorican Massif landmass (Fig. 1a), in the western part of the Anglo-Paris Basin. Palaeontological, stratigraphical and palaeoenvironmental aspects of the Feuguerolles-sur-Orne section have been studied by several authors (e.g. Rioult 1968; Dugué et al. 1998; Vernhet et al. 2002).

Although comprising sediments that are strongly reduced in thickness, the section allows us to establish a well-constrained stratigraphical scale based on ammonites, following the chronozone concept introduced by Page (2003); it covers parts of the Lower and Middle Jurassic (lower Pliensbachian to lower Bajocian). Our study focused on the upper Pliensbachian ("Domerian") and the lower Toarcian beds. The most complete section out of 20 field-logs is chosen herein as the representative section (Fig. 1c). The Pliensbachian sediments overly the Palaeozoic basement, with a thickness of ca. 1.7 m; the upper part of the Pliensbachian beds has been dated by a single specimen of *Amaltheus* sp., found in situ 30 cm below the base of bed T1a. This occurrence indicates the Margaritatus Chronozone or the Apyrenum Subchronozone of the Spinatum Chronozone. Concerning the Toarcian deposits, the Semicelatum Zonule, Semicelatum Subchronozone, Tenuicostatum Chronozone has been identified (beds T1a–c). Bed T1a is a 0.04–0.06-m-thick layer of sandy, fossiliferous marls. It contains bivalve and brachiopod shells (Thecideida indet. and *Koninckella liasiana* Bouchard in Davidson and Morris 1847), echinoderms, fish teeth, numerous belemnites and a single ammonite specimen *Dactylioceras semicelatum* (Simpson 1843). The calcareous layer T1b, with a thickness of 0.10–0.14 m, contains the same dactylioceratid ammonite fauna. Bed T1c corresponds to sandy marls, similar to T1a, with a similar fossil assemblage but more numerous *Dactylioceras semicelatum*. It is followed by 0.2-m-thick greyish marls, dated from the Serpentinum Chronozone, Elegantulum Subchronozone, with numerous belemnites at the base. The very thin layer between T1c and T2 ("Couche à Koninckella" of local authors) contains numerous fossils, e.g. belemnites and the brachiopod *Koninckella davidsoni* (Eudes-Deslongchamps 1853); no ammonites have been found in this T1c/T2 boundary bed at Feuguerolles-sur-Orne, but the age of the "Couche à Koninckella" in Normandy is given as Tenuicostatum Chronozone (Rioult 1980). Records of *Lissajousibelus harleyi* are mainly distributed in beds T1a–c, a few records come from the transition bed T1c/2a and the base of T2. The distribution of coeval belemnite taxa (passaloteuthids, megateuthidids and salpingoteuthidids) will be investigated in a separate paper.

Systematic palaeontology

Terminology follows Doyle and Kelly (1988) and Weis et al. (2012). Symbols (*; v; cf.; ?) are used according to the recommendations of Matthews (1973). Measurements: L,

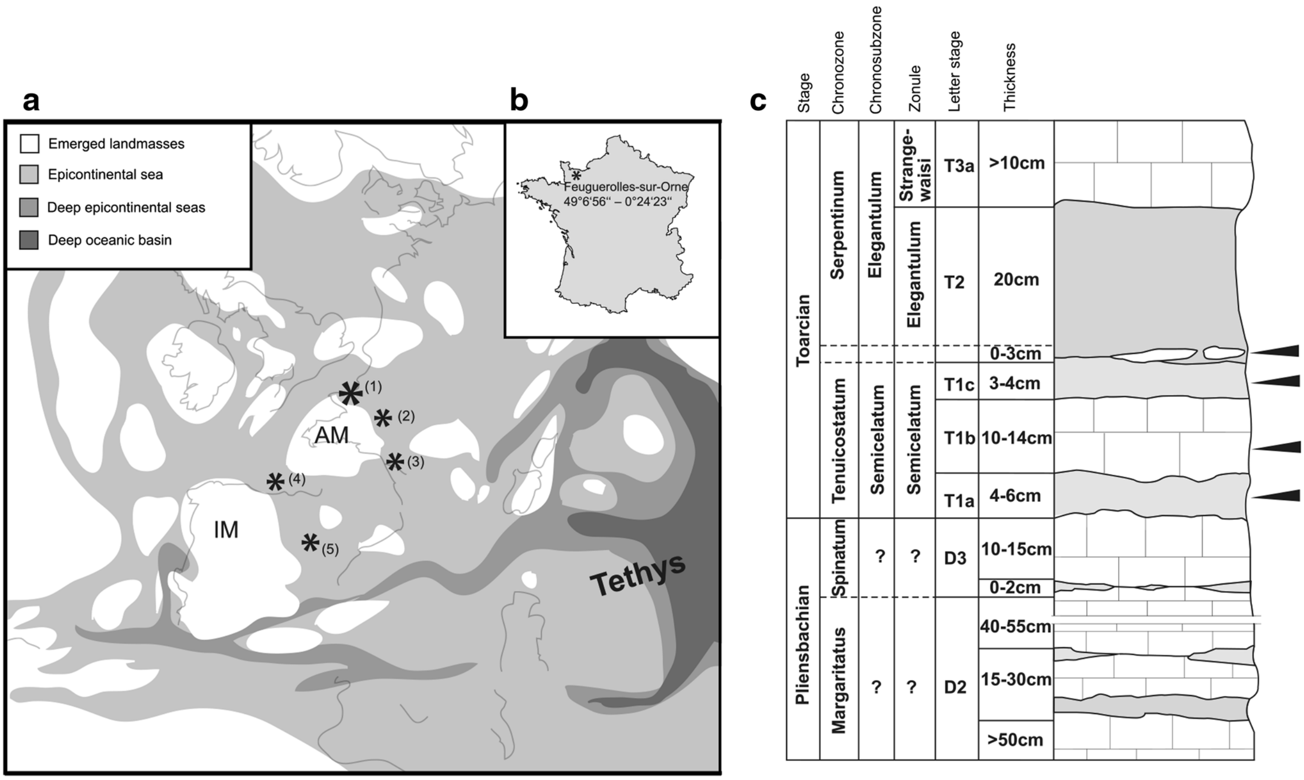


Fig. 1 Geographical and geological setting of the Feugerolles-sur-Orne section. **a** Palaeogeographical map of western Europe during the Toarcian (modified from Dera et al. 2010), with occurrences of *Lissajousibelus harleyi*: *(1)* Calvados (including Feuguerolles-sur-Orne), *(2)* Sarthe, *(3)* Vendée, *(4)* Asturias, *(5)* Iberian range; landmass abbreviations: IM, Iberian Massif, AM, Armorican Massif. **b** Position of the studied section in northwestern France. **c** Stratigraphy of the Feuguerolles-sur-Orne section (*pars*), showing the Pliensbachian/Toarcian boundary beds. The occurrence of *Lissajousibelus harleyi* is marked by the belemnite rostrum symbol

total preserved length; X, length from apex to protoconch (length of the rostrum solidum); Dv, dorso-ventral diameter at alveolar opening; Dl, lateral diameter at alveolar opening; Ie, elongation index, ratio between dorsal and ventral diameter at alveolar opening and length from apex to protoconch (Dv/X); Ic, compression index, ratio between dorsal and ventral diameter and lateral diameter, calculated at the level of the alveolar opening: values of >1 indicate a compressed rostrum, values of <1 indicate a depressed rostrum; Ls, length of the splitting surface; A, alveolar angle.

Subclass Coleoidea Bather, 1888
Order Belemnitida Zittel, 1895
Suborder ?Belemnopseina Jeletzky, 1965
Family uncertain (?Holcobelidae)
Genus *Lissajousibelus* Weis nov. gen.
Type species Belemnites harleyi Mayer 1866

Derivatio nominis In honour of the French geologist Marcel Lissajous (1863–1921), who was the first to recognize the outstanding systematic position of "*Belemnites harleyi*".

Diagnosis Small to medium sized, conical rostrum. Outline symmetrical, conical to cylindroconical. Profile slightly asymmetrical, conical. Apical region elongate and moderately acute. Cross sections depressed all along the rostrum. Short and weakly developed dorsolateral apical grooves. Long intermediate ventral groove, with smooth edges, extending from the apical to the alveolar region, and fading out towards the alveolar border, with variably developed splitting surface. Short dorsoalveolar depression or flattening, not reaching the alveolar border. Apical line cyrtolineate. Alveolus ventrally displaced, occupying circa one-third of the rostrum.

Differential diagnosis The genus differs from *Holcobelus* (upper Aalenian–lower Bajocian) by its overall depressed rostrum, the presence of short dorsolateral apical grooves and by its broader ventral groove, with smooth borders; it differs from *Acrocoelites* (upper Pliensbachian–lower Aalenian) by its overall depressed rostrum and the different morphology of the ventral groove, long and intermediate with splitting surface.

Remarks The genus *Lissajousibelus* Weis nov. gen. is tentatively assigned to the Belemnopseina, on the base of the intermediate ventral groove with splitting surface. It is not possible to assign *Lissajousibelus* to a known family with certainty, although it shows some affinities with the Holcobelidae, an Aalenian–Bajocian family to which "*Belemnites harleyi*" had previously been assigned. The depressed rostrum, the morphology of the ventral groove and splitting surface, and the dorsolateral apical grooves are not typical characters for Holcobelidae (see also Weis et al. 2012, p. 17); however, some holcobelids (few individuals of *Holcobelus munieri* (Eudes-Deslongchamps 1878) and *Calabribelus pallinii* Weis, Mariotti and Riegraf, 2012) show both a rudimentary splitting surface and remnants of reduced dorsolateral grooves (Weis et al. 2012). Nevertheless, evidence about the phylogenetic relationships between *Lissajousibelus* and the holcobelids is considered inadequate (see also chapter "Discussion") at the present stage of investigations.

Occurence Lowermost Toarcian (Tenuicostatum Chronozone) of western France (Calvados, Sarthe, Vendée) and northern and eastern Spain (Asturìas and Iberian Range). Possibly also upper Pliensbachian of western France (Vendée and Calvados).

Lissajousibelus harleyi (Mayer 1866)
Figures 2a–k, 3a–i

non 1820 *Belemnites canaliculatus*—Schlotheim, p. 49. [= *Pachybelemnopsis canaliculata* (von Schlotheim 1820), *fide* Riegraf 2000]
1853 *Belemnites canaliculatus*—Harlé, p. 14.
*1866 *Belemnites harleyi*—Mayer, p. 362.
1878 *Belemnites canaliculatus* Schlotheim—Eudes-Deslongchamps, p. 58, pl. VII, Figs. 21–26.
1915 *Belemnopsis harleyi* Mayer—Lissajous, p. 146
1919 *Belemnites canaliculatus*—Lissajous, p. 43f.
v.1927 *Aulacoteuthis harleyi* Mayer—Lissajous, p. 35, pl. IV, Figs. 1–3.
1927 *Belemnites canaliculatus* Deslongchamps—Stolley, p. 122.
1971 *Belemnites harleyi* Mayer—Mouterde, p. 378ff.
1974 *Aulacoteuthis harleyi* (Mayer)—Suarez-Vega, p. 51.
1994 *Acrocoelites harleyi* Lissajous (*sic*)—Doyle, p. 113.
2002 *Aulacoteuthis harleyi* (Mayer)—Vernhet et al., p. 98.
v.2012 *Holcobelus harleyi* (Mayer)—Weis et al., p. 22, pl. 2, Figs. 1–7 and text-Fig. 3c (*cum syn.*)

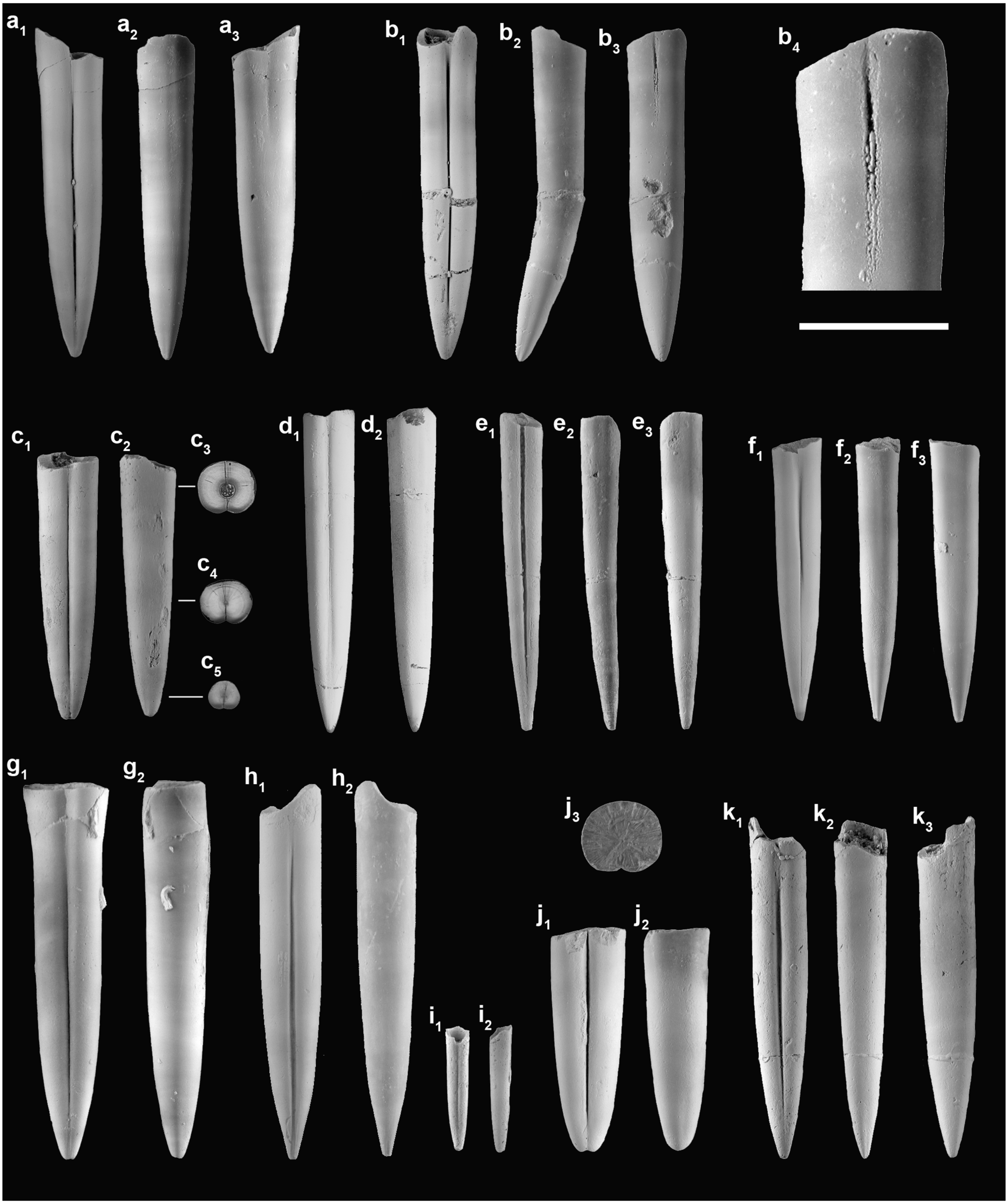
Type material Mayer (1866) did not designate a holotype. He mentions the presence of specimens in several collections, which constitute then the type series. One of the mentioned collections is the "École des mines" (Paris), which is now partially held by the Geological Museum of the University Claude Bernard, Lyon-Villeurbanne (France). The "École des Mines" collection in Lyon contains several historical specimens with handwritten determination "*Belemnites harleyi*". One of them, no. UCBL EM18076, from the lowermost Toarcian of Fontaine-Etoupefour (Calvados, France) is hereby designated as the lectotype and re-illustrated herein (Fig. 2h; also figured in Weis et al. 2012: pl. 2, Fig. 5a–b, with erroneous stratigraphic information). Five additional specimens figured in Weis et al. (2012) from the same collection and nearby localities are hereby designated as paralectotypes (Weis et al. 2012: pl. 2, Figs. 1a–c, 3a–b, 4a–b, 6a–b, 7).

Fig. 2 *Lissajousibelus harleyi* (Mayer 1866). **a** Adult stage (MNHNL BEL373a); a_1 ventral view, a_2 lateral view, venter right, a_3 dorsal view. **b** (Sub)adult stage (MHNLM 2015.1.1); b_1 ventral view, b_2 lateral view, venter left, b_3 dorsal view, b_4 detail of the dorsal "groove", *scale bar* equals 10 mm. **c** (Sub)adult stage, anterior part broken (MHNLM 2015.1.6); c_1 ventral view, c_2 lateral view, venter right, c_3 cross section of the alveolar region, c_4 cross section of the stem region, c_5 cross section of the apical region. **d** Subadult stage (UCBL FSL.27508); d_1 ventral view, d_2 lateral view; figured also in (Lissajous 1927, pl. IV, Fig. 3). **e** Subadult stage, extremely slender individual with broken anterior part (MHNLM 2015.1.2); e_1 ventral view, e_2 lateral view, venter right, e_3 dorsal view. **f** Subadult stage (MHNLM 2015.1.4); f_1 ventral view, f_2 lateral view, venter right, f_3 dorsal view. **g** Adult stage (MHNLM 2003.1.2107a); g_1 ventral view, g_2 lateral view, venter left. **h** Lectotype, herein designated (UCBL EM18076), figured also in Weis et al. 2012, pl. 2, Fig. 5; h_1 ventral view, h_2 lateral view. **i** Early juvenile stage (MHNLM 2003.1.2107b); i_1 ventral view, i_2 lateral view, venter left. **j** Adult-gerontic stage, apical region and part of stem region (MHNLM 2015.1.3); j_1 ventral view, j_2 lateral view, venter left, j_3 cross section at broken end. **k** (Sub)adult stage (MHNLM 2015.1.5); k_1 ventral view, k_2 lateral view, venter left, k_3 dorsal view. Specimens originate from the lower Toarcian, Tenuicostatum Chronozone, Semicelatum Subchronozone of Feuguerolles-sur-Orne, Normandy (**b**–**c**, **e**, **j**, **k**), lowermost Toarcian of Montceaux-en-Bessin (**f**), lowermost Toarcian of unknown locality in Normandy (**a**), "Domerian" (?) of Subles, Calvados (**d**), lowermost Toarcian of Fontaine-Etoupefour, Calvados (**h**), Toarcian of Asnières-sur-Vègre and Prévigné, Sarthe (**g**, **i**)

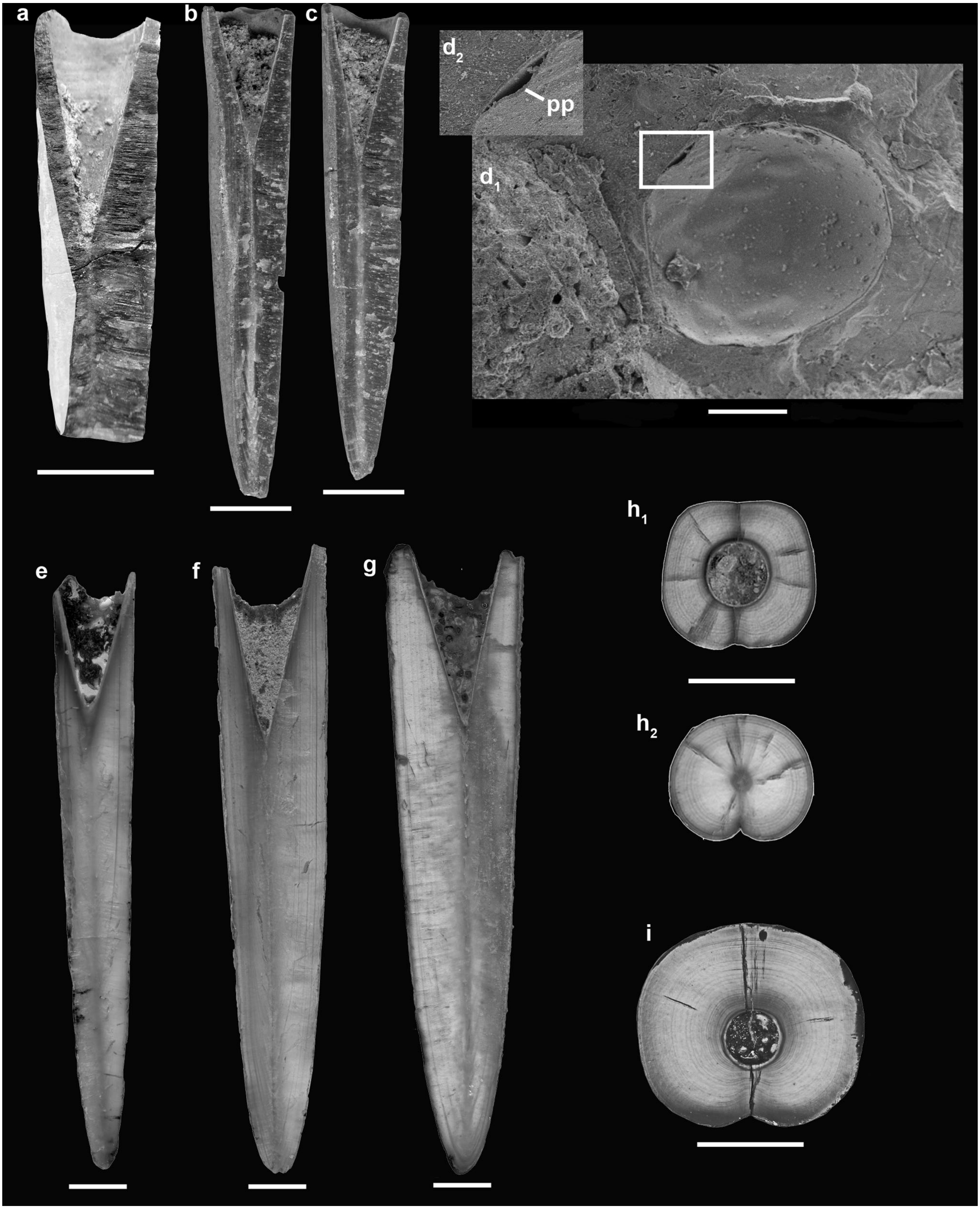
Studied material Sixty-nine complete or subcomplete specimens from the Tenuicostatum Chronozone, Semicelatum Subchronozone, Semicelatum Zonule of Feuguerolles-sur-Orne (MHNLM no. 2015.1.1–11 and collection Chesnier); six complete to subcomplete specimens from the ?uppermost Pliensbachian or basal Toarcian, Monceaux-en-Bessin (collection Chesnier); two alveolar fragments from the ?Pliensbachian or lowermost Toarcian of Surain (Vieux-Pont), collection Chesnier; six complete specimens from the Toarcian of Asnières-sur-Vègre and Prévigné (Sarthe, France), coll. MHNLM no. 2003–1–2107; four specimens without locality (UCBL EM20.407–410); three specimens from the Pliensbachian–Toarcian boundary beds of Luron (Vendée, France), coll. UCBL EM20.404–406); four specimens from the Toarcian of Calvados, France, former collection Pellat (MNHNL BEL350 and 373).

Diagnosis As for the genus.

Description Small to medium sized, moderately robust and conical rostrum. The outline is symmetrical and conical to slightly cylindroconical. The profile is slightly



asymmetrical and conical. The apical region is tapering regularly to an elongate and moderately acute apex, which becomes obtuse in late ontogenetic stages. Cross sections are depressed elliptical on the entire length of the rostrum; the depression is more marked on the stem and apical region than on the alveolar region. At the anterior margin of the rostrum, close to the alveolar border, cross sections are almost subquadrate, due to the dorsoalveolar flattening.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◀**Fig. 3** *Lissajousibelus harleyi* (Mayer 1866). **a** Longitudinal split of the alveolar and stem region, the outline of the splitting surface is evidenced by the whitened area on the left (UCBL FSL.27509); *scale bar* equals 10 mm; figured also in Lissajous 1927, pl. IV, Fig. 3. **b** Longitudinal split, with the splitting surface visible along the left rostrum margin (MHNLM 2015.1.10). **c** Longitudinal split, with the splitting surface visible along the left rostrum margin (MHNLM 2015.1.11). **d** SEM image showing the protoconch and surrounding rostral mass in a splitted section (MHNLM 2003.1.2107c); *d_1* complete view of the egg-shaped protoconch, *d_2* close-up of the upper protoconch wall (dorsal) showing the protoconch pocket (pp); *scale bar* equals 100 µm. **e** Longitudinal thin section of a slender, subadult individual, ventral side left (MHNLM 2015.1.9); *scale bar* equals 5 mm. **f** Longitudinal thin section of a (sub)adult individual, ventral side left (MNHNL BEL373b); *scale bar* equals 5 mm. **g** Longitudinal thin section of an adult individual, ventral side right (MHNLM 2015.1.8); *scale bar* equals 5 mm. **h** Thin cross section (MHNLM 2015.1.7); *h_1* anterior alveolar region, showing the dorsal depression (*on the top*) and the outfading ventral groove; *h_2* stem region, showing the ventral groove, progressively deepening during growth; *scale bar* equals 5 mm. **i** Thin cross section at the posterior alveolar region, showing the ventral groove, progressively deepening during growth (MHNLM 2015.1.6); *scale bar* equals 5 mm. Specimens originate from the lower Toarcian, Tenuicostatum Chronozone, Semicelatum Subchronozone of Feuguerolles-sur-Orne, Calvados (**b**–**c**, **e**, **g**–**i**), the lower Toarcian of Calvados, unknown locality (**f**), the "Domerian" (?) of Mervent, Vendée (**a**) and the Toarcian of Asnières-sur-Vègre or Prévigny, Sarthe (**d**)

Short dorsolateral apical grooves are commonly developed. A broad intermediate ventral groove extends from close the apex to the alveolar border, fading out into a broad depression on the alveolar region. A reduced, clearly delimited splitting surface is developed; it does not reach the alveolar wall or the apical line and appears thus to have developed only at later ontogenetic stages (adult). A short and shallow dorsoalveolar depression is commonly present; in some individuals, it is replaced by a dorsoalveolar flattening. Lateral lines consist in two parallel running indistinct depressions in lateral and ventrolateral position and confined to the alveolar region. The apical line is sharply delimited, cyrtolineate. The alveolus occupies approximately one-third of the total length of the rostrum and is slightly ventrally eccentric: the eccentricity of the protoconch (EP) varies between 10 and 13 %. The alveolar angle varies between 22° and 24°.

Phragmocone structures Traces of the siphuncle have been observed, indicating that the position of the groove is ventral. The dimensions of the protoconch in one measured specimen are 0.29 mm (width) and 0.31 mm (length). An enigmatic hollow structure, designated as "protoconch pocket" by Doguzhaeva et al. (2014) is present on the dorsal edge of the protoconch (Fig. 3d), and appears similar to those observed in *Holcobelus* and *Pachybelemnopsis* (Doguzhaeva et al. 2014, Fig. 4).

Ontogeny The primordial rostrum has not been observed in the studied material. Early juvenile stages are slender elongate, cylindrical in profile and cylindrical or subhastate in outline. A dorsoalveolar flattening and a broad intermediate ventral groove are well developed, but no splitting surface is developed at this early stage. The subadult–adult stages are characterized by an increase in length and elongate conical shape. At adult–gerontic stages, the acute apical region is more attenuated and rostra more robust due to an increase in width. The splitting surface develops only at the adult stage.

Remarks Measurements of the rostrum are given in Table 1, in addition to those given by Weis et al. (2012, p. 23). The elongation index (Ie) varies between 0.23 and 0.26, which are typical values for *Passaloteuthis* and *Acrocoelites* (Schlegelmilch 1998). The compression index (Ica) varies between 0.88 and 0.98 (or 0.82–0.98 taking into consideration data from Weis et al. 2012), which is a typical range for *Pachybelemnopsis* (Schlegelmilch 1998). The length of the splitting surface (Ls) varies considerably, occupying between 24 and 60 % of the total rostrum length. The size of the protoconch is comparable with that of *Holcobelus* given by Doguzhaeva et al. (2014, Table 1). Protoconch pockets are reported to date only in *Lissajousibelus* (herein), *Holcobelus* and *Pachybelemnopsis* (Doguzhaeva et al. 2014); their function and taxonomic value are unknown.

One specimen shows an irregularly shaped, incised dorsoalveolar groove (Fig. 2b). The occasional presence of such poorly developed dorsoalveolar grooves ("Dorsalrinne" in Riegraf 1980) is known in some taxa and considered to be of little taxonomic value (Stevens 1965, p. 41; Riegraf 1980, p. 36; Doyle 1992, p. 53), though this feature may contribute to highlight phylogenetic relationships (Jeletzky 1980, p. 4).

Occurrence As for the genus.

Discussion

Palaeobiogeography and biostratigraphy

Belemnite assemblages from the lowermost Toarcian Tenuicostatum Chronozone and corresponding units (Page 2003) are known from several localities in the United Kingdom (Doyle 1990–1992), southwestern Germany (Riegraf 1980; Riegraf et al. 1984), Bulgaria (Stoyanova-Vergilova 1993), the Rif mountains, Morocco (Sanders et al. 2013), central Italy and Sicily (Weis et al. 2015), Belgium and Luxembourg (Maubeuge 1952; Delsate 1997). All these assemblages contain one or more of the following taxa: *Passaloteuthis laevigata* (von Zieten 1830), *Passaloteuthis milleri* (Phillips 1867), *Acrocoelites* ssp., *Parapassaloteuthis* ssp. and *Pseudohastites longiformis*

Table 1 Measurements of *Lissajousibelus harleyi* (Mayer 1866)

Specimen no.	L	X	Dv	Dl	Ie	Ica	Ls	A
MHNLM 2003.1.2107d	54	38	10	10.2	0.26	0.98	20	–
MHNLM 2003.1.2107e	55	39	8.8	10.1	0.23	0.87	(27)	–
UCBL FSL.20.407	64	(44)	(9.6)	(11.4)	(0.22)	(0.84)	–	–
UCBL FSL.20.408	73	46	11.8	13.4	0.26	0.88	38	–
MHNLM 2015.1.10	58	37	9.3	10	0.25	0.93	37	22
MHNLM 2015.1.11	62	40	9.9	10.9	0.25	0.91	(37)	24

(Blake in Tate and Blake 1876). In southwestern Germany only, *Micropassaloteuthis fistulata* Riegraf, Werner and Lörcher, 1984 is also present. The presence of a peculiar form such as *Lissajousibelus harleyi* could hardly have been overlooked. It is therefore probable that the species had a more limited palaeobiogeographic distribution than the aforementioned taxa; this distribution area is part of the western Tethys and comprises the epicontinental seas surrounding parts of the Armorican Massif and the Iberian Massif (Fig. 1b). The same area is known as the transitional zone in the Aalenian–Bajocian, where (Sub)Boreal and (Sub)Mediterranean faunas were mingling (Weis and Mariotti 2008; Mariotti et al. 2010). A similar pattern with mixed faunas has been reported for Pliensbachian–Toarcian brachiopod assemblages (Alméras and Bécaud 2002). In ammonites, a pattern of northwards migration of Mediterranean ammonites towards southern England has been evidenced for the Tenuicostatum Chronozone; this palaeobiogeographic pattern can be correlated with a major transgression after a regressive period at the end of the late Pliensbachian, facilitating the connection between Mediterranean and northwestern Europeans basins (Morard et al. 2003; Dera et al. 2011).

The stratigraphic range of *Lissajousibelus harleyi* in Feuguerolles-sur-Orne is entirely within the Tenuicostatum Chronozone, Semicelatum Subchronozone. Slightly older records of *Belemnites harleyi* have been reported by Lissajous (1927; uppermost Pliensbachian) based on historical collection data; however, their exact stratigraphic position needs confirmation. No records of *Lissajousibelus* are known after the Toarcian Oceanic Anoxic Event (T-OAE) which coincides with the Tenuicostatum–Serpentinum zonal boundary and marks an important extinction event in marine biota, including belemnites (Ullmann et al. 2014; Dzyuba et al. 2015).

Morphological affinities

The peculiar morphological characters of *Lissajousibelus harleyi* were outlined by several authors, but led to different taxonomic interpretations; "*Belemnites*" *harleyi* has been subsequently assigned to *Belemnopsis* (Lissajous 1915; Stolley 1927), *Aulacoteuthis* (Lissajous 1927), *Acrocoelites* (Doyle 1994) and *Holcobelus* (Riegraf 1995; Weis et al. 2012). The new material from Feuguerolles-sur-Orne allows a more detailed understanding of the morphology of *Lissajousibelus* and a better differential diagnosis towards the mentioned genera. The distinctive features of *Lissajousibelus* are the broad ventral groove with smooth edges, the clearly delimited splitting surface, the overall depressed rostrum and the presence of short dorsolateral apical grooves and a dorsoalveolar depression; the combination of these characters allow us to distinguish *Lissajousibelus* from the genus *Holcobelus* (family Holcobelidae). The similar rostrum shape and the similar position of the intermediate ventral groove in *Lissajousibelus* and *Holcobelus* could represent a case of homeomorphism; this hypothesis is supported by the different ages of *Lissajousibelus* (earliest Toarcian) and *Holcobelus* (Aalenian–Bajocian), and the lack of connecting forms. On the other hand, *Lissajousibelus* is distinguished from *Pachybelemnopsis* by its short cylindroconical shape, its dorsolateral apical grooves, and the long intermediate ventral groove, a feature that is not equivalent with the alveolar groove and splitting surface of *Pachybelemnopsis* (Combémorel et al. 1994; see also below).

Lissajousibelus harleyi also bears some similarities with "*Holcobelus*" *kinasovi* Sachs, in Sachs and Nalnjaeva 1975, from the lower Toarcian (Commune Zone) to possibly Bajocian of northern Siberia and northeastern Russia. Both species have a depressed cross section and a long incised ventral groove. Re-investigation of "*H.*" *kinasovi*, stored in the Central Siberian Geological Museum (Novosibirsk, Russia) revealed that the holotype of this species (Sachs and Nalnjaeva 1975, pl. 12, Fig. 3) possesses feeble dorsolateral apical grooves. "*H.*" *kinasovi* may be distinguished from *Lissajousibelus harleyi* by its more elongate rostrum, with the ventral groove beginning at the apex and not associated with splitting surface. The taxonomic position of "*H.*" *kinasovi* is yet unclear. It certainly does not belong to *Holcobelus* (Weis et al. 2012) and possibly represents a new genus directly related to *Acrocoelites* (Megateuthididae, Belemnitina). Other "*Holcobelus*" sensu Tuchkov (1954), Sachs and Nalnjaeva (1975), and Nalnjaeva (in Challinor et al. 1992) from northern and eastern Russia do not belong to *Holcobelus* as well (Weis et al. 2012). They are revised herein:

Table 2 Morphological comparison of the discussed taxa

Genus/species	Grooves				Splitting surface	Rostrum shape	Cross section	Alveolar depth	Alveolar angle
	Apical		Interm.	Alveolar					
	Dorsolat.	Ventral							
Acrocoelites	Yes	Yes	–	–	No	Conical–cylindrical, moderatley robust to elongated	Rounded subquadrate to compressed	ca. 1/4	21°–30°
Lissajousibelus	Yes	–	Yes	–	Yes	Conical–cylindroconical, moderatley robust	Depressed	ca. 1/3	22°–24°
“*Holcobelus*” *kinasovi*	Yes	Yes	–	–	no	Cylindrical, elongated	Rounded subquadrate to depressed	ca. 1/5	24°
Holcobelus	–	–	Yes	–	Yes	Conical–cylindroconical, robust to elongated	Rounded subquadrate to compressed	ca. 1/3 to 1/4	20°–24°
Pachybelemnopsis	–	–	–	Yes	Yes	Subcylindrical-hastate, elongated	Depressed	ca. 1/3 to 1/4	ca. 17°–23°
Holcobeloides	–	Yes	–	–	No	Conical–cylindrical, elongated	Depressed	ca. 1/4 to 1/2	23°–29°
Boreioteuthis	–	Yes	–	–	No	Cylindrical–cylindroconical, moderately robust	Depressed to slightly compressed	ca. 1/3 to 1/2	17°–27°
Aulacoteuthis	–	Yes	–	–	No	Cylindroconical-subhastate, moderately elongate	Subrounded	ca. 1/3	ca. 16°–20°

Acrocoelites umarensis (Tuchkov 1954), *Lenobelus gravis* Gustomesov, 1966, ?*Lenobelus* sp. (=*Holcobelus* sp. in Challinor et al. 1992, pl. 132, Fig. 4). Thus, the rostra of *Lissajousibelus harleyi* and “*Holcobelus*” *kinasovi* show a remarkable morphological resemblance, although the specifics of ventral groove as well as the absence of evidence for a splitting surface in “*H.” kinasovi* argues for attributing these species to different genera, families and even suborders.

The genus *Lissajousibelus* shows strong homeomorphism with some other ventrally flattened and grooved Boreal taxa of the Belemnitina, such as *Holcobeloides* (Lagonibelinae) and *Boreioteuthis* (Pachyteuthidinae) from the Cylindroteuthididae, especially *Holcobeloides altdorfensis* (Ducrotay de Blainville 1827) and *Boreioteuthis absoluta* (Fischer 1837), and *Aulacoteuthis* from the Oxyteuthididae, especially *A. ernsti* Mutterlose and Baraboshkin 2003. According to Gustomesov (1964), some individuals of *Holcobeloides altdorfensis* and *H. beaumontianus* (d’Orbigny 1842–1851) possess a narrow slit-like depression at the bottom of a broad and long ventral groove. Besides homeomorphic similarity, the species *Aulacoteuthis ernsti*, like *Lissajousibelus harleyi*, is characterized by the central to slightly ventrally displaced apical line. The genera *Holcobeloides* (middle Callovian to Oxfordian), *Boreioteuthis* (Oxfordian to Aptian) and *Aulacoteuthis* (late early Barremian) are distinguished by their non-canaliculate ventral groove, which starts from the apex, and by the absence of splitting surface and dorsolateral apical grooves. In addition, adult *Boreioteuthis* are more robust and larger in size than *Lissajousibelus*.

It can be deduced from the above information that taxa morphologically similar to *Lissajousibelus* (Table 2) appear to have developed independently in several evolutionary lineages, belonging to different families: “*Holcobelus*” *kinasovi* (family uncertain) in the Early–Middle Jurassic, *Holcobelus* (Holcobelidae) in the Middle Jurassic, *Holcobeloides* (Cylindroteuthididae) in the Middle–Late Jurassic, *Boreioteuthis* (Cylindroteuthididae) in the Late Jurassic–Early Cretaceous, *Aulacoteuthis* (Oxyteuthididae) in the late Early Cretaceous (Fig. 4). On the other hand, our data do not definitely preclude the possibility of a yet unrecognized phylogenetic relationship between *Lissajousibelus harleyi* and the Boreal-Arctic “*Holcobelus*” *kinasovi* or the (Sub) Mediterranean *Holcobelus*.

Changes in groove morphology amongst Early–Middle Jurassic belemnites

For the later Early Jurassic and early Middle Jurassic (late Pliensbachian–early Bajocian), it is possible to observe a clear trend regarding the ventral groove element of belemnites occurring in the Western Tethys (Fig. 4). A first morphological step relevant in this discussion is represented by the Pliensbachian–Aalenian genus *Acrocoelites* (Megateuthididae, Belemnitina) which develops a well-

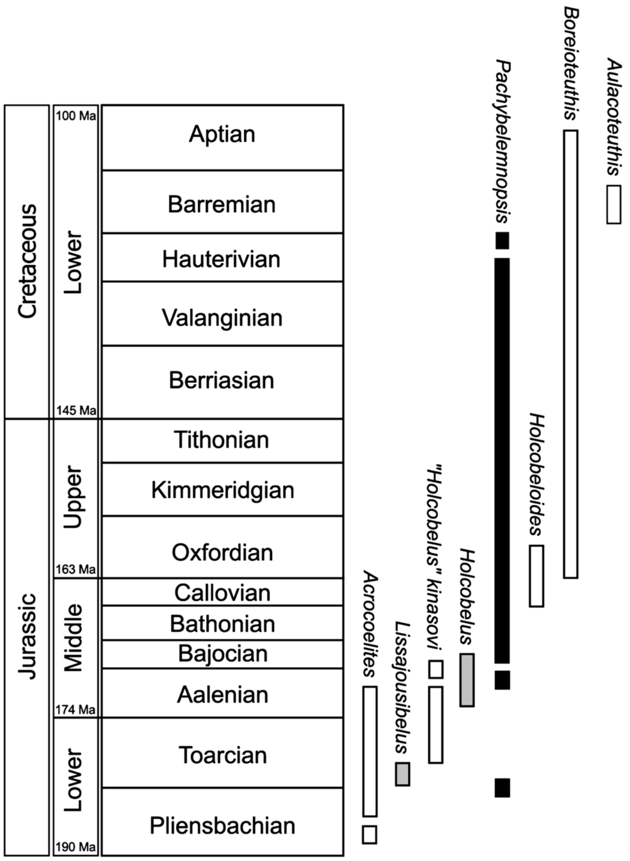

Fig. 4 Stratigraphical distribution of the discussed taxa in the order of first occurrence. The morphological trends in the ventral groove element are evidenced by the pattern of the *vertical distribution lines* (*transparent*: presence of an apical ventral groove, without splitting surface; *grey shaded*: intermediate ventral groove, with more or less developed splitting surface; *black*: alveolar ventral groove, with fully developed splitting surface). Chronostratigraphy is in accordance with Cohen et al. (2013)

incised ventral apical groove, without splitting surface. The apical ventral groove of the Boreal family Cylindroteuthididae (Belemnitina) can be considered equivalent to the apical ventral groove of megateuthids; a direct derivation of Cylindroteuthididae from Megateuthididae, or a common origin of both, is therefore deemed possible, as supported by Jeletzky (1966, p. 139), Combémorel et al. (1994, p. 48) and Sachs and Nalnjaeva (1975, p. 135). A second step is represented by *Lissajousibelus* and *Holcobelus* (Holcobelidae, Belemnopseina): here, the dorsolateral apical grooves are being reduced and the ventral groove extends from the apical region to the alveolar region (intermediate position sensu Riegraf 1980). This intermediate ventral groove is associated with a more or less developed splitting surface. A different morphology is represented by the mesohibolitids, e.g. *Pachybelemnopsis*; here the groove is confined to the stem and alveolar part of the rostrum and a well-defined triangular splitting surface is present. It is not clear if the alveolar groove of *Pachybelemnopsis* evolved from the intermediate groove of holcobelids and/or morphologically similar forms (e.g. *Lissajousibelus*), as has been suggested by Riegraf (1980) and Weis et al. (2012), or if it evolved independently, as suggested by Jeletzky (1966: from Hastitidae, Belemnitina), Combémorel et al. (1994), and discussed also by Iba et al. (2014). Future studies detailing the evolution of the lateral line patterns and investigating phragmocone details of these taxa may contribute to unravel the phylogeny of the early canaliculate belemnites (suborder Belemnopseina).

Conclusions

The new material collected in the type area has provided evidence that (1) "*Belemnites*" *harleyi* belongs to a new genus, *Lissajousibelus* nov. gen. Weis, characterized by the presence of short dorsolateral apical grooves and a long intermediate groove with splitting surface; (2) the previously uncertain stratigraphic position of *L. harleyi* is now confirmed as lowermost Toarcian, Tenuicostatum Chronozone; (3) its geographic distribution is limited to western France and northeastern Spain; (4) the taxon is amongst the earliest belemnites worldwide to have developed a long intermediate ventral groove with a rudimentary developed splitting surface, a feature considered a major step in the evolutionary history of belemnites.

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