The belemnite family Holcobelidae (Coleoidea) in the European Jurassic: systematics, biostratigraphy, palaeobiogeography and evolutionary trends

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Abstract

The belemnite family Holcobelidae Gustomesov, 1977 is revised, based on ca. 200 rostra from recent fieldwork as well as historical museum collections. The studied specimens originate from various European localities and are dated from the Early Aalenian to the Early Bajocian (Middle Jurassic). Eight species of the genera *Holcobelus* Stolley, 1927 (including *H. elmii* n. sp.) and *Calabribelus* n. gen. (with type species *C. pallinii)* are described. The evolution of the morphological characters at the family level is outlined and compared with acrocoelitids (Belemnitina) and pachybelemnopseids (Pachybelemnopseina); the possible phylogenetic links between the Holcobelidae and the latter are discussed. The stratigraphic and palaeobiogeographic distribution of holcobelids is analysed in respect to morphological changes, leading to a hypothesis on different lifestyles among the investigated taxa. The peculiar distribution pattern of Holcobelidae represents a colonization event by belemnites in the northern Tethys and a distinctive belemnitid Tethyan fauna developed during the Bajocian, dominated by *Pachybelemnopsis* and *Hibolithes*.

Keywords: Systematics, biostratigraphy, palaeobiogeography, Holcobelidae, *Holcobelus*, *Calabribelus*, Middle Jurassic, Aalenian, Bajocian, Europe.

Zusammenfassung

Anhand von ca. 200 Rostren aus neuen Geländeaufsammlungen und älteren Museumsbeständen wird eine Revision der Belemnitenfamilie Holcobelidae Gustomesov, 1977 vorgenommen. Die untersuchten Exemplare entstammen unterschiedlichen europäischen Fundstellen und reichen vom frühen Aalenium bis in das frühe Bajocium (Mittlerer Jura). Im systematischen Teil werden acht Arten der Gattungen *Holcobelus* Stolley, 1927 (mit *H. elmii* n. sp.) und *Calabribelus* n. sp. (mit der Typusart *C. pallinii*) beschrieben. Die Verfasser legen die Evolution der morphologischen Merkmale innerhalb der Familie dar und vergleichen sie mit acrocoelitiden (Belemnitina) sowie pachybelemnopseiden (Pachybelemnopseina) Belemniten. Mögliche phylogenetische Beziehungen zwischen Holcobelidae und Letztgenannten werden dargelegt. Die Untersuchung der stratigraphischen und paläobiogeographischen Verbreitung der Holcobeliden ermöglicht unter Berücksichtigung der morphologischen Veränderungen eine neue Hypothese bezüglich verschiedener Lebensweisen der hier behandelten Taxa. Insbesonders das auffällige Verbreitungsmuster der Holcobelidae stellt ein erstes Stadium zur Besiedelung der Tethys durch Belemniten und die Ausbildung einer eigenen Tethys-Belemnitenfauna während des Bajociums dar, charakterisiert durch die Vorherrschaft von *Pachybelemnopsis* und *Hibolithes*.

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1. Introduction

Early Middle Jurassic belemnites from Europe have been little investigated in the past two decades. Recent studies by us (Mariotti et al. 2007, 2010; Weis & Mariotti 2007) have attempted to combine the taxonomic results with palaeobiogeographic and biostratigraphic data, recognising the key role of Holcobelidae in the distribution patterns and evolution of the Early Middle Jurassic belemnites. The present work aims at completing these preliminary studies, by integrating unpublished data derived from the study of collections stored at the University Claude Bernard (Lyon) and from additional field work in southern Italy (Calabria) and France (Normandy, Haute-Provençe). Based on the analysed material, relevant changes in the rostrum morphology at the Aalenian/Bajocian boundary are outlined. Finally, the role of holcobelid belemnites as biostratigraphic and palaeobiogeographic markers is discussed.

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Acronyms of repositories

NHMW	Naturhistorisches Museum, Wien (A)
NMBa	Naturhistorisches Museum, Basel (CH)
NMBe	Naturhistorisches Museum, Bern (CH)
MNHN	Musée national d'histoire naturelle, Paris (F)
MNHNL	Musée national d'histoire naturelle, Luxembourg (L), including donations from Riegraf, Clement, Chesnier and Rulleau
MUSR NS	Museo di Paleontologia, Università 'La Sapienza', Roma (I)
RNGHP	Musée de la Réserve Naturelle Géologique de Haut-Provence, Digne-les-Bains (F)
SMNS	Staatliches Museum für Naturkunde, Stuttgart (D)
UBD	Université de Bourgogne, Dijon (F)
UCBL	Université Claude Bernard, Lyon (F), including collection École des Mines de Paris
UJFG	Université Joseph Fourier, Institut Dolomieu, Grenoble (F)

2. Previous works

Belemnites assigned to the family Holcobelidae have been reported many times from the Aalenian and Bajocian sediments, which are widely distributed in Europe. However, the exact stratigraphic position of these records is poorly known, also because of the condensed character and the stratigraphic hiatuses within these deposits. Records of stratigraphically older taxa, such as *Holcobelus suprapalatinus* (Kolb, 1942) from the Toarcian of southern Germany (Schlegelmilch 1998), most probably represent juvenile *Acrocoelites* with reduced dorsolateral grooves. Recently, Ippolitov et al. (2010) have recorded from the Upper Toarcian of SW Crimea (Ukraine) some fragmentary rostra of *Holcobelus* sp., which need further systematic investigation.

Reliable records of holcobelids come from the following areas: France (Voltz 1830; d'Orbigny 1842-51; Eudes-Deslongchamps 1878; Haug 1891; Roman & Gennevaux 1912; Lissajous 1925; Stolley 1927; Roché 1939; Riegraf

1980b; Mariotti et al. 2010), southern England (Phillips 1869), Luxembourg (Weis & Mariotti 2007; Guérin-Franiatte & Weis 2010), southern Germany (Quenstedt 1848, 1856; Riegraf 1980a; Schlegelmilch 1998; Weis & Mariotti 2007), Switzerland (Ooster 1857), Austria (v. Hochstetter 1897), Bulgaria (Stoyanova-Vergilova 1982, 1990, 1993; Metodiev & Koleva-Rekalova 2008), Romania (Preda 1975), eastern Slovakia and southern Poland (Gavrilishin & Kruglov 1972; Krawczyk et al. 1992), Ukraine (Nikitin 1969, 1977), the Caucasus (Krimholz 1931, 1953; Nutsubidze 1966), southern Italy (Combémorel et al. 1994a; Mariotti et al. 2007), Spain (Mallada 1891), and Portugal (Choffat 1880).

Extra-European occurrences of *Holcobelus* are rare and controversial. The only reliable records are those from the Maghreb area in Northern Africa (Morocco, Algeria and Tunisia). Termier (1936) was amongst the first to mention "*Belemnopsis blainvillei* Voltz" from the Tisfoula area (Morocco). A rock slab with a belemnite battlefield composed of *Holcobelus* specimens is stored in the collections of the Université de Bourgogne (Dijon, coll. Pierre & Durlet n° 2096). It originates from the Propinquans Zone of Amellago (Higher Atlas) and demonstrates that holcobelid belemnites are abundant at this stratigraphic level. *Holcobelus* sp. has also been recorded by Sadki (1997) from the Concavum and Propinquans zones of the Higher Atlas. A few fragmentary specimens from the Lower Bajocian of Algeria were collected by S. Elmi (collection of the University Claude Bernard, Lyon).

As concerns North America, the only evidence is by Jeletzky (in Frebold 1969; 1980), recording *Holcobelus* associated to *Acrocoelites* from the Toarcian of the Fernie Basin (Alberta, Canada); however these rostra have never been figured. For this reason there is no proof that they represent true *Holcobelus* or rather slender *Acrocoelites* with a prominent ventral and reduced dorsolateral grooves, as commonly found in the European Toarcian. From South America, Möricke (1894) recorded ?*Holcobelus* cf. *tetramerus* from the Bajocian Humphriesianum Zone of Chile, but this unique and unfigured specimen was later referred to as *Megateuthis* sp. by Doyle et al. (1996). *Belemnites admirandus* Steinmann, 1881 from the Middle Jurassic of Bolivia, previously regarded as *Holcobelus* (Stolley 1927), has been reassigned to *Dicoelites* (Riegraf 1995: 87).

Concerning south-eastern Asia, the records of Soergel (1913), figured as *Belemnites subblainvillei* Deslongchamps, have been reviewed by Stolley (1929), Stevens (1965) and Challinor (1991a). These specimens, originating from isolated boulders, had been erroneously dated as Aalenian by Soergel; the previously mentioned authors showed that they are of Callovian age and belong to *Pachybelemnopsis persulcata* (Stolley, 1929). The specimens identified as *Cylindroteuthis* (*Holcobelus*) by Stevens (1965: 65f, 169) from the Indo-Pacific region are not holcobelids s.s. and their poor preservation state does not allow to assign them unambiguously to any known genus.

Holcobelus umaraensis Tuchkov, 1954, *H. gravis* (Gustomesov, 1966) and *H. kinasovi* Sachs, 1975, were described from uppermost Lower Toarcian–Aalenian of northern Siberia and north-eastern Russia (Tuchkov 1954, Sachs & Nalnjaeva 1975, Meledina et al. 2005); *H.* cf. *blainvillii* (Voltz, 1830) was recorded from Bajocian(?) sediments of the Viliga River Basin (Pacific coast of Russia) by Tuchkov (1962, fide Dzyuba & Nalnyaeva 2011). Challinor et al. (1992) reported *H. kinasovi* from the middle Toarcian and *H. umaraensis* from Lower Aalenian of the Northeast Russia (northern coast of Okhotsk Sea) and also *Holcobelus* sp. from the Lower Aalenian of the Far East Russia (Bureya River basin). In our opinion, these taxa should be revised in order to clarify their possible phylogenetical relation to Megateuthididae and/or Cylindroteuthididae.

Finally, alleged *Holcobelus*-like belemnites associated with *Hastites* have also been reported from the Bajocian of the Xizang-Qinghai Plateau, Tibet (Wu Shunbao 1982; Chen Pei-ji 2003).

3. Material and methods

Several hundred rostra from different European localities were examined.

The terminology herein used follows Doyle & Kelly (1988), Doyle (1990) and Mariotti (2003). The description of ontogenetic stages follows Pugaczewska (1961) and Doyle (1990). To avoid confusion, the following terms and their synonyms are defined for the use in this paper (Figs. 1, 2):

Apical groove: A groove starting from the tip of the apex without reaching the alveolar part. Its position is usually dorso-lateral or ventral.

Intermediate groove: A groove that does neither reach the tip of the apex nor the alveolar border (sensu Riegraf 1980a). Its position is usually ventral. It is associated with a rudimentary splitting surface in holcobelids.

Alveolar groove: A groove starting at the alveolar border and extending towards the apical region without reaching the apex. Such a groove is not underlain by a clearly defined splitting surface. Its transverse section is generally U-shaped. However, the limit between groove and canal can not always be clearly drawn, as the alveolar groove represents a transitional evolutionary step towards a "true" alveolar canal; this is the case especially for *Calabribelus* n. gen.

Alveolar canal: An incised, V-shaped groove starting at the alveolar border and fading out towards the apical part without reaching the apex. Its position can be ventral (as in

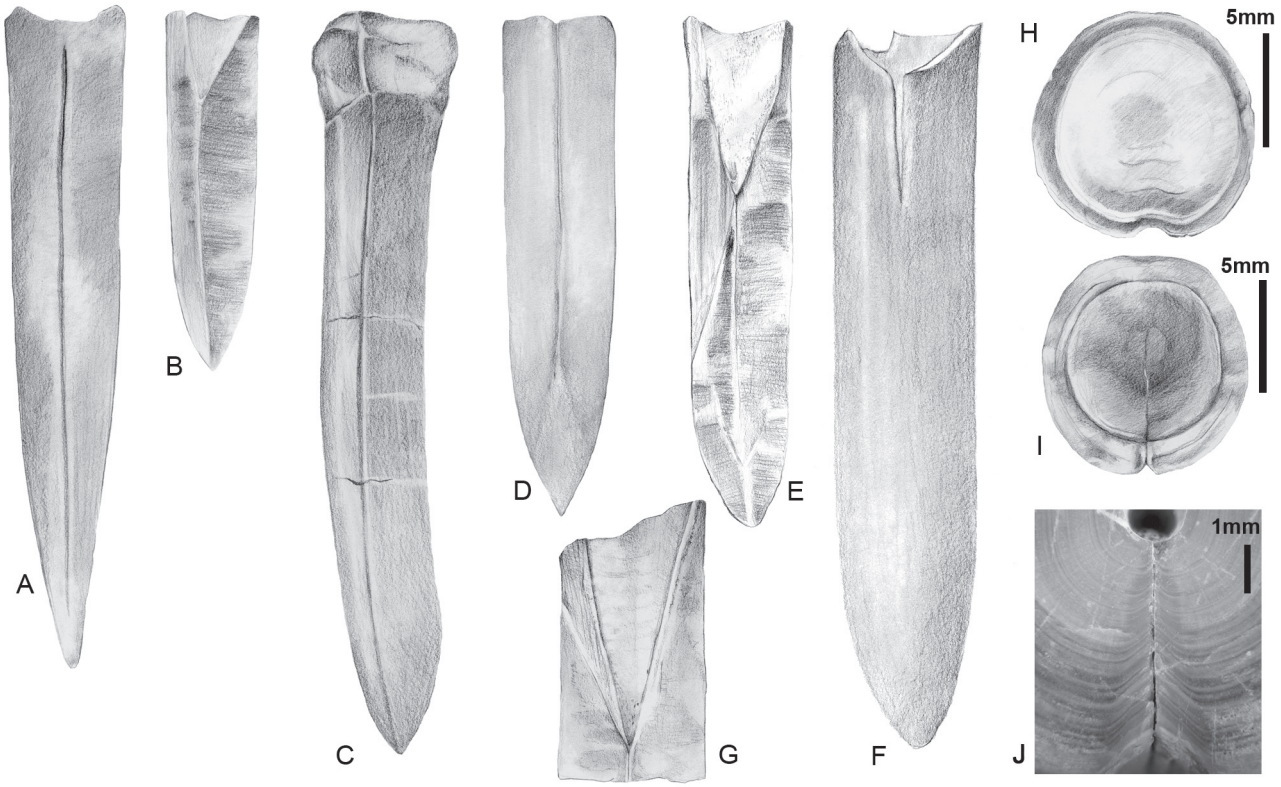

Fig. 1. Different types of grooves and splitting surfaces. – **A**. Intermediate ventral groove in *Holcobelus munieri* (Eudes-Deslongchamps); from the Aalenian/Bajocian of Croisilles, NW France (MNHN R07132). – **B**. Rudimentary splitting surface in *Holcobelus* sp.; from the Aalenian/Bajocian boundary of Fontaine-Etoupefour, NW France (UCBL, coll. École des Mines, not numbered). – **C**. Alveolar ventral groove (fading out towards the alveolar border) in *Calabribelus pallinii* n. gen, n. sp.; from the Lower Bajocian, Propinquans Zone of Lac du Castillon, Castellane, SE France (MNHNL BEL003) – **D**. Alveolar canal in *Pachybelemnopsis* sp., from the Bajocian of Saint-Honoré, western France (coll. Pellat, MNHNL 320.09). – **E**. Well-defined triangular splitting surface in *Pachybelemnopsis* sp.; from the Bajocian of Feuguerolles-sur-Orne, NW France (MNHNL BEL097). – **F**. Ventral fissure in *Belemnitella* sp.; Upper Cretaceous, unknown locality (MNHNL BEL104). – **G**. Typical belemnitellid splitting surface in *Belemnitella* sp.; Upper Cretaceous, unknown locality (MNHNL BEL133). – **H**. Transverse section of *Holcobelus brevicanalis* (Eudes-Deslongchamps), showing the "U"-shaped ventral groove; from the Aalenian/Bajocian boundary of Fontaine-Etoupefour, NW France (UCBL EM18039). – **I**. Transverse section of the alveolar part of *Pachybelemnopsis* sp., showing the "V"-shaped ventral canal; from the Bajocian of Saint-Honoré, western France (coll. Pellat, MNHNL 320.09). – **J**. Macrophoto of *Pachybelemnopsis* sp. in a transverse section, showing the growth discontinuity; from the Bajocian of Feuguerolles-sur-Orne, NW France (MNHNL, not numbered). – All specimens in natural size unless otherwise specified.

Pachybelemnopsis or *Hibolithes*) or dorsal (*Duvalia*). By definition, the canal is underlain by a splitting surface.

Splitting surface: A smooth area that can be observed in longitudinally split rostra possessing an alveolar canal. The term is used sensu Jeletzky (1966) and is equivalent to the fissural area sensu Pugaczewska (1961), and the Schlitzfeld of German authors (Riegraf 1980a, Schlegelmilch 1998).

Ventral fissure: It corresponds to an incision located on the ventral alveolar area, characteristic for Belemnitellidae (= open fissure sensu Jeletzky 1966; = alveolar fissure sensu Pugaczewska 1961).

Primordial rostrum: The first rostrum deposited on the top of the conotheca, characterised by alternating aragonitic and organic layers (Bandel & Spaeth 1988). In thin sections, it is easily distinguished by the shape of its apical, "saucer"-like part (= calcar primordialis sensu Müller-Stoll 1936).

Earliest juvenile rostrum: It corresponds to the first distinct growth stage after the primordial rostrum. Two main types are distinguished: conirostrid (or cone-like), and clavirostrid (or spindle-like) (Abel 1916; Jeletzky 1966).

Individual descriptions include size measurements in the cases of complete or almost complete specimens. All measures are in millimeters. Estimated values for incomplete specimens are marked by an asterisk (*). Dimensional adjectives are used as in Doyle & Kelly (1988);

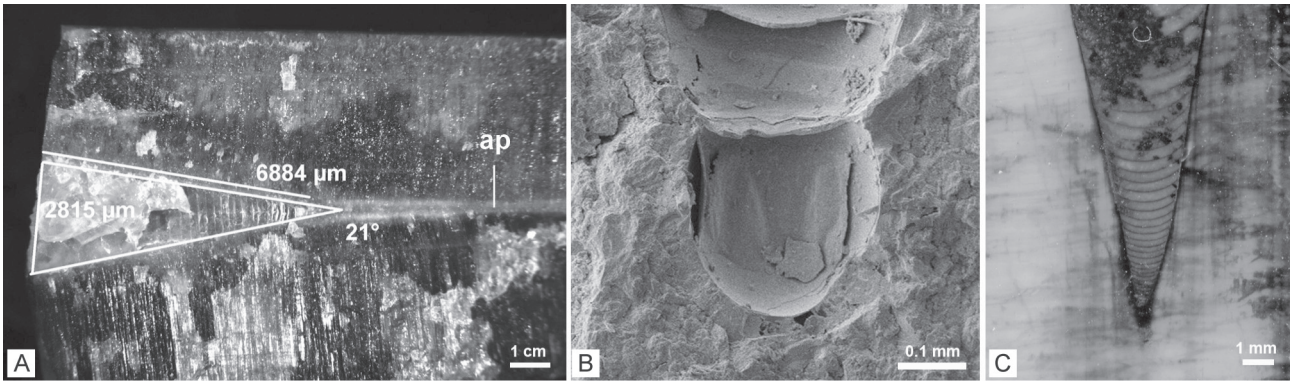

Fig. 2. Phragmocone structures. – **A**. Splitted alveolar region of *Holcobelus munieri* (Eudes-Deslongchamps), showing the position of the apical line (ap) and the alveolar angle value; from the Aalenian/Bajocian boundary of Fontaine-Etoupefour, NW France (UCBL, EM18094); photo D. Fuchs. – **B**. SEM picture showing the protoconch in *Holcobelus munieri* (Eudes-Deslongchamps); from the Aalenian/Bajocian boundary of Fontaine-Etoupefour, NW France (UCBL, EM18091); photo D. Fuchs. – **C**. Thin section showing the phragmocone of *Calabribelus pallinii* n.gen, n. sp., and the chambers without cameral deposits; from the Lower Bajocian, Propinquans Zone of Galabrun near Gap, SE France (MNHNL BEL045).

the terms small, medium and large, related to the length of the rostrum (L), are respectively referred to L < 80 mm, L between 80 and 110 mm and L > 110 mm. Abbreviations as in Mariotti (2003): L, total length; Dv, dorso-ventral diameter at alveolar opening; Dl, lateral diameter at alveolar opening; Dv_{max}, maximum dorso-ventral diameter; Dl_{max}, maximum lateral diameter; X, length from apex to protoconch (length of the rostrum solidum); Ic, compression index, the ratio between dorsal-ventral diameter and lateral diameter, calculated at the level of the alveolar opening (Ica), and at the level of the maximum dorso-ventral diameter (Icm): a value of > 1 indicates a compressed rostrum, a value of < 1 indicates a depressed rostrum.

The statistical use of ratios of the above mentioned features is regarded herein as a mere support and illustration for a qualitative taxonomic approach sensu Schwegler (1961) and Jeletzky (1980).

4. Systematic palaeontology

The systematics used herein follows Riegraf et al. (1998).

Order Belemnitida MacGillivray, 1840

Suborder Pachybelemnopseina Riegraf, in Riegraf et al., 1998
= Belemnopseina Jeletzky, 1966

Remarks. – The family Holcobelidae is included herein in the suborder Pachybelemnopseina due to the absence of apical grooves and the presence of a long ventral groove, which is regarded as anterior to the alveolar canal. The distinct feature of the Pachybelemnopseina, the splitting surface linked to the alveolar canal, is rudimentary developed in Holcobelidae. Riegraf (in Riegraf et al. 1998) proposed Pachybelemnopseina Riegraf, 1998 as a junior subjective synonym of Belemnopseina Jeletzky, 1965, considering that the type genus of the later, *Belemnopsis* auct., not Bayle, 1878, is preoccupied, an older subjective synonym of the Boreal genus *Lagonibelus* Gustomesov, 1958 and should be replaced by its next junior subjective synonym, *Pachybelemnopsis* Riegraf, 1980 (Riegraf 1999).

Family Holcobelidae Gustomesov, 1977 (emend. Riegraf, 1980)

Type genus: *Holcobelus* Stolley, 1927.
Other genera: *Calabribelus* n. gen.
Stratigraphic range and geographical distribution: Lower Aalenian (Opalinum Zone) – Lower Bajocian (Humphriesianum Zone) of mainland Europe, SW England, the Caucasus, northern Africa and possibly Tibet.

Diagnosis. – Small to large sized Pachybelemnopseina with a narrow intermediate ventral groove that extends from the apical to the alveolar region, covering almost the whole rostrum. Transverse sections generally compressed to subcircular. Splitting surface only rudimentary developed. Distinct lateral lines observable in all species on well preserved individuals. Earliest juvenile rostrum conirostrid, short conical to elongate conical. Epirostrum commonly developed in most species. Alveolar angle 20–24°. Vestigial cameral deposits.

Remarks. – The subfamily Holcobelinae has been established by Gustomesov (1977), who included several

genera with very different morphologic characters and no close phylogenetic relationship (*Holcobelus* Stolley, 1927; *Salpingoteuthis* Lissajous, 1915; *Hartmannibelus* Gustomesov, 1977). For this reason, Riegraf (1980a) emended the original diagnosis of Gustomesov (1977), but maintained the rank as a subfamily. Later, Riegraf (1998) raised the Holocobelinae to the rank of family within the suborder Pachybelemnopseina.

The Holcobelidae display morphological characters that are interpreted as intermediate between typical early Belemnitina (apically grooved, cameral deposits in the phragmocone, conirostrid earliest juvenile guard) and typical Pachybelemnopseina (alveolar canal underlain by a splitting surface, absence of cameral deposits, clavirostrid earliest juvenile guard). Due to these apparently ambiguous characters, holcobelids have been previously classified following different systematic approaches: earlier researchers included them either within the Polyteuthidae Stolley (Stolley 1927) or within the Cylindroteuthididae Stolley (Stolley 1919; Jeletzky 1966). Riegraf (1980a: 167) in contrast regarded the ventral depression of cylindroteuthids (including the early Bajocian genus *Eocylindroteuthis*) as a convergent morphologic feature to the intermediate ventral groove of holcobelids. The same author (Riegraf in Riegraf et al. 1998) included the Holcobelidae within the suborder Pachybelemnopseina, a view that is tentatively adopted herein, considering the rudimentary splitting surface present in holcobelids and the absence of apical grooves, as well as the reduced cameral deposits.

Genus *Holcobelus* Stolley, 1927

Type species: *Belemnites munieri* Eudes-Deslongchamps, 1878.

Other species: *H. blainvillii* (Voltz), *H. tetramerus* (Eudes-Deslongchamps), *H. brevicanalis* (Eudes-Deslongchamps), *H. trauthi* (Stolley), *H. harleyi* (Mayer), *H. tschegemensis* (Krimholz), *H. elmii* n. sp.

Stratigraphic range and geographical distribution: Lower Aalenian (Opalinum Zone) to Lower Bajocian (Humphriesianum Zone) of mainland Europe, SW England, the Caucasus, northern Africa and possibly Tibet.

Diagnosis. – Small to large sized, conical to cylindriconical Holcobelidae, with usually elongated apical region and compressed transverse sections. A more or less long narrow intermediate ventral groove is present. Splitting surface rudimentary developed. Alveolus penetrates deeply, one third to three quarters of the rostrum. Earliest juvenile rostrum conirostrid, short to elongate conical. Epirostrum commonly developed. Alveolar angle 20°–24°. Vestigial cameral deposits.

Remarks. – The genus includes the early representatives of the family; the earliest species, *H. blainvillii*, shows remarkable similarities with *Acrocoelites* and related Belemnitina from the Late Toarcian and Early Aalenian. Although sharing the general shape and the acute apex, *Holcobelus* differs from Toarcian and Early Aalenian Belemnitina by possessing a long intermediate ventral groove extending from the apical to the alveolar region. On the other hand, the distinction between *Holcobelus* and *Pachybelemnopsis* is often difficult because of some morphologic similarities. This is particularly true for some species of *Holcobelus* (namely *H. harleyi*) that have partially depressed transverse sections; vice-versa some *Pachybelemnopsis* show a circular section and a long ventral canal that may even reach the apex (*Pachybelemnopsis persulcata* Stolley). However, true *Pachybelemnopis* is characterised by a broader ventral alveolar canal that extends towards the apical region. The canal is combined with a well marked splitting surface (see also remarks under 5.1.3.). Furthermore, cameral deposits within the phragmocone are unknown in *Pachybelemnopsis*. In *Holcobelus* the ventral groove is intermediate (Riegraf 1980a) and the splitting surface is only rudimentary developed, fading out indistinctively towards the apical end of the rostrum. Vestigial cameral deposits have been observed in *Holcobelus* (Jeletzky 1966).

Holcobelus blainvillii (Voltz, 1830)
Figs. 3B, 3F; Pl. 1, Figs. 1–9

non	1827	*Belemnites unisulcatus*. – de Blainville, p. 81, pl. 5, fig. 2.1 [= *Acrocoelites* sp.]
*	1830	*Belemnites blainvillii*. – Voltz, p. 37, pl. 1, fig. 9.
pars?	1836	*Belemnites blainvilli*. – Roemer, p. 176.
	1855	*Belemnites blainvillei* Voltz. – Terquem, p. 25.
non	1856	*Belemnites blainvillei*. – Oppel, p. 484. [= *Holcobelus munieri* (Eudes-Deslongchamps, 1878)]
non	1857	*Belemnites blainvillei*. – Ooster, p. 13, pl. 2, figs. 7–8. [= *Holcobelus tschegemensis* (Krimholz, 1931)]
v	1857	*Belemnites infracanaliculatus*. – Quenstedt, pp. 411, 484, pl. 65, fig. 1.
v	1861	*Belemnites infracanaliculatus*. – Quenstedt, p. 565.
pars?	1867	*Belemnites infracanaliculatus*. – Waagen, p. 588.
pars	1869	*Belemnites blainvillei*. – Phillips, p. 102, pl. 25, fig. 60v', v'''. [non fig. 60v'' = *Holcobelus munieri* (Eudes-Deslongchamps, 1878)]
	1878	*Belemnites blainvillei* (Voltz). – Eudes-Deslongchamps, p. 55, pl. V, figs. 7–11, pl. VI, figs. 2–4.
	1878	*Belemnopsis unicanaliculata* Hartmann. – Bayle, pl. XXX, fig. 5.
	1880	*Belemnites blainvillei*. – Choffat, p. 40.
	1883	*Belemnites (Belemnopsis) blainvillei* Voltz. – Mayer-Eymar, p. 642.
	1883	*Belemnites (Belemnopsis) infracanaliculatus* Quenstedt. – Mayer-Eymar, p. 642.
	1891	*Belemnites blainvillei* Voltz. – Mallada, p. 114.

1912 *Belemnites (Belemnopsis) blainvillei* Voltz. – Roman & Gennevaux, p. 64.
1915 *Acrocoelites blainvillei* (Voltz). – Lissajous, p. 133.
pars? 1920 *Cylindroteuthis blainvillei*. – Bülow-Trummer, p. 198.
non 1921 *Belemnites blainvillei*. – Hauff, p. 27, pl. 8–12. [= *Acrocoelites* ?]
pars 1922 *Belemnites blainvillei*. – Naef, p. 246, fig. 89c. [non fig. 89b = *Holcobelus munieri* (Eudes-Deslongchamps, 1878)]
1925 *Acrocoelites infracanaliculatus*. – Lissajous, p. 99.
1925 *Acrocoelites blainvillei*. – Lissajous, p. 18, fig. 8.
v 1927 *Belemnites infracanaliculatus*. – Stolley, p. 124.
1927 *Holcobelus blainvillei* Voltz. – Stolley, p. 114.
1931 *Cylindroteuthis blainvillei* Voltz. – Krimholz, pl. 2, figs. 33–35, 39.
? 1936 *Belemnopsis blainvillei* Voltz. – Termier, p. 1352.
1939 *Acrocoelites blainvillei* (Voltz). – Roché, p. 147.
pars 1947 *Holcobelus blainvillei*. – Krimholz, p. 206, pl. 43, fig. 5. [non fig. 4 = *H. munieri*]
v 1949 *Belemnites infracanaliculatus*. – Schwegler, p. 304.
pars 1958 *Holcobelus blainvillei*. – Krimholz, pl. 67, fig. 4. [non pl. 47, fig. 4 = *H. munieri*]
v 1961 *Belemnites infracanaliculatus*. – Schwegler, p. 61.
? 1966 *Holcobelus blainvillei*. – Nutsubidze, p. 167, pl. XXXIX, figs. 7–8.
v 1971 *Belemnites infracanaliculatus*. – Schwegler, p. 124, fig. 126.
1972 *Holcobelus blainvillei* (Voltz). – Gavrilishin & Kruglov, pl. 3, fig. 3.
pars ? 1975 *Holcobelus blainvillei* (Voltz). – Preda, p. 6, pl. 2, fig. 10. [non pl. 2, figs. 3–4 = *H. tschegemensis* (Krimholz)]
v 1980a *Holcobelus blainvillii* (Voltz). – Riegraf, p. 168, text-fig. 152, pl. 1, figs. 1–5 (cum syn.).
1990 *Holcobelus blainvillei* (Voltz). – Stoyanova-Vergilova, pl. 1, fig. 2.
non 1992 *Holcobelus blainvillei* (Voltz). – Krawczyk et al., p. 1, pl. 1, fig. 1. [= *H. munieri* (Eudes-Deslongchamps)]
1993 *Holcobelus blainvillei* (Voltz). – Stoyanova-Vergilova, pl. XXXVII, figs. 1–2.
1995 *Holcobelus blainvillii* (Voltz). – Riegraf, p. 73.
1995 *Holcobelus infracanaliculatus* (Quenstedt). – Riegraf, p. 73.
non 1995 ?*Holcobelus unisulcatus* (De Blainville). – Riegraf p. 73. [= *Acrocoelites* sp.]
1998 *Holcobelus blainvillii* (Voltz). – Schlegelmilch, p. 76, pl. 16, figs. 2–3.
1998 *Holcobelus blainvillii* (Voltz). – Riegraf et al., pp. 66, 97, 238, 270.
1999 *Holcobelus blainvillei* (Voltz). – Riegraf, text-fig. 36.
? 2003 *Holcobelus blainvillei*. – Chen, p. 429.
2007 *Holcobelus blainvillii* (Voltz). – Weis & Mariotti, p. 167, pl. 7, figs. 4–6.
v 2010 *Holcobelus blainvilli* (Voltz). – Mariotti et al., fig. 4a–b.

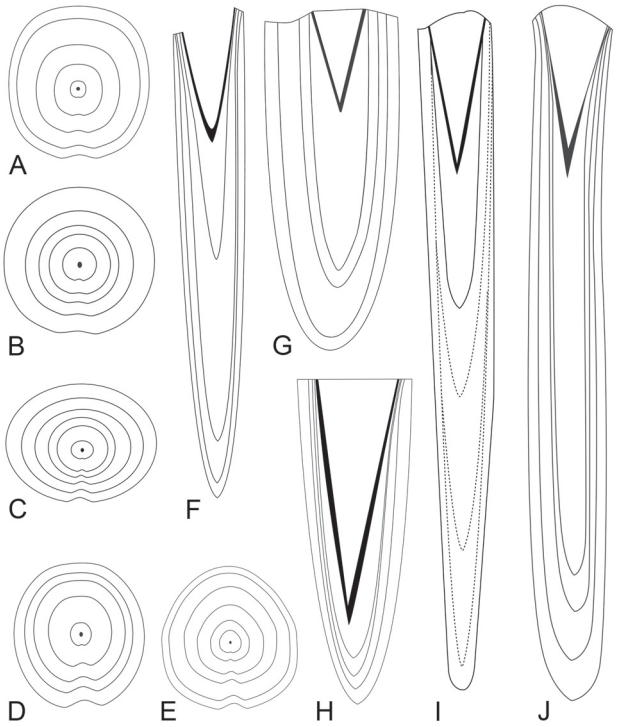

Fig. 3. Sketches of selected ontogenetic stages of holcobelids. The shape of the earliest juvenile rostrum is marked in black. In longitudinal section, the ventral side is orientated to the right; all transverse sections are at the protoconch level. – **A**. *Calabribelus pallinii* n. gen, n. sp., transversal section; Lower Bajocian of Caloveto, southern Italy (MUSR NS20/1180); ×1.5. **B**. *Holcobelus blainvillii* (Voltz), transvsersal section; from the Upper Aalenian, Concavum Zone of Blumberg-Achdorf, SW Germany (MNHNL DOT182 b); ×1.5. **C**. *Holcobelus harleyi* (Mayer), transversal section; from the Aalenian/Bajocian boundary (?) of Département Calvados, NW France (UCBL EM18078); ×1.5. **D**. *Holcobelus munieri* (Eudes-Deslongchamps), transversal section; from the Aalenian/Bajocian boundary of Fontaine-Etoupefour, NW France (UCBL EM18101); ×1.5. **E**. *Holcobelus brevicanalis* (Eudes-Deslongchamps), transversal section; from the Aalenian/Bajocian boundary of Fontaine-Etoupefour, NW France (UCBL EM18039); ×1.5. **F**. *Holcobelus blainvillii* (Voltz), longitudinal section; from the Upper Aalenian, Concavum Zone of Blumberg-Achdorf, SW Germany (MNHNL DOT182 a); ×0.75. **G**. *Holcobelus elmii* n. sp., longitudinal section; from the Lower Bajocian of Caloveto, southern Italy (MUSR NS20/1017); ×0.75. **H**. *Holcobelus brevicanalis* (Eudes-Deslongchamps), longitudinal section; from the Aalenian/Bajocian boundary of Fontaine-Etoupefour, NW France (UCBL EM18039); ×0.75. **I**. *Holcobelus munieri* (Eudes-Deslongchamps), longitudinal section, the epirostral growth stages are marked by a dashed outline; from the Aalenian/Bajocian boundary of Croisilles, NW France (UCBL FSL391828); ×0.75. **J**. *Calabribelus pallinii* n. gen, n. sp., longitudinal section; from the Lower Bajocian of Caloveto, southern Italy (MUSR NS20/772); ×0.75.

Type material: The collection of Voltz in Strasbourg has been destroyed by fire in the 1960's (personal communication Jean-Claude Gall in 1998), however, the species is morphologically well defined by the original figure of Voltz (1830, pl. 1, fig. 9). The designation of a neotype is therefore unnecessary. Voltz's specimen is from the "calcaires jurassiques des environs de Caen" (Aalenian–Bajocian of Normandy).

Additional material: 28 specimens from: Lower Bajocian, "Sowerbyschichten" of Betznau and Grossmatt, Switzerland (NMBa J11920, board 44; regional collection); Upper Aalenian of Saint-Quentin-Fallavier, Isère, France (MNHNL BEL001; coll. Rulleau); Aalenian of Louvigny near Caen, Normandy (MNHNL BEL024; coll. Chesnier); Aalenian Murchisonae and Concavum zones of Rumelange, Luxembourg (MNHNL HU210, HU225, HU227, HU286); Bajocian Discites Zone of the Plettenberg hill near Balingen, SW Germany (MNHNL DOT175; coll. Riegraf); Aalenian Concavum Zone of Blumberg-Achdorf, Wutach River, SW Germany (MNHNL DOT182; coll. Riegraf); Aalenian/Bajocian boundary of Torcieu, Ain, SE France (UCBL FSL391–822/824; coll. Juventin); Aalenian/Bajocian boundary of Fontaine-Etoupefour, Normandy (UCBL EM18035–18036).

Stratigraphic range and geographic distribution: Aalenian–Lower Bajocian (Opalinum–Laeviuscula zones) of France (Languedoc, Normandy, Bourgogne), Luxembourg, SW Germany, N Switzerland, Caucasus (Daghestan), Bulgaria (Teteven area), Portugal (Cabo Mondego), United Kingdom (Dorset), Spain.

Diagnosis. – Small sized, slender, cylindriconical *Holcobelus*. Outline symmetrical, cylindriconical. Alveolar outline slightly constricted. Profile symmetrical, conical, apex acute. Transverse sections subcircular to depressed in the rostrum solidum, subcircular to compressed in the alveolar region. Narrow intermediate ventral groove well developed, moderately long, not reaching the alveolar region.

Description. – Medium sized, relatively slender and elongate cylindriconical rostrum. The outline is symmetrical and cylindriconical with a slight constriction in the alveolar area. The profile is symmetrical to slightly asymmetrical, and strictly conical. The apical region is elongated and acute. Transverse sections are characteristic: they vary from compressed at the alveolar end to subcircular in the medium part and depressed in the posterior part of the rostrum. Stratigraphically younger specimens seem to be more compressed. The rostrum bears a narrow intermediate ventral groove, which covers nearly the whole rostrum solidum. It extends from the apical region – without reaching the tip of the apex – to the alveolar region. The groove usually does not go beyond the protoconch, although it may fade out as a slight depression on the alveolar region for a few millimetres. Usually the apical line is central. The phragmocone penetrates approximately one quarter of the rostrum. The alveolar angle varies between 20° and 22°.

Ontogeny. – The earliest juvenile stage is short and conical. Subsequent stages resemble adult individuals, being slightly slender and with a less incised and shorter ventral groove. Juvenile forms have been figured by Weis & Mariotti (2007, pl. 7, figs. 5–6).

Differential diagnosis. – *H. blainvillii* resembles both juvenile *H. munieri* and *H. harleyi*. It can however be distinguished from the former by its shorter ventral groove, and the depressed transverse section in the apical region. *H. harleyi* distinguishes itself for an overall depressed transverse section, whereas *H. blainvillii* is depressed only in the apical part. Moreover, *H. harleyi* is more robust and conical in shape, with a longer intermediate ventral groove, covering the alveolar region.

Remarks. – In the past, the name *H. blainvillii* has been overused. Some authors, considering only the character "long ventral groove", ascribed their specimens to *H. blainvillii*, although some specimens represented juvenile or subadult forms of *H. munieri* (see synonymy list). The same occurred for citations without figures. The species has been described in detail and figured by Riegraf (1980a), based on material from SW Germany. It has been considered as the stem-form for all holcobelids by the same author, and our recent investigations tend to confirm this position, as evidenced in the Discussion.

Eudes-Deslongchamps (1878) figured individuals with a very short ventral groove. A similar specimen has been found in the Aalenian of Rumelange, Luxembourg (Pl. 1, Fig. 9a–b). These morphologically intermediate forms between *Acrocoelites* with reduced dorsolateral grooves and *H. blainvillii*, are considered herein as *H.* cf. *blainvillii*.

Measurements (mm)

Specimen	L	X	Dv	Dl	Dv_{max}	Dl_{max}	Ica	Icm
MNHNL BEL001a	62	–	9.5	9.4	10.7	10.3	1.01	1.04
MNHNL BEL001b	47	47	9.7	9.3	–	–	1.04	–
UCBL FSL391822	72	–	8.5	8.6	–	–	0.99	–
UCBL FSL391824	59	–	9.0	8.5	10.5	9.0	1.06	1.17
MNHNL DOT175a	68	–	7.9	8.1	8.9	8.7	0.98	1.02
MNHNL DOT175b	61	–	7.4	7.4	8.5	8.1	1.00	1.05
MNHNL DOT182a	57	–	6.8	7.5	7.2	8.0	0.91	0.90
MNHNL DOT182b	50	–	7.6	7.8	7.7	7.8	0.97	0.99
UCBL EM18035	57	42	7.6	7.7	7.9	7.9	0.99	1.00
UCBL EM18036	52	30	7.2	7.3	7.6	7.6	0.99	1.00

Holcobelus brevicanalis (Eudes-Deslongchamps, 1878)
Figs. 1H, 3E, 3H; Pl. 1, Figs. 10–17

1869 *Belemnites canaliculatus*. – Phillips, p. 103, pl. XXV, fig. 61.
* 1878 *Belemnites brevicanalis*. – Eudes-Deslongchamps, p. 66, pl. VI, figs. 14–23.
1883 *Belemnites (Belemnopsis) heberti.* – Mayer-Eymar, p. 642.
1883 *Belemnites (Belemnopsis) brevicanalis* Deslongchamps. – Mayer-Eymar, p. 642.
1915 *Belemnopsis brevicanalis* (Deslongchamps). – Lissajous, p. 146.
1925 *Belemnopsis brevicanalis* (Deslongchamps). – Lissajous, p. 61.
1927 *Holcobelus brevicanalis* (Deslongchamps). – Stolley, p. 118.
1939 *Belemnopsis brevicanalis* (Eudes-Deslongchamps). – Roché, p. 153.
? 1985 *Belemnopsis* aff. *nalisbrevica* [sic] (Deslongchamps). – Stoyanova-Vergilova, p. 41, pl. II, figs. 3–4.
? 1990 *Belemnopsis* aff. *brevicanalis* (Deslongchamps). – Stoyanova-Vergilova, pl. 1, fig. 5.
? 1993 *Belemnopsis* aff. *brevicanalis* (Deslongchamps). – Stoyanova-Vergilova, pl. XXXIX, figs. 4–5.
1995 *Holcobelus brevicanalis* (Eudes-Deslongchamps). – Riegraf, p. 73.
1995 *Holcobelus heberti* (Mayer). – Riegraf, p. 73.
1997 *Belemnopsis brevicanalis* (Deslongchamps). – Combémorel, p. 159, pl. 27, fig. 19.
1998 *Holcobelus heberti* (Mayer). – Riegraf et al., p. 239.
v 2010 *Holcobelus brevicanalis* (Eudes-Deslongchamps). – Mariotti et al., fig. 4c–d.

Type material: The type material of Eudes-Deslongchamps in Caen has been destroyed during World War II (Combémorel et al. 1994b). According to Article 75.2 of the 4th edition of the ICZN, the designation of a neotype is not retained necessary herein, as the species is well defined by the original description and figures of Eudes-Deslongchamps (1878).

Additional material: 18 specimens originating from: Upper Aalenian of Feuguerolles-sur-Orne, Normandy (MNHNL BEL023; coll. Chesnier); Lower Bajocian of Baugé-les-Fours, Maine-et-Loire, France (UBD, coll. Badillet); Lower Bajocian of Commune de Corpe, Vendée, France (UCBL FSL391830); Lower Bajocian of Sully, Normandy, France (UCBL FSL391831; coll. De Riaz); Aalenian/Bajocian boundary of Caloveto, Calabria, Italy (MUSR NS20/817).

Stratigraphic range and geographic distribution: Middle and Upper Aalenian (Murchisonae–Concavum zones) and Lower Bajocian of France (Normandie, Aquitaine, Mâconnais), United Kingdom (Dorset), Italy (Calabria) and Bulgaria (Teteven area).

Diagnosis. – Small sized, robust, conical *Holcobelus*. Outline symmetrical and conical. Profile asymmetrical, conical, venter generally inflated. Apex acute. Transverse section compressed, elliptical to pyriform. Broad, intermediate ventral groove covering nearly the complete rostrum. Short epirostrum sometimes present.

Description. – Small sized, robust and strongly conical rostrum. The outline is symmetrical and conical to cylindriconical. The profile is weakly asymmetrical and conical, usually with an inflated venter. The apex is very acute. Transverse sections are compressed and elliptical to pyriform, more subquadrate in the alveolar region, due to flattened flanks. The intermediate ventral groove extends from the apical region (2–3 mm from the tip of the apex) until the alvolar border where it broadens and flattens out. The most remarkable feature is certainly the extremely deep alveolus: it can occupy more than 9/10 of the whole rostrum. The apical line is markedly eccentrical, towards the venter. The alveolar angle is 23°. In some specimens, a very short epirostrum can be observed. Vestigial cameral deposits have been observed.

Ontogeny. – The earliest juvenile stage is short and conical. The subsequent stages are characterised by a regularly asymmetric growth. At the adult stage, a short epirostrum is developed.

Differential Diagnosis. – By its short and conical rostrum, broad groove and its deep alveolus, *H. brevicanalis* occupies a peculiar position amongst holcobelids. These characters distinguish it easily from other species. Less robust and conical variants may resemble juvenile *H. tetramerus* that however can be distinguished by the cylindrical profile and the shorter apical region. *H. brevicanalis* greatly resembles another common species at the Aalenian/Bajocian boundary, *Brevibelus gingensis* (Oppel), but the latter, however, lacks any grooves.

Remarks. – Mayer-Eymar (1883: 642) indicated *Belemnites brevicanalis* Deslongchamps, 1878 as synonym of his *Belemnites heberti*. As *B. brevicanalis* Eudes-Deslongchamps is a valid species, *Belemnites heberti* Mayer-Eymar is considered herein a junior objective synonym of *H. brevicanalis*.

Some individuals show an eroded apex where an epirostrum was present (Pl. 1, Fig. 13a–b). Furthermore, a single specimen with a preserved epirostrum shows a short and narrow epirostrum (Pl. 1, Fig. 11a–c).

Measurements (mm)

Specimen	L	X	Dv	Dl	Dv_{max}	Dl_{max}	Ica	Icm
UCBL FSL391831	37	–	6.6	6.4	10.1	9.2	1.03	1.10
UCBL FSL391830	34	–	7.3	6.7	9.9	9.5	1.09	1.04
MUSR NS20.817	44	28	12.3	11.9	13.6	12.4	1.03	1.10
UCBL EM18037 (NT)	52	(6)	(8.5)	(7.5)	17.6	15.4	(1.13)	1.14
UCBL EM18038+040	28	1.8	–	–	9.8	8.7	–	1.13

Holcobelus elmii n. sp.
Fig. 3G; Pl. 1, Figs. 18–20

1997 Belemnopsidé n. gen., n. sp. – Sadki, p. 55.

Type material: Holotype, herein designated (MNHNL BEL006). One paratype, herein designated (UCBL FSL391834), from the Bajocian of Hassi Bou Lakhal (Algeria).

Derivatio nominis: Dedicated to the French palaeontologist Serge Elmi (1935–2007), who collected numerous fossils in Algeria, included the paratype of the species.

Locus typicus: Lac du Castillon, north of the town of Castellane (Alpes de Haute-Provençe, France), along the border of the road between the barrage of Castillon and the first tunnel direction Saint-Julien du Verdon. The section, protected by a net, is described in Assenat (1972) and Mariotti et al. (2012).

Stratum typicum: "Formation des Calcaires à *Zoophycos*", Cremon unit. The rostrum originates from the base of the unit, directly upon the hardground reported in Assenat (1972). According to Kerckhove (1976), the base of the Cremon unit is ascribed to the Lower Bajocian. Mariotti et al. (2012) recorded a specimen of *Kumatostephanus perjucundus* (Buckman), indicating the Propinquans Zone.

Additional material: Three specimens from the Lower Bajocian of the Lac du Castillon near Castellane, Haute-Provençe, France (MNHNL BEL049) and the Aalenian/Bajocian boundary of Caloveto, Italy (MUSR NS20/1500, NS20/1017).

Stratigraphic range and geographic distribution: Lower Bajocian (Propinquans Zone) of SE France (Alpes de Haute-Provençe), southern Italy (Calabria) and northern Africa (Algeria, Morocco).

Diagnosis. – Small to medium sized, cylindriconical *Holcobelus*. Outline symmetrical, cylindrical or cylindriconical. Profile asymmetrical, cylindriconical. Apex short and moderately obtuse. Transverse sections strongly compressed and sub-trapezoidal. Well developed narrow ventral groove extending from the apical to the alveolar region.

Description. – Small to medium sized, robust and cylindriconical rostrum. The outline is symmetrical and cylindrical or cylindriconical. The profile is asymmetrical and cylindriconical, the "beak-like" and short apical region being slightly orientated towards the dorsal side of the rostrum. In juveniles, the apex is more centrally placed. The tip of the apex is moderately acute to obtuse. The transverse section is highly compressed (compression ratio at protoconch in the holotype: 1.27) and has a distinctive subtrapezoidal section, with the venter larger than the dorsum. The flanks are flattened. A well developed narrow ventral groove is present and extends from the apical to the alveolar region. The apical line is excentrical, bending towards the venter. The phragmocone penetrates approximately one half to one third of the rostrum. The alveolar angle is 21°.

Ontogeny. – The ontogenetic growth of *H. elmii* is allometric. Juvenile rostra are cylindrical and stout, with a central apical line. At the adult stage, the apical line is progressively displaced towards the venter, due to an increased growth on the dorsal part of the apical region. This discontinuity in growth finally results into the "beak-like" apex.

Differential Diagnosis. – *H. elmii* can be distinguished from other holcobelids by its large, robust, cylindriconical rostrum with a short, "beak-like" apex and a strongly compressed, subtrapezoidal section. Individuals of *H. tetramerus* may resemble subadult *H. elmii*, but are less robust, less compressed and have a subquadrate section. *H. trauthi* has a more elongate and symmetrical apex and is less compressed, with an elliptical section.

Remarks. – This species may correspond to the unfigured specimens recorded by Sadki (1997, and personal communication 2011) as "Belemnopsidé n. gen., n. sp." from the Propinquans Zone of the Rich area (Higher Atlas, Morocco). Our material consists of five incomplete rostra, lacking most of the alveolar region, except the first chambers of the phragmocone. Nonetheless, the distinctive morphological characters as defined herein are deemed to be sufficent for establishing a new species.

Measurements (mm)

Specimen	L	X	Dv	Dl	Ica
UCBL FSL391834 (fragm.)	45	37	14.9	12.7	1.17
MNHNL BEL006 (fragm.)	47	42	15.3	12.0	1.27
MNHNL BEL049	63	37	15.3	–	–

Holcobelus harleyi (Mayer, 1866)
Fig. 3C; Pl. 2, Figs. 1–7

non 1820 *Belemnites canaliculatus*. – Schlotheim, p. 49.
1842 *Belemnites canaliculatus*. – d'Orbigny, p. 109, pl. XIII, fig. 1.
1850 *Belemnites canaliculatus*. – d'Orbigny, p. 244.
1853 *Belemnites canaliculatus*. – Harlé, p. 14.
1863 *Belemnites canaliculatus*. – Mayer, p. 168.
* 1866 *Belemnites harleyi*. – Mayer, p. 362.
1870 *Belemnites blainvillii*. – Phillips, p. 102, pl. XXV, fig. 60'''.
1878 *Belemnites canaliculatus* Schlotheim. – Eudes-Deslongchamps, p. 58, pl. VII, figs. 21–26.
1883 *Belemnites (Belemnopsis) harleyi* Mayer. – Mayer-Eymar, p. 641.
1915 *Belemnopsis harleyi* Mayer. – Lissajous, p. 146.
1919 *Belemnites canaliculatus* Deslongchamps. – Stolley, p. 27.
1925 *Belemnites harleyi* Mayer. – Lissajous, p. 35.
1927 *Aulacoteuthis harleyi* Mayer. – Lissajous, p. 35, pl. IV, figs.1–3.
1927 *Belemnites canaliculatus* Deslongchamps. – Stolley, p. 118.
1952 *Belemnites hartleyi* Mayer-Eymar. – Roger, p. 715.
? 1956 *Belemnopsis* sp. – Delattre, p. 42.

1994b ?*Belemnopsis canaliculatus* (Schlotheim). – Combémorel et al., p. 16.
1995 ?*Holcobelus harleyi* (Mayer). – Riegraf, p. 73.
1998 *Holcobelus hartleyi* (Mayer in Roger). – Riegraf et al., p. 239.
v 2010 *Holcobelus harleyi* (Mayer). – Mariotti et al., fig. 4e–f.

Type material: Mayer (1866) did not designate a holotype, subsequently Lissajous (1927) named as "topotype" the specimen figured in his paper (pl. IV, fig. 1) coming from Tilly-sur-Seilles, Calvados (UCBL FSL27510). The term "topotype" is not ruled by the ICZN. Therefore, the designation of a neotype is requested. The following observations must be evidenced: a) the type material of Mayer (1866) has not yet been retraced; b) the "topotype" designated by Lissajous (1927) does not belong to the type series; c) Eudes-Deslongchamps (1878) described and illustrated specimens referred to "*Belemnites canaliculatus* Schlotheim" which subsequently were ascribed to *H. harleyi* by Lissajous (1927); d) after Mayer (1866), the stratigraphic distribution of *H. harleyi* was Late Pliensbachian–Early Toarcian, Eudes-Deslongchamps (1878: 59) corrected it into Aalenian ("Couches à *Ammonites murchisonae*"). In conclusion, since the type material of Mayer (1866) is lost, the most appropriate solution would be to designate the "topotype" of Lissajous (1927) as neotype.

Additional material: 18 specimens originating from: ?Aalenian of Nanteuil near Ruffec, Charente, France (UCBL EM18001); ?Aalenian/Bajocian boundary of Fontaine-Etoupefour and Fontenay le Pesnel, Calvados, France (UCBL EM18076–18090); ?Lower Bajocian of Baugé-les-Fours, Maine-et-Loire, France (UBD, coll. Badillet).

Stratigraphic range and geographic distribution: ?Pliensbachian/Toarcian boundary and/or Aalenian to Lower Bajocian of western France (Normandie; Charente; Sarthe; Maine-et-Loire) and United Kingdom (Dorset).

Diagnosis. – Small sized, conical *Holcobelus*. Outline symmetrical, conical to cylindriconical. Profile slightly asymmetrical, conical, apical region elongated and moderately acute. Transverse sections depressed all along the rostrum. Long intermediate ventral groove, with smooth edges, from the apical to the alveolar region.

Description. – Small sized, moderately robust and conical rostrum. The outline is symmetrical and conical to slightly cylindriconical. The profile is slightly asymmetrical, due to a weakly inflated venter and always conical. The apical region is tapering regularly to an elongate and moderately acute apex. The transverse sections are always depressed, the depression is stronger on the rostrum solidum (average depression index: 0.90) than on the rostrum cavum (average depression index: 0.94). A broad, intermediate ventral groove extends from the apical region (2–4 mm from the tip of the apex) to the alveolar border, where it flattens out to a broad depression. The apical line is central. The phragmocone penetrates approximately one third of the rostrum. The alveolar angle is 24°.

Ontogeny. – The growth of *H. harleyi* is almost regular throughout all stages, and thus comparable to that of *H. blainvillii*.

Differential Diagnosis. – At first sight, *H. harleyi* resembles *H. blainvillii*, with which it shares the small size and the general shape. However, *H. blainvillii* is less robust, less conical and has a shorter ventral groove. A further major difference is the depression of the rostrum which is stronger and constant in *H. harleyi*, while *H. blainvillii* has a slightly depressed rostrum solidum, but a compressed rostrum cavum. *H. harleyi* is easily distinguished from other holcobelids by its strong depression and smooth, broad groove. It is distinguished from depressed *Pachybelemnopsis* by its intermediate ventral groove, a feature that can not be assimilated with the alveolar canal of pachybelemnopseids.

Remarks. – The species has been formerly reported as "*Belemnites canaliculatus* Schlotheim" due to its depressed rostrum. Originals from the Ecole des Mines collection (UCBL) bear handscript determinations: "*Belemnites canaliculatus* = *Belemnites harleyi*, Mayer". The stratigraphic position of this species, as given by different authors, is ambiguous: Harlé (1853) and Lissajous (1927) report it from the late Pliensbachian and the early Toarcian, meanwhile according to Eudes-Deslongchamps (1878), it would be present exclusively in the "couches à *Ammonites murchisonae*" (Aalenian). The investigated material originates from old collections with little or invalid stratigraphic information. A validation of the stratigraphic occurrence of *H. harleyi* would need more material with reliable stratigraphic data.

Measurements (mm)

Specimen	L	X	Dv	Dl	Dv_{max}	Dl_{max}	Ica	Icm
UCBL EM18087	57	40	9.5	10.1	10.6	11.2	0.94	0.95
UCBL EM18076	67	45	9.2	9.9	9.7	9.9	0.93	0.98
UCBL EM18090	58	40	8.3	9.4	9.6	10.5	0.88	0.91
UCBL EM18081	52	36	6.1	6.5	6.6	6.9	0.94	0.96
UCBL EM18083	48	30	6.5	7.6	7.5	8.3	0.86	0.90
UCBL EM18077 (fragm.)	40	–	6.4	6.8	–	–	0.94	–
UCBL EM18079	59	43	5.8	7.1	–	–	0.82	–

Holcobelus munieri (Eudes-Deslongchamps, 1878)
Figs. 1A, 2A–B, 3D, 3I; Pl. 2, Figs. 8–16; Pl. 3, Figs. 1–12

1827 *Belemnites acutus*. – De Blainville, p. 69, pl. 2, fig. 2.
v 1842 *Belemnites blainvillii* Voltz. – d'Orbigny, pl. 12, figs. 9–16.
1850 *Belemnites unicanaliculatus* Hartmann. – d'Orbigny, p. 260.
1853 *Belemnites unicanaliculatus*. – Pictet, p. 614, pl. XLIX, fig. 12.
pars 1869 *Belemnites blainvillii*. – Phillips, pl. XXV, figs. 59, 60v''. [non fig. 60v', v''' = *Holcobelus blainvillii* (Voltz, 1830)]
* 1878 *Belemnites munieri.* – Eudes-Deslongchamps, p. 63, pl. V, figs. 3–6, 12–14; pl. VI, figs. 5–11.
1878 *Belemnites subblainvillei.* – Eudes-Deslongchamps, p. 60, pl. V, figs. 15, 17; pl. VII, figs. 5–9.
pars 1878 *Belemnopsis unicanaliculata* Hartmann. – Bayle, pl. XXX, fig. 2. [non fig. 5 = *Holcobelus blainvillii* (Voltz, 1830)]
? 1878 *Belemnopsis sulcata* Miller. – Bayle, pl. XXX, fig. 3. [= ? *Pachybelemnopsis* sp.]
non 1883 *Belemnites (Belemnopsis) munieri* Deslongchamps. – Mayer-Eymar, p. 642.
1883 *Belemnites (Belemnopsis) deshayesi.* – Mayer-Eymar, p. 642.
1883 *Belemnites (Belemnopsis) sub-Blainvillei* Deslongchamps. – Mayer-Eymar, p. 642.
1897 *Belemnites eduardi.* – v. Hochstetter, p. 119, pl. III, figs. 1–2.
non 1913 *Belemnites subblainvillei* Desl. – Soergel, p. 621, pl. 24, figs. 4–8. [figs. 4, 6–8 = *Pachybelemnopsis persulcata* (Stolley, 1929); fig. 5 = *Pachybelemnopsis* cf. *parva* (Stolley, 1929); all from the Callovian]
1915 *Acrocoelites munieri* (Deslongchamps). – Lissajous, p. 154.
1915 *Belemnites sub. Blainvillei* Deslongchamps. – Lissajous, p. 146.
1920 *Belemnopsis eduardi*. – Bülow-Trummer, p. 129.
1920 *Belemnites munieri* Deslongchamps. – Bülow-Trummer, pp. 200, 201.
1920 *Belemnites subblainvillei* Deslongchamps. – Bülow-Trummer, pp. 200, 201.
1922 *Belemnopsis unicanaliculata* Hartmann. – Naef, fig. 89a.
pars 1922 *Belemnites blainvillei*. – Naef, fig. 89b. [non fig. 89c = *Holcobelus blainvillii* (Voltz, 1830)]
1925 *Acrocoelites munieri* Deslongchamps. – Lissajous, p. 55.
1925 *Acrocoelites deshayesi* Mayer. – Lissajous, p. 55.
1927 *Holcobelus munieri*. – Stolley, p. 114 ff., pl. XXIV, figs. 1–4.
1927 *Holcobelus subblainvillei*. – Stolley, p. 114 ff., pl. XXIV, fig 5.
1927 *Holcobelus eduardi* v. Hoch. – Stolley, p. 114, pl. XXIV, fig. 6.
1939 *Acrocoelites munieri* (Eudes-Deslongchamps). – Roché, p. 147.
1952 *Holcobelus munieri* Deslongchamps. – Roger, p. 717.
1966 *Holcobelus munieri* Deslongchamps. – Jeletzky, p. 96, pl. 25, fig. 1.
1966 *Holcobelus munieri*. – Nutsubidze, p. 166, pl. XXXIX, figs. 5–6.
1975 *Holcobelus munieri* (Deslongchamps). – Preda, p. 6, pl. 1, figs. 9–12; pl. 2 figs. 5–7, 9.
1977 *Holcobelus deshayesi* (Mayer). – Nikitin, p. 91, pl. 1, figs. 1–3.
1977 *Holcobelus munieri* (Deslongchamps). – Nikitin, p. 89, pl. 1, figs. 4, 7.
1980 *Holcobelus munieri* (Deslongchamps). – Riegraf, p. 168.
1990 *Holcobelus munieri* (Deslongchamps). – Stoyanova-Vergilova, pl. 1, fig. 1.
1992 *Holcobelus blainvillei* (Voltz). – Krawczyk et al., p. 1, pl. 1, fig. 1.
1993 *Holcobelus munieri* (Deslongchamps). – Stoyanova-Vergilova, pl. 35, figs. 1–4; pl. 36, figs. 1–5.
1993 *Holcobelus deshayesi* (Mayer). – Stoyanova-Vergilova, pl. XXXVIII, figs. 1–6.
1994b *Holcobelus munieri* (Eudes-Deslongchamps). – Combémorel et al., p. 15, pl. 2, figs. 7–8.
1994b *Holcobelus subblainvillei* (Eudes-Deslongchamps). – Combémorel et al., p. 16.
1995 *Holcobelus eduardi* (v. Hochstetter). – Riegraf, p. 73.
1995 *Holcobelus munieri* (Eudes-Deslongchamps). – Riegraf, p. 73.
1995 *Holcobelus deshayesi* (Mayer-Eymar). – Riegraf, p. 73.
1995 *Holcobelus subblainvillei* (Eudes-Deslongchamps). – Riegraf, p. 73.
1997 *Holcobelus munieri* (Deslongchamps). – Combémorel, p. 159.
1998 *Holcobelus munieri* (Eudes-Deslongchamps). – Riegraf et al., pp. 150, 238.
1998 *Holcobelus subblainvillei* (Eudes-Deslongchamps). – Riegraf et al., p. 129.
1998 *Holcobelus deshaiesi* (Mayer in Krimholz). – Riegraf et al., p. 238.
1999 *Holcobelus munieri* (Eudes-Deslongchamps). – Riegraf, fig. 37.
? 1999 *Holcobelus subblainvillei* (Eudes-Deslongchamps). – Riegraf, fig. 38. [= ? *Pachybelemnopsis* sp.]
v 2007 *Holcobelus munieri* (Eudes-Deslongchamps). – Mariotti et al., p. 9, pl.1, figs. 2, 5.
v 2007 *Holcobelus subblainvillei* (Eudes-Deslongchamps). – Mariotti et al., p. 9. pl. 1, fig. 7.
v 2010 *Holcobelus munieri* (Eudes-Deslongchamps). – Mariotti et al., fig. 4i–j.
v 2012 *Holcobelus munieri* (Eudes-Deslongchamps). – Mariotti et al., p. 104, figs. 4 (3–7), 5 (5–6).

Type material: The original collection of Eudes-Deslongchamps in Caen has been destroyed during World War II (Combémorel et al. 1994b: 16); for this reason, Combémorel et al. (1994b) have chosen a neotype from the collection Puzos

(studied by D'ORBIGNY): n° EM75010 from the locality Les Moutiers (stored nowadays at UCBL and re-illustrated herein: Pl. 2, Fig. 10a–b).

Additional material: 53 specimens originating from the Lower Bajocian, "Oolithe inférieure" of St. Vigors and Bayeux, Normandy, France (SMNS 66260; 66261/1–2); Lower Bajocian of Département Calvados, France (SMNS 66262); Aalenian/Bajocian boundary of Truc de Balduc near Mende, Lozère, France (MNHNL BEL022; coll. RIEGRAF); Lower Bajocian of Baugé-les-Fours, Main-et-Loire, France (UBD, coll. BADILLET); Aalenian/Bajocian boundary of Normandy (Caen, Les Moutiers, Fontaine-Etoupefour, Valognes, Croisilles and St. Vigors) (UCBL FSL391828; FSL391829, EM18010–18012, 18024–18028, 18034); Lower Bajocian of Croisilles, Normandy, France (UCBL FSL391828); Upper Aalenian of Lac de Castillon near Castellane, Alpes de Haute-Provençe, France (MNHNL BEL010); Lower Bajocian of Croisilles, Normandy, France (MNHN R07132); Bajocian of Hassi Lakhal, Algeria (UCBL FSL391827); Lower Bajocian, Humphriesianum Zone of Feuguerolles-sur-Orne, Normandy, France (MNHNL BEL030–031); Aalenian, Murchisonae Zone of "Côte folle" near Gap, Hautes-Alpes, France (UJFG n° UJF.ID9000; coll. HAUG); Aalenian/Bajocian boundary of Caloveto, Calabria, Italy (MUSR NS20/880, 843, 838, 768, 878, 831).

Stratigraphic range and geographic distribution: Middle Aalenian to Lower Bajocian (Murchisonae–Humphriesianum zones) of France (Mont d'Or, Cévennes, Haute-Provençe, Hautes-Alpes, Normandie, Aquitaine, Bourgogne), Italy (Calabria), Ukraine (Kanev region), Poland and Slovakia (Carpathians), Bulgaria, Romania (Rosia area), United Kingdom (Dorset), Algeria (Hassi Bou Lakhal).

Diagnosis. – Medium to large sized, conical *Holcobelus*. Outline symmetrical, cylindriconical to conical. Profile asymmetrical, conical. Transverse sections subquadrate to elliptical, compressed. Apex acute. Long narrow intermediate ventral groove extending from the apical to the alveolar region. Epirostrum commonly developed.

Description. – Medium to large sized, elongate and slender rostrum. The outline is symmetrical, cylindriconical in juveniles and conical to slightly subhastate in adults; in the alveolar region the rostrum is commonly constricted, producing a slightly subhastate outline. The profile is asymmetrical, with an inflated venter and a dorsally curved apex in juveniles (those specimens known as *Belemnites subblainvillei*) becoming more irregular in adults (specimens with epirostrum), and always conical. Transverse sections are compressed and elliptical to subquadrate. A long narrow intermediate and well incised ventral groove extends for nearly the total length of the rostrum. In most individuals, it fades out 2–3 mm before the tip of the apex. In the alveolar region, the groove fades out adapically, continued as a shallow depression on the last few millimeters. A rudimentary splitting surface is observable. The shape of the apical region changes throughout ontogeny (see below). Well developed lateral lines can be distinguished. The apical line is central. The phragmocone penetrates approximately one third to one quarter of the rostrum. An epirostrum, varying from one quarter to two thirds of the total length, is commonly developed.

Ontogeny. – The early juvenile stage is elongate conical. The ontogentic growth is regular, even if the dimensions of the rostrum at the adult stage present a considerable variability. In juvenile individuals ("*Belemnites subblainvillei* EUDES-DESLONGCHAMPS"), the apical region is relatively short, acute and slightly incurved towards the dorsum. At the adult stage, an epirostrum with long, irregular striae develops; it is particularly elongate, acute and its apex is commonly eroded or hollow. The penetration of the phragmocone varyies following the ontogenetic stages, approximately one third of the rostrum in juveniles and one quarter in adults. The alveolar angle varies from 21°–23°.

Differential diagnosis. – Despite their variable morphology, adult and subadult *H. munieri* are easily distinguished from other *Holcobelus*. *H. blainvillii* is similar in shape to juvenile *H. munieri*, but has a much shorter intermediate ventral groove, that does not cover the rostrum cavum. Slender and younger individuals of *H. trauthi* strongly resemble subadult *H. munieri*, but differ by the more elongate apical region and namely the stronger lateral compression. *H. tschegemensis* approaches very slender individuals of *H. munieri*, but is strictly cylindrical.

Remarks. – The highly variable morphology has led to some taxonomic confusion in the past. EUDES-DESLONGCHAMPS (1878) described *Belemnites munieri* and *Belemnites subblainvillei* as two distinct species; the latter represents an earlier ontogenetic stage of the former (COMBÉMOREL et al. 1994b) (Pl. 2, Figs. 8c, 11). MAYER-EYMAR (1883: 642) reports *B. subblainvillei* EUDES-DESLONGCHAMPS as an objective synonym of his *Belemnites deshayesi*. There is no reason that EUDES-DESLONGCHAMPS' species should be invalid, therefore *B. deshayesi* MAYER-EYMAR has to be considered a junior objective synonym of *B. subblainvillei* EUDES-DESLONGCHAMPS, which in turn is considered now a junior objective synonyme of *H. munieri*. On the other hand, some specimens from stratigraphically younger beds ("Oolithe ferrugineuse", Humphriesianum Zone, Normandy) developed a slender rostrum without epirostrum (Pl. 2, Fig. 15a–b). A similar, slender form without epirostrum has been described as *Belemnites eduardi* by V. HOCHSTETTER (1897) (Pl. 2, Fig. 9a–c), which is here considered as a subjective synonym of *H. munieri*. In addition to the two specimens published by V. HOCHSTETTER (1897), another specimen of the "*eduardi*"-type could be identified in the material from the Ecole des Mines collection (UCBL) (Pl. 3, Fig. 3). It is characterised by weak and short dorsolateral grooves evidenced only by lateral light. This peculiar character might be of great phylogenetic interest, documenting the relation between *Holcobelus* and *Acrocoelites*.

In *H. munieri*, the groove never reaches the alveolar border; as most rostra lack the thin anterior border, there

has been an erroneous interpretation concerning the extension of the ventral groove supposed to reach the alveolar border (Stolley 1927).

Measurements (mm)

Specimen	L	X	Dv	Dl	Dv_{max}	Dl_{max}	Ica	Icm
UCBL EM18006	89	(53)	9.3	9.1	10.9	10.5	1.02	1.04
UCBL EM18004	95	61	8.5	8.5	10.5	10.5	1.00	1.00
UCBL EM18005	92	52	10.3	9.3	11.3	10.9	1.11	1.04
UCBL EM18003	81	49	8.4	8.2	10.9	10.8	1.02	1.01
UCBL EM18009	95	53	9.2	8.6	10.8	10.5	1.07	1.03
UCBL EM18007	98	(61)	9.3	9.1	10.0	9.4	1.02	1.06
UCBL EM18008	84	55	10.3	9.1	11.5	10.5	1.13	1.09
UCBL EM18011	69	37	8.9	8.8	9.9	9.6	1.01	1.03
UCBL EM18012	65	34	9.3	8.9	10.4	9.8	1.04	1.06
UCBL EM18010	52	29	9.7	9.6	11.3	10.7	1.01	1.06
UCBL EM18033	58	(32)	9.7	8.6	12.1	11.5	1.13	1.05
UCBL EM18032	55	(28)	8.4	7.6	9.4	8.3	1.11	1.13
UCBL FSL391828	90	67	9.9	–	10.6	–	–	–
UCBL EM18027	62	41	8.7	–	9.2	–	–	–
UCBL EM18028	61	61	10.6	11.1	–	–	0.95	–
UCBL BEL031	55	48	8.3	7.5	–	–	1.11	–
UCBL EM18014	73	(49)	9.4	8.3	9.5	8.7	1.13	1.09
UCBL EM18016	68	42	8.8	7.9	9.2	8.4	1.11	1.10
UCBL EM18017	66	47	9.3	8.5	–	–	1.09	–
UCBL EM18020	50	30	6.8	6.4	8.5	7.9	1.06	1.08
UCBL EM18022	55	31	7.2	6.9	8.6	8.2	1.04	1.05
UCBL EM18023	56	32	8.4	7.9	9.9	9.2	1.06	1.08
UCBL EM18019	57	39	8.4	7.8	–	–	1.08	–

Holcobelus tetramerus (Eudes-Deslongchamps, 1878)
Pl. 4, Figs. 1–7

* 1878 *Belemnites tetramerus*. – Eudes-Deslongchamps, p. 67, pl. 7, figs. 10–20.
1883 *Belemnites (Belemnopsis) tetramerus*. – Mayer-Eymar, p. 641.
non 1894 *Belemnites* cf. *tetramerus* Deslongchamps. – Möricke, p. 9. [= *Megateuthis* sp., fide Doyle et al. 1996]
1927 *Holcobelus tetramerus* (Deslongchamps). – Stolley, p. 118.
? 1927 *Belemnopsis angusta* n. sp. – Stolley, p. 123, pl. XXIV, fig. 9.
1995 *Holcobelus tetramerus* (Eudes-Deslongchamps). – Riegraf, p. 73.
? 1995 ?*Holcobelus angusta* (Stolley). – Riegraf, p. 73.
v 2007 *Holcobelus tetramerus* (Eudes-Deslongchamps). – Mariotti et al., p. 10, pl. 1, figs. 4, 6, 8.
v 2010 *Holcobelus tetramerus* (Eudes-Deslongchamps). – Mariotti et al., fig. 4g–h.

Type material: The type material of Eudes-Deslongchamps in Caen was destroyed during World War II (Combémorel et al. 1994b). According to Article 75.2 of the 4th edition of the ICZN, the designation of a neotype is not necessary, as the species is well defined by the original description and figures of Eudes-Deslongchamps (1878, pl. VII, figs. 10–20).

Additional material: 15 specimens from the Aalenian/Bajocian boundary of Fontaine-Etoupefour and other unspecified localities in Normandy (UCBL EM18068–18073); Bajocian of Vieux-Pont, Calvados, France (UCBL EM18074–18075); Lower Bajocian(?) of Peault, Vendée, France (UCBL FSL391832–33); Aalenian ("Mâlière") of Feuguerolles-sur-Orne, Calvados, France (MNHNL BEL025–026).

Stratigraphic range and geographic distribution: Middle and Upper Aalenian (Murchisonae–Concavum zones) and possibly Lower Bajocian of France (Normandie, Vendée) and Italy (Calabria).

Diagnosis. – Small sized, cylindrical *Holcobelus*. Outline symmetrical, cylindrical. Profile slightly asymmetrical, cylindrical to weakly cylindriconical. Apex moderatly acute to obtuse. Transverse sections compressed, subquadrate. Long narrow intermediate ventral groove. Epirostrum short.

Description. – Small sized, robust, cylindrical rostrum. The outline is symmetrical and cylindrical; the apical region is particularly short. The profile is asymmetrical and cylindrical to weakly cylindriconical, with the venter slightly inflated. The apex is generally smooth and rounded, reminding the genus *Dactyloteuthis*, although some ontogenetic stages show a more acute apex. A short epirostrum is developed, mostly broken. In this case, the apex of the orthorostrum is blunt, covered with striae and devoid of grooves. Transverse sections are markedly compressed and characteristically subquadrate. Most individuals are more compressed in the juvenile stages. The long narrow intermediate and well incised ventral groove extends on nearly the total lenght of the rostrum from the

alveolar to the apical region, but does not reach the apex itself. The groove generally fades out 3–4 mm before the tip of the apex. Lateral lines are well developed. The apical line is slightly excentrical, towards the venter. The phragmocone penetrates at least one third to one half of the rostrum. The alveolar angle is 21°.

Ontogeny. – The earliest juvenile stage is conical, but more elongate than in other representatives of the genus. Outline and profile are slightly subhastate in subsequent juvenile stages (Pl. 4, Fig. 7a–b).

Differential diagnosis. – *H. tetramerus* can be easily distinguished from other holcobelids by its robust, cylindrical rostrum with a relatively short apical region, and a highly compressed, subquadrate transverse section. More cylindriconical variants approach *H. trauthi*. However, typical specimens of *H. trauthi* have a clearly subhastate shape, and an inflated, elongate apical region.

Remarks. – The single rostrum figured as *Belemnopsis angusta* n. sp. by Stolley (1927) possibly represents a juvenile specimen of *H. tetramerus* with a reduced ventral groove.

Measurements (mm)

Specimen	L	X	Dv	Dl	Ica
MNHNL BEL025 (fragm.)	27	25	9.1	8.3	1.10
UCBL EM18068	56	31	11.8	10.5	1.12
UCBL EM18069 (juvenile)	30	17	7.5	5.7	1.32
UCBL EM18072 (juvenile)	35	20	8.6	7.4	1.16
UCBL EM18073	43	18	9.6	8.4	1.14
UCBL EM18071 (fragm.)	27	–	9.2	8.4	1.10
UCBL EM18061 (juvenile)	31	16	6.4	5.4	1.19
UCBL EM18060	41	20	9.3	8.2	1.13
UCBL EM18062 (juvenile)	40	19	9.5	7.6	1.25
UCBL EM18059	52	24	9.2	8.4	1.10
UCBL EM18002	53	23	12.2	10.2	1.20
UCBL EM18057	55	25	12.1	10.6	1.14
UCBL EM18074 (cf. *tetramerus*)	62	32	11.8	10.0	1.18

Holcobelus trauthi (Stolley, 1927)
Pl. 4, Figs. 8–10

* v 1927 *Holcobelus trauthi*. – Stolley, p. 118, pl. XXIV, figs. 7–8.
? 1993 *Holcobelus* sp. – Stoyanova-Vergilova, pl. XXXVII, fig. 3.
v 1994a *Holcobelus trauthi* Stolley. – Combémorel et al., p. 47, pl. XXIV, fig. 4.
1995 *Holcobelus trauthi* Stolley. – Riegraf, p. 73.
v 2007 *Holcobelus trauthi* Stolley. – Mariotti et al., p. 8, pl. 1, figs. 3–4.
v 2010 *Holcobelus trauthi* Stolley. – Mariotti et al., fig. 4k–l.
v 2012 *Holcobelus trauthi* Stolley. – Mariotti et al., p. 104, fig. 4 (10–11).

Type Material: The type material of Stolley is composed of two rostra (NHMW 1868/0011/0016a–b), but he did not designate the holotype. The specimen figured by Stolley (1927, pl. XXIV, fig. 7) is designated herein as lectotype (NHMW 1868/0011/0016a). It originates from the "unterer Dogger … im Niveau körniger Kalke" (= "Oolithe ferrugineuse", Lower Bajocian, Propinquans or Humphriesianum Zone) of Bayeux, Calvados, France.

Additional material: 9 specimens originating from the Aalenian/Bajocian boundary of Caloveto, Calabria, Italy (MUSR, NS20/1181, /1179, /862, /1178, /1400, /1403); Lower Bajocian, Laeviuscula Zone, La Baume near Castellane, Alpes de Haute-Provençe, France (RGHP 010012–010014).

Stratigraphic range and geographic distribution: Lower Bajocian (Laeviuscula–?Humphriesianum zones) of France (Normandie, Haute-Provençe) and southern Italy (Calabria).

Diagnosis. – Small sized, cylindriconical to subhastate *Holcobelus*. Outline symmetrical, subhastate. Profile slightly asymmetrical, cylindriconical, apical region elongated. Apex moderately acute. Transverse sections clearly compressed. Intermediate narrow ventral groove from the apical to the alveolar region. Short epirostrum developed in the adult stage.

Description. – Small sized, more or less slender rostrum. The outline is symmetrical and subhastate, due to an inflated medium part of the rostrum. The profile is slightly asymmetrical and cylindriconical. The apical region is inflated and elongated. The apex is moderately acute. Weak apical striae can be observed, indicating the presence of a short epirostrum in the adult stage. A well developed narrow intermediate ventral groove extends from the apical region (starting 3–4 mm from the tip of the apex) to the alveolar border. On the last 2–3 mm, it fades out to a depression. Transverse sections are elliptical and markedly compressed. The apical line is slightly eccentrical, towards the venter. The phragmocone penetrates approximately one third of the rostrum. The alveolar angle is 21°.

Differential diagnosis. – H. *trauthi* is distinguished from *H. munieri* by its shorter, more robust and compressed rostrum. It shows close similarities with cylindriconical individuals of *H. tetramerus*, which however differs by a shorter apical region and a subquadrate transverse section.

Measurements (mm)

Specimen	L	X	Dv	Dl	Ica
NHMW 1868/0011/0016a (LT)	75	–	(12.0)	(10.0)	1.20
NHMW 1868/0011/0016b	76	–	(10.8)	(9.3)	1.16
UCBL EM18064 (cf. *trauthi*)	57	27	10.0	9.3	1.08
RGHP 010012	82	42	15.8	14.3	1.10

Remarks. – The section of La Baume in SE France (Mariotti et al. 2012) has yielded three short and robust specimens (Pl. 4, Fig. 8) whose morphologic characters match well the more slender specimens of Stolley (1927). The species appears to be rare.

Holcobelus tschegemensis (Krimholz, 1931)
Pl. 4, Fig. 11

v 1857 *Belemnites blainvillei* Voltz. – Ooster, pl. 2, figs. 7–8.
* 1931 *Belemnopsis tschegemensis* sp. n. – Krimholz, p. 27, pl. 1, figs. 26–32. [LT designated herein]
? 1966 *Holcobelus* cf. *tschegemensis*. – Nutsubidze, p. 167, pl. XXXIX, figs. 9–10.
1975 *Holcobelus blainvillei* (Voltz). – Preda, p. 6 (pars), pl. 2, figs. 3–4. [non pl. 2, fig. 10]
1990 *Holcobelus tschegemensis* (Krimholz). – Stoyanova-Vergilova, pl. 1, fig. 3.
1993 *Holcobelus tschegemensis* (Krimholz). – Stoyanova-Vergilova, pl. XXXVII, fig. 4.
1995 *Holcobelus tschegemensis* (Krimholz). – Riegraf, p. 73.
1998 *Holcobelus tchegemensis* [sic] (d'Orbigny in Stoyanova-Vergilova). – Riegraf et al., p. 239.
? 2007 *Holcobelus tschegemensis* (Krimholz). – Mariotti et al., p. 10, pl. 1, fig. 11.
v 2010 *Holcobelus tschegemensis* (Krimholz). – Mariotti et al., fig. 4m–n.

Type material: Krimholz (1931) reports 11 specimens and 69 fragments from the Aalenian of Chegem (northern Caucasus) and Gouniv (Daghestan) collected by V.P. Renngarten. Two of them are illustrated (Krimholz 1931, pl. 1, figs. 26–32), but no holotype is designated. For this reason, it is retained to designate herein the specimen figured in Krimholz (1931, pl. 1, figs. 29–32), originating from the Aalenian of Cheghem, as lectotype.

Additional material: 7 specimens originating from: the "Dogger" of Hohmad, Sulzgraben and Blattenheid, Stockhornkette, Switzerland (NMBe 5018816, 5018818, 5015826–27; coll. Ooster); the Aalenian/Bajocian boundary of Caloveto, Calabria, Italy (MUSR NS20.847/865/777).

Stratigraphic range and geographic distribution: Aalenian of Caucasus (Cheghem region and Daghestan), Bulgaria (Trojan area), central Switzerland (Stockhornkette, Préalpes Médianes) and Aalenian/Bajocian boundary of southern Italy (Calabria).

Original diagnosis. – "Long and thin, cylindrical rostrum with gradual taper throughout the whole length. Transverse section elliptical, becoming more circular towards the posterior end. The alveolus penetrates 1/5 of the rostrum. Narrow ventral groove extending throughout the rostrum, passing on to an alveolar slit" (Krimholz 1931; translated from Russian).

Description. – Medium sized, gracile and elongate, cylindrical rostrum. The outline is symmetrical and cylindrical, the profile symmetrical and cylindriconical. The apical region is elongate and tapers gradually. The apex is acute. A long narrow ventral groove extends from nearby the apex towards the alveolar border. The studied material did not allow to decide whether an alveolar slit is present or not. Transverse sections are elliptical, subcircular or slightly compressed. The phragmocone occupies approximately one fifth to one sixth of the total rostrum length.

Differential diagnosis. – *H. tschegemensis* is chiefly distinguishable from other holcobelids by its "tubular", slender and long rostrum. Slender individuals of *H. munieri* show some similarities, but are distinguished by a more robust rostrum with a shorter apical area.

Remarks. – The studied rostra are historical findings from the original collection of W.A. Ooster. It was not possible to re-study the type material of Krimholz (1931), so that the description presented herein is based largely on the material from Switzerland and Italy (Mariotti et al. 2007). The geographical distribution of *H. tschegemensis* compared with other holcobelids appears as peculiar: the species has been reported only from the Caucasus, Bulgaria, Italy and Switzerland and is absent in western Europe.

Genus *Calabribelus* n. gen.

Type species: *C. pallinii* n. sp.

Derivatio nominis: Derived from the southern Italian region of Calabria, from where the type material originates.

Other species included: *C.* aff. *pallinii* (= Belemnitida incertae sedis sp. 2, Mariotti et al. 2012).

Stratigraphic range and geographic distribution: Lower Bajocian (Discites and Propinquans zones) of southern Italy (Calabria) and SE France (Gap, Hautes-Alpes; Castellane, Alpes de Haute-Provençe).

Diagnosis. – Large sized, elongate, cylindrical to subhastate Holcobelidae. Transverse sections compressed to subcircular. Long narrow alveolar ventral groove beginning close to the apex and reaching the alveolar border. Apical region short, apex obtuse or moderately acute. The phragmocone penetrates one fourth to one fifth of the rostrum. Splitting surface rudimentary developed. Earliest juvenile rostrum conirostrid, elongate conical. Epirostrum developed in the adult stage. Alveolar angle between 23°–24°. Cameral deposits absent.

Remarks. – *Calabribelus* n. gen. closely resembles early representatives of the family Mesohibolithidae, especially *Pachybelemnopsis* with which it shares the elongate, subhastate rostrum. Morphologically, *Calabribelus* occupies an intermediate position between *Holcobelus* and *Pachybelemnopsis*. In *Holcobelus* the long intermediate ventral groove reaches the alveolar region without touching the border, in *Calabribelus* n. gen. it ends at the alveolar border, with a shallow depression. In *Pachybelemnopsis* it is reduced to a shorter, alveolar canal with a marked al-

veolar slit. *Calabribelus* displays a compressed transverse section on the complete length of the rostrum, a feature which distinguishes it from *Pachybelemnopsis*, characterised by a depressed section in the stem and apical region. Few individuals of *Calabribelus* (Pl. 4, Fig. 12a) show remnants of reduced dorsolateral grooves, indicating a possible phylogenetic relationship with *Acrocoelites* through *Holcobelus*. The stratigraphic range of *Calabribelus* comprises the Early Bajocian Propinquans Zone, as recent field work in SE France revealed (Mariotti et al. 2012). The Propinquans Zone coincides with the highest occurence of *Holcobelus* and the lowest occurence of *Pachybelemnopsis* in Europe (Weis & Mariotti 2007, Mariotti et al. 2010).

Calabribelus pallinii n. sp.
Figs. 1C, 2C, 3A, 3J; Pl. 4, Figs. 12–14; Pl. 5, Figs. 1–7

v pars 1994a Belemnitida incertae sedis. – Combémorel et al., p. 48, pl. 1, figs. 1, 6–10. [non fig. 11 = *H. brevicanalis* (Eudes-Deslongchamps)]
v pars 2007 Belemnitida incertae sedis. – Mariotti et al., p. 12, pl. 2, figs. 1–3. [non figs. 6, 10]
v pars 2010 Belemnitida incertae sedis. – Mariotti et al., p. 140.
v 2012 Belemnitida incertae sedis. – Mariotti et al., p. 105, fig. 5 (7–8).

Type material: The holotype hereby designated is specimen MUSR NS20/799. 6 paratypes are also designated (MUSR NS20.769/772/816/858/1175/1180).

Derivatio nominis: Dedicated to our friend Giovanni "Jack" Pallini (1949–2003), Italian palaeontologist, expert in Early Jurassic and Early Cretaceous ammonites.

Locus typicus: Caloveto, "Cozzo di Mastro Pasquale", natural outcrop along the road from Caloveto to Bocchigliero (Cosenza, Italy). The exposure is described in detail by Mariotti et al. (2007).

Stratum typicum: Red marls of the lower part of the "Sant'Onofrio Formation" (Lower Bajocian, Discites Zone).

Additional material: 9 apical fragments from the Lower Bajocian, Discites Zone of Caloveto, Calabria, Italy (N S20.810/811/813/814/917/920/1499/1501/1502); 4 complete specimens from the Lower Bajocian, Propinquans Zone, of Lac du Castillon near Castellane, Alpes de Haute-Provençe, France (MNHNL BEL003, 004, 007, 045).

Stratigraphic range and geographic distribution: Lower Bajocian, Discites Zone of southern Italy (Calabria) and Propinquans Zone of SE France (Castellane, Alpes de Haute-Provençe).

Diagnosis. – Medium to large sized, elongate *Calabribelus*. Outline symmetrical, subhastate. Profile symmetrical, subhastate to cylindrical, alveolar region short, obtuse to moderately mucronate. Transverse sections subcircular or compressed. Long narrow alveolar ventral groove extending from the apex and reaching the alveolar border. Splitting surface rudimentary developed. Epirostrum developed at the adult stage.

Description. – Medium to large sized, very elongate and subhastate rostrum. The outline is symmetrical, subhastate in adults and more cylindrical in juveniles. The profile is symmetrical and subhastate to cylindrical in adults, more cylindrical in juveniles. The apical region is very short, moderately acute with a mucro-like tip in some individuals or more obtuse in others. A more or less long epirostrum is visible in longitudinal sections of adult specimens. A long narrow alveolar ventral groove extends from the apical region (starting 3–5 mm from the tip of the apex) and reaches the alveolar border. A splitting surface is rudimentary developed. Transverse sections are elliptical, subcircular or slightly compressed. The apical line is central. The phragmocone penetrates one fifth to one sixth of the rostrum. The alveolar angle varies between 23°–24°.

Ontogeny. – The earliest juvenile stage is elongated and slender conical. Subsequent juvenile stages are elongate and cylindrical, with an acute apex. At the adult stage, the profile tends to a slightly subhastate shape, and a zone of looser growth at the apex indicates the formation of a short epirostrum; at the same stage, the apex tends towards an obtuse and mucronate shape.

Differential diagnosis. – *C. pallinii* is easily distinguishable from most holcobelids by its elongate and subhastate rostrum, with a short and obtuse apex. *H. tetramerus* is much shorter and more compressed and has no subhastate outline in adults. *H. tschegemensis* is a long and slender form, but has a more cylindriconical outline and a more acute apex. *C. pallinii* is closest to gracile *Pachybelemnopsis*, but can be distinguished by its long ventral groove, that extends to nearly the tip of the apex, and the compressed transverse sections.

Remarks. – This new species has first been reported by Combémorel et al. (1994a) and later by Mariotti et al. (2007, 2012) as "Belemnitida incertae sedis". These authors pointed out the peculiar combination of characters which are found separately in belemnites belonging to different genera and families (Mariotti et al. 2007: 12). For this reason, a new species and a new genus is established herein to classify these peculiar rostra. Similar characters have been reported in specimens from the Upper Bajocian–Bathonian from SW Germany determined as *Pachybelemnopsis persulcata* (Stolley, 1929) by Riegraf (1980a); being very close to *C. pallinii*, these specimens are distinguished by a depressed apical region. *C. pallinii* shows some affinities with *"Belemnopsis" mackayi* Stevens, 1965 from the Lower Temaikan (Bajocian–Bathonian) of New Zeland (Stevens 1965, pl. 2, figs. 1–3), but it differs by a lesser hastation and a shorter and obtuse apical region with a mucronate apex. Furthermore, a striking, convergent resemblance in shape of the rostrum and the transverse section and the length of the ventral groove is found with cylindrical variants of *Hibolithes arkelli* Stevens, 1965 from the Lower Tithonian of New Zealand (Stevens 1965, pl. 15, figs. 1–3).

Measurements (mm)

Specimen	L	X	Dv	Dl	Dv_{max}	Dl_{max}	Ica	Icm
MUSR NS20/1180	130	115	8.1	7.3	10.0	9.2	1.11	1.09
MUSR NS20/799	116	84	10.3	8.7	11.5	9.8	1.18	1.17
MUSR NS20/772 (fragm.)	67	65	11.4	9.5	11.9	10.7	1.20	1.11
MUSR NS20/858 (fragm.)	65	63	10.0	9.4	–	–	1.06	–
MUSR NS20/697 (juvenile)	70	55	7.6	6.7	9.3	8.2	1.13	1.13
MNHNL BEL003	100	7.5	10.7	9.1	–	–	1.18	–
MNHNL BEL045	73	55	9.9	9.1	–	–	1.09	–

Calabribelus aff. *pallinii*
Pl. 5, Fig. 8

v 2007 Belemnitida incertae sedis. – Mariotti et al., p. 12, pl. 2, fig. 10.
v 2012 Belemnitida incertae sedis. – Mariotti et al., p. 105, fig. 5 (1–4).

Material: 4 specimens from the earliest Lower Bajocian, Discites Zone of Caloveto, Calabria, Italy (MUSR NS20/1397); Lower Bajocian, Propinquans Zone, of Gap, Hautes-Alpes and Castellane, Haute-Provençe, France (MNHNL BEL013, 034, 043).

Stratigraphic range and geographic distribution: Lower Bajocian (Discites and Propinquans zones) of southern Italy (Calabria) and SE France (Gap, Hautes-Alpes; Castellane, Alpes de Haute-Provençe).

Description. – Medium sized, robust and strongly cylindrical rostrum. The outline is symmetrical and cylindrical, the profile asymmetrical and cylindrical, with the "beak-like" tip of the apex being orientated towards the dorsal side. The apical region is short. A long broad (1.5 mm) alveolar groove extends from the apical region (starting about 5 mm from the tip) towards the alveolar border. A splitting surface is rudimentary developed. The transverse section is elliptical and distinctly compressed. The apical line is eccentrical, displaced towards the venter. The phragmocone penetrates approximately one third to one half of the rostrum. The alveolar angle is 23°.

Remarks. – The specimens herein studied show a general affinity with *Calabribelus pallinii*. However they differ by the asymmetrical apex, the shorter, robust and cylindrical rostrum, the deeper alveolus, the broader groove and the eccentrical apical line. All these morphological differences might indicate a new taxon, but considering the low number of specimens, albeit well-preserved, introducing a new species appears not advisable.

Measurements (mm)

Specimen	L	X	Dv	Dl	Dv_{max}	Dl_{max}	Ica	Icm
MUSR NS20/1397	84	70	13.8	13.4	14.3	1.27	1.03	1.13
MNHNL BEL043	104	59	14.3	12.8	–	–	1.12	–

5. Evolutive trends in Holcobelidae and allies

The Aalenian/Bajocian boundary represents an important time interval for the differentiation of belemnites. Whereas the suborder Belemnitina was largely dominant in Early Jurassic times, in the early Middle Jurassic belemnites mark a turnover characterised by the fast evolution of early representatives of the suborder Pachybelemnopseina (Holcobelidae and Mesohibolithidae). During the time interval comprised between the Early Aalenian and the Early Bajocian, the following characters were subject to changes.

5.1. Morphologic features of the rostrum

5.1.1. Rostrum shape and alveolus

A trend from cylindriconical, short rostra (*Acrocoelites*, *Holcobelus*) to elongate and subhastate rostra (*Calabribelus*, *Pachybelemnopsis*) is observable. The tendency to a subhastate rostrum, with a slight constriction in the initial alveolar region, is inherent in most holcobelid species, except for *H. brevicanalis*, which has an extremely short and conical rostrum.

The transverse sections are circular, depressed or compressed. Acrocoelitids show compressed or circular sections meanwhile *Pachybelemnopsis* is characterised by depressed sections at the stem and apical region. Holcobelids display a high variation of sections, ranging from markedly compressed (*H. elmii*, *H. tetramerus* and *H. trauthi* with ratios ranging from 1.10 to 1.32) to depressed (*H. harleyi* with ratios ranging from 0.82 to 0.94). This remarkable variation of an otherwise rather stable character is interpreted as a further evidence for the highly adaptative morphology of holcobelids and their possible position between Belemnitina and Pachybelemnopseina.

The asymmetry grade of the rostrum, in lateral view (profile), can be evaluated observing also the apical line. *C. pallinii*, *H. munieri*, *H. blainvillii* and *H. tschegemensis* show a central apical line; *H. trauthi* and *H. tetramerus* are characterised by a slightly excentrical apical line. Finally, *C.* aff. *pallinii*, *H. brevicanalis* and *H. elmii* show a strong

eccentrical apical line. Another character to take into consideration is the penetration depth of the phragmocone into the rostrum. All the previously mentioned species with a strong eccentrical apical line, show a deep penetration (from two third to one third). The species with a central or slightly eccentrical apical line are characterised by an inferior penetration depth (from one third to one seventh). *C. pallinii* and *H. tschegemensis* are the species with the minimum penetration, one fifth and one seventh respectively. The combination of these two characters, asymmetry grade and phragmocone penetration could influence the animal's center of mass (sensu Monks et al. 1996), determinating different lifestyles and consequently different environments.

A further character which should be taken into consideration is the alveolar angle. In acrocoelitids it varies roughly among 22° to 29° (Schlegelmilch 1998), in holcobelids from 20° to 24° (Fig. 2A and own observations herein) and in pachybelemnopseids from 17° to 23° (Schlegelmilch 1998). Thus, a general tendency to reduce the alveolar angle can be postulated. The reduction of the alveolar angle results in a narrower and possibly longer proostracum.

5.1.2. Apical and alveolar grooves

The ventral groove changes progressively from:

- an apical ventral groove, typical for *Acrocoelites* (Opalinum Zone) to
- a moderately long narrow intermediate ventral groove, not reaching the alveolar region, typical of *Holcobelus blainvillii* (Opalinum–Murchisonae zones), to
- a long narrow intermediate ventral groove (Fig. 1A), extending on the alveolar region without reaching the alveolar border, typical for *Holcobelus munieri* and related species (Concavum–Propinquans zones), to
- a long narrow ventral groove (Fig. 1C), extending from near the tip of the apex to the alveolar border, typical for *Calabribelus* (Discites and Propinquans zones), to
- a shorter and broader alveolar canal (Fig. 1D), with a distinct alveolar slit area, starting from the alveolar border and fading out at the beginning of the apical region, typical for *Pachybelemnopsis* (Propinquans Zone).

The dorsolateral grooves, typical of *Acrocoelites*, are reduced in the Holcobelidae. Some individuals maintain remnants of those short dorsolateral grooves. "*Belemnites eduardi* v. Hochstetter" is a typical example, few individuals of *H. munieri* (Pl. 3, Fig. 3a) and *C. pallinii* (Pl. 4, Fig. 12a) show the same feature, indicating their possible phylogenetic origin from acrocoelitids.

The shape of the transverse section of the ventral groove, observed at the protoconch level, is smooth and broad (U-shaped; Fig. 1H) in *H. blainvillii*, *H. harleyi*, *H. munieri*, *H. brevicanalis*, but it is sharper and more incised (V-shaped; Fig. 1I) in *H. tetramerus*, *Calabribelus* and *Pachybelemnopsis*. According to Jeletzky (1980: 32), the presence of a V-shaped profile, combined to a relative depth, indicates the presence of a canal underlain by a splitting surface.

5.1.3. The splitting surface

The splitting surface sensu Jeletzky (1966, 1980) (or slit area sensu Pugaczewska 1961) is a typical feature of early belemnites of the Pachybelemnopseina. Both above mentioned authors distinguish between the splitting surface (or slit area) in Jurassic pachybelemnopseids (Fig. 1E) and hibolithids and the ventral fissure common in Cretaceous belemnites (Fig. 1F). By definition, (Jeletzky 1966: 147; Riegraf 1980a) a splitting surface is found in combination with an alveolar canal; thus, a canal is distinguished from a groove by the fact that the latter is not underlain by a clearly discernable splitting surface. The splitting surface itself consists in a growth discontinuity of the rostrum lamellae. This discontinuity could also be interpreted as a zone of looser growth, with (post)diagenetic dissolution causing, in some cases, a visible discontinuity on transverse sections (Fig. 1J). On longitudinal sections, a smooth area with delicate longitudinal striae is discernable, extending along the cleavage plane between the apical line and the external ventral groove. The length of this splitting surface is equivalent to the length of the ventral canal; it is generally shorter in *Hibolithes* and longer in *Pachybelemnopsis* (Fig. 1E), whereas it is strongly reduced in *Belemnitella* (Fig. 1G). While the splitting surface generally displays a well marked triangular shape in the above-mentioned genera, it is only rudimentarily developed in *Holcobelus* (Fig. 1B), so that the posterior extension of the surface is unclearly recognizable (Riegraf 1980a). Thus, holcobelids could represent a transitional stage towards the development of a clearly defined alveolar canal associated with a splitting surface, characteristic for Middle and Late Jurassic Pachybelemnopseina.

5.2. Morphologic features of the phragmocone

The preservation potential of phragmocones is highly variable because of taphonomic, sedimentological and diagenetical constraints. In our material, only few rostra that can be referred to *H. munieri*, *H. brevicanalis* and *C. pallinii*, show a partially preserved phragmocone within the alveolus. Thus, our observations on the internal structure of the phragmocone are provisional, until further better preserved material is available.

5.2.1. Protoconch

The protoconch has been observed in one specimen of *H. munieri* (Fig. 2B). With a diameter of 0.3 mm, it appears of smaller size than other belemnitid protoconchs (Fuchs, personal communication 2011); nonetheless, this single observation cannot yet be retained as a general value, unless more individuals have been examined.

5.2.2. Cameral deposits

According to Jeletzky (1966, 1980), cameral deposits are characteristic for Early Jurassic Belemnitina (including Hastitidae), but are absent in Pachybelemnopseina. An evolutionary trend toward reduction and complete disappearance of the cameral deposits in Belemnitida has been observed by Jeletzky (1966: 133). The same author records vestigial cameral deposits in *H. munieri* (Jeletzky 1966: 96). In our material, a specimen of *H. brevicanalis* shows also vestigial cameral deposits. Thus, the genus *Holcobelus* may represent a transitional stage in the trend of reduction of the cameral deposits. In *Calabribelus*, one single rostrum with a partially preserved phragmocone was available to study (Fig. 2C): at least in the preserved septa, no remnants of cameral deposits could be observed.

5.3. Ontogenetical features

5.3.1. Primordial rostrum

It has been assumed that Belemnitina are generally characterised by a "saucer-like" apical part of the primordial rostrum, and Pachybelemnopseina by a "low cone-like" structure (Jeletzky 1966: 130). Bandel et al. (1984) found a conical primordial rostrum in *Hibolithes*, consisting of two distinct parts, respectively aragonitic and organic. Although the primordial rostrum has been observed in the studied material, it was impossible to study in detail the shape of its apical part, due to diagenetic alteration.

5.3.2. Earliest juvenile rostrum

In *Holcobelus*, the earliest juvenile growth stage is easily distinguishable in most species; it corresponds to a conirostrid type, with slight variations. In *H. blainvillii* and *H. brevicanalis*, the earliest juvenile growth stage is short and conical. In *H. munieri*, *H. tetramerus* and *Calabribelus pallinii*, it is elongate and conical.

According to Jeletzky (1966: 136), belemnites with a conirostrid juvenile stage (early Belemnitina) possess also cameral deposits, and vice-versa belemnites with a clavirostrid juvenile stage (Pachybelemnopseina and late Belemnitina) lack cameral deposits. Following this author, this correlation is related to the function of the belemnitid juvenile guard as an organ of balance. The clavirostrid rostrum would have been insufficient as a counterweight to keep the animal in a horizontal position and therefore was assisted in the balancing by the cameral deposits. In clavirostrid juvenile rostra, the counterbalancing effect of cameral deposits was not needed anymore, due to the significant postalveolar length of the rostrum. A secondary balancing effect in conirostrid belemnites was probably given by the formation of an epirostrum (Jeletzky 1966: 136 and own observations, see also 5.3.3.), a structure unknown in clavirostrid belemnites, except *Neohibolites minimus* (Miller, 1826).

5.3.3. Epirostrum

As recently emphasized by Fuchs (2012), the rostrum of Belemnitida is composed of at least three structures: conotheca, primordial rostrum, and orthorostrum. A fourth structure, the epirostrum, is known in some species. This more or less developed extension is either observable on the outer shape of the rostrum (as in *Holcobelus munieri*, or the well-known *Pleurobelus lagenaeformis*, *Youngibelus tubularis* and *Dactyloteuthis semistriata* from the Early Jurassic), or in the longitudinal section only (as in *Holcobelus trauthi* or *Megateuthis elliptica*). The function and composition of this peculiar structure has been discussed by several authors, and a possible sexual dimorphism has been suggested (d'Orbigny 1842, Doyle 1985). Several Early Jurassic Belemnitina developed an epirostrum; nonetheless it is documented only in two species among the Pachybelemnopseina, *Neohibolithes minimus* from the Albian (Bandel & Spaeth 1988) and *Hibolithes escragnolensis* Delattre, 1952 from the Hauterivian. It is therefore remarkable that holcobelid species develop an epirostrum. This feature is particularly marked in *H. munieri*, to the point that specimens without epirostrum were differently named by Eudes-Deslongchamps (1878) as *Belemnites subblainvillei*. Short epirostra have also been evidenced in *H. tetramerus*, *H. trauthi* and *H. brevicanalis*, but have not been observed in *H. blainvillii* and *H. harleyi*. In *Calabribelus*, fully adult specimens show also an epirostrum (Pl. 5, Fig. 1d).

6. Phylogenetic problems

The genus *Holcobelus* has been suggested as a possible phylogenetic link between the Belemnitina and the Pachybelemnopseina (Riegraf 1980a). Although including *Holcobelus* in his family Belemnitidae, Stolley (1919) already

suggested that it could be ancestral to the taxon currently named *Pachybelemnopsis*.

6.1. *Holcobelus* vs. *Acrocoelites*

Several authors stated that *Holcobelus* derives from acrocoelitids (Lissajous 1915, Riegraf 1980a, Combémorel et al. 1994a, Mariotti et al. 2010). Many acrocoelitids, especially juvenile specimens, show a dominant ventral groove and weaker dorsolateral grooves which often are not developed in juvenile stages. *Belemnites suprapalatinus* Kolb, from the Upper Toarcian of Franconia (SE Germany), reported as *Holcobelus* by Schlegelmilch (1998), most likely represents such a juvenile *Acrocoelites* with reduced dorsolateral grooves. On the other hand, some individuals of *Holcobelus* (*Belemnites eduardi* v. Hochstetter) and *Calabribelus* show remnants of dorsolateral grooves, a further clue for a hypothetical lineage *Acrocoelites – Holcobelus – Calabribelus*.

6.2. *Holcobelus* and *Calabribelus* vs. *Pachybelemnopsis*

Riegraf (1980a) suggested a direct derivation of Pachybelemnopseina from holcobelids, arguing that the intermediate ventral groove and the rudimentary developed splitting surface of holcobelids represent an evolutionary stage towards the ventral alveolar canal and the well defined slit area of Pachybelemnopseina.

A different interpretation was developed by Combémorel et al. (1994a): "No close comparison can be made between *Holcobelus* and the Belemnopseina, and particularly the Belemnopseidae. This is because an apomorphy for all Belemnopseina is the possession of an alveolar groove that is commencing in the alveolar region and fading adapically." Combémorel et al. (1994a) support Jeletzky (1966) who observed that ancestors of Pachybelemnopseina must have possessed a claviform rostrum during the juvenile stage, alveolar grooves and a tendency to a split area. Consequently, Jeletzky (1966: 143) supposed the hastate and "Doppellinien"-bearing Hastitidae from the Early Jurassic to be the ancestors of Pachybelemnopseina, observing specimens with ventroalveolar furrows accompanied by poorly developed splitting surfaces, occurring from the middle Early Jurassic to earliest Middle Jurassic.

The newly described genus *Calabribelus* might be regarded as a possible link between *Holcobelus* and *Pachybelemnopsis* for its peculiar combination of the following characters:

1) a long ventral groove extending from the alveolar border to the apical region. The length and narrowness of the groove remind *Holcobelus*;
2) a short and slightly mucronate apical region, reminiscent of *Pachybelemnopsis*;
3) a rudimentary slit area, similar as in *Holcobelus*, whereas in *Pachybelemnopsis* this character is fully developed;
4) compressed to subcircular transverse sections, reminiscent of *Holcobelus*;
5) subhastate to cylindrical profile, typical of *Pachybelemnopsis*;
6) presence of a slightly developed epirostrum, common in *Holcobelus,* but unknown in *Pachybelemnopsis.*

6.3. *Holcobelus* vs. *Cylindroteuthis*

The hypothesis of a direct phylogentic relationship between Holcobelidae and Cylindroteuthididae, as advanced by Jeletzky (1966) on the base of cameral deposits in *Holcobelus* and in some insufficiently understood Bathonian forms tentatively placed in the Cylindroteuthididae, is not retained herein following Combémorel et al. (1994a); Cylindroteuthididae possibly derived from a peculiar genus present in the Early Bajocian of the European subboreal region, *Eocylindroteuthis* Riegraf, following Riegraf (1980; 1981, text-fig. 252) and Weis & Mariotti (2007). This view supports the opinion of Mutterlose (1988: 528), who suggested that the cylindroteuthids derived from the Aalenian genus *Homaloteuthis*, recently interpreted as the direct ancestor of *Eocylindroteuthis* (Weis & Mariotti 2007).

7. Stratigraphic and palaeobiogeographic distribution of Holcobelidae and coeval allies

Mariotti et al. (2010, 2012) evidenced the palaeobiogeographic distribution of holcobelid belemnites and their allies at the Aalenian/Bajocian boundary (Murchisonae–Propinquans zones; Figs. 4, 5) as follows:

7.1. Subboreal association

A Subboreal fauna, characterized by *H. blainvillii* – associated with *Homaloteuthis*, *Brevibelus*, *Eocylindroteuthis*, *Megateuthis* – is present in some areas of northwestern and central Europe: Luxembourg, Lorraine, Burgundy, Lyonnais (France), NW Switzerland, Swabia (SW Germany). The stratigraphic distribution of this fauna is well known in southern Germany (Riegraf 1980a, Schlegelmilch 1998) and Luxembourg (Weis & Mariotti 2007, Guérin-Franiatte & Weis 2010). More specifically the only holcobelid, *H. blainvillii*, occurs from the Middle Aalenian (Murchisonae Zone) to the Early Bajocian (Discites Zone). This relatively wide stratigraphic occurrence makes it not the best choice for a biozonal index, but its presence might, however, be considered as a field marker for the Aalenian/Bajocian boundary region, in a wider sense.

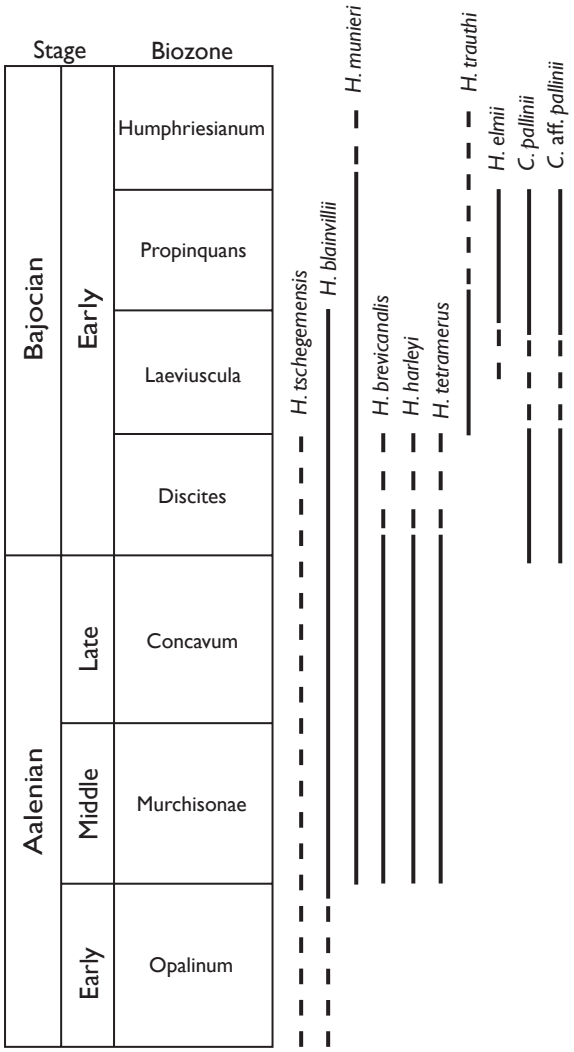

Fig. 4. Biostratigraphic distribution of the Holcobelidae. Compiled after Eudes-Deslongchamps (1878), Riegraf (1980), Weis & Mariotti (2007), Mariotti et al. (2007, 2010, 2012). Verified occurrences are marked by a continous line, inferred occurrences by a dashed line.

7.2. Submediterranean association

The Submediteranean fauna is characterised by diverse species of holcobelids (namely *H. munieri*, *H. trauthi*, *C. pallinii*, *C.* aff. *pallinii*) associated with early *Pachybelemnopsis* and *Hibolithes*. This association has been recorded from Calabria (southern Italy) (Combémorel et al. 1994a, Mariotti et al. 2007) and the Gap-Digne-Castellane area (SE France) (Mariotti et al. 2012). In particular, the Gap-Digne-Castellane area is characterized by the exclusive presence of *Holcobelus munieri* in the Late Aalenian (Concavum Zone), meanwhile *H. trauthi* appears limited to the Early Bajocian (Laeviuscula Zone). Furthermore, the presence of *H. elmii* and the genus *Calabribelus* characterises the Early Bajocian and namely the Propinquans Zone.

Another fauna of the Submediterranean assemblage, characterized by holcobelids, has been recorded from the Late Aalenian (Concavum Zone) to the Early Bajocian (Propinquans Zone) of Morocco (Sadki 1997) and the Early Bajocian of Algeria (coll. Elmi, UCBL).

7.3. Mixed association

A mixed fauna, comprising several elements distinctive of Subboreal and Submediteranean associations, has been evidenced in western France (Normandy, Aquitaine; Eudes-Deslongchamps 1878 and Mariotti et al. 2010) and south-western England (Dorset; Phillips 1869). This fauna is composed by representatives of holcobelids *(H. munieri*, *H. blainvillii*, *H. tetramerus*, *H. brevicanalis*, *H. trauthi*, *H. harleyi)* and Belemnitina *(Brevibelus*, *Megateuthis)* at the Aalenian/Bajocian boundary and, from the Early Bajocian on, also by *Pachybelemnopsis* and *Hibolithes.* The stratigraphic range of this association is comprised between Early Aalenian (Opalinum Zone) and Late Bajocian (Humphriesianum Zone).

Similarly composed faunas have also been reported from Romania (Preda 1975), Bulgaria (Stoyanova-Vergilova 1982, 1985, 1990) and the Caucasus (Krimholz 1931; Nutsubidze 1966), making it apparent that the interaction between the Subboreal and Submediterranean faunas was present all along the European margins of the Tethys Ocean.

8. Discussion

The Bajocian represents an important interval of belemnite faunal turnover. Throughout most of the Early Jurassic, the composition of belemnite faunas was rather uniform (Doyle 1987, 1994; Doyle & Mariotti 1991). At the end of the Early Jurassic, in Toarcian times, a distinct Boreal fauna developed in the northern hemisphere (Greenland, Arctic Siberia and Arctic Canada) (Jeletzky 1980; Doyle 1987, 1991; Doyle & Pirrie 1999; Meledina et al. 2005). However, only in Bajocian times a clearly distinguishable Tethyan fauna developed. This event is probably related to the evolution and expansion of ventrally grooved Pachybelemnopseina.

According to Doyle & Howlett (1989), the Pachybelemnopseina were able to migrate freely in the expanse of Tethys and the Tethyan borders of the Palaeo-Pacific realm. Namely *Pachybelemnopsis* has been encountered in deeper marine as well as in the shelf environments (Doyle & Howlett 1989: 178). In contrast, most of the Early Jurassic Belemnitina were apparently not able to expand into deep marine environments and thus they were largely limited to shelf or near-shore environments (Doyle 1987).

The holcobelids were confined to the NW and NE European margins of the Tethys ocean and along the emerged

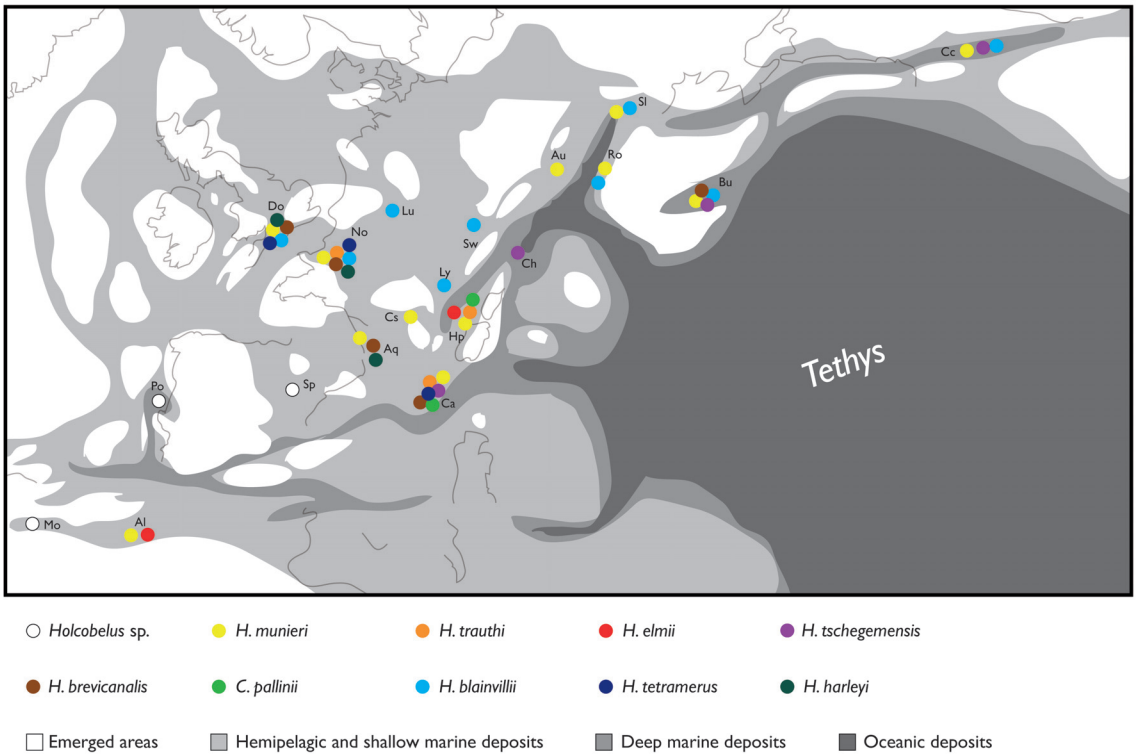

Fig. 5. Palaeobiogeographic distribution of Holcobelidae from the Late Aalenian (Concavum Zone) to the Early Bajocian (Propinquans Zone). Al = Algeria; Aq = Aquitaine; Au = Austria (Vienna); Bu = Bulgaria; Ca = Calabria; Cc = Caucasus; Ch = central Switzerland; Cs = Causses; Do = Dorset; Hp = Haute-Provençe; Lu = Luxembourg; Ly = Lyonnais; Mo = Morocco, middle Atlas; No = Normandy; Po = Portugal; Ro = Romania; Sl = eastern Slovakia; Sp = Spain, Aragón; Sw = Swabia. Palaeogeographic map modified after Thierry & Barrier (2000).

ridges of the Maghreb. Their center of origin is most probably the western Anglo-Paris Basin (Riegraf 1980a: 167). As reported by Mariotti et al. (2010: 142), the holcobelids thrived in areas surrounding continental masses, along rifted margins or in epicontinental seas, but their further spread into the Boreal provinces was hampered as well as the colonization of oceanic environments. In contrast to the limited geographical distribution of holcobelids, the pachybelemnopseid and hibolithid belemnites had a subsequent wider geographical distribution, reaching southern and south-eastern Tethyan regions such as India, Indonesia, New Zealand (e. g., Stevens 1965, 1973; Doyle 1987; Challinor 1991a, 1991b; Challinor et al. 1992) and Madagascar (Combémorel 1988). Thus, Doyle & Howlett (1989) established the hypothesis that the "Tethyan" pachybelemnopseids were migratory cephalopods in analogy with modern oegopsid squids, which have a pelagic lifestyle but come inshore periodically to spawn or feed. Among the diverse Mesozoic belemnite families, different lifestyles and habitats as well as important ontogenetic migrations were represented in an analogue way as it occurs in modern squids (e. g., Arkhipkin et al. 2008).

The above discussed elements, combined with the distribution patterns of Holcobelidae and the coeval *Pachybelemnopsis* and *Hibolithes*, indicate that the early representatives of Pachybelemnopseina took advantage of the environmental variation (such as eustatic changes and ocean currents, water temperatures …) during the Bajocian transgression, gradually adapting their morphology to their lifestyle. These adaptations (see also chapter 5.) allowed the Pachybelemnopseina to expand beyond the European margins of the Tethys Ocean in the early Middle Jurassic, giving birth to a wide distribution area (Tethyan Realm sensu Doyle 1987).

9. Conclusions

The systematic review of holcobelid belemnites provides for the first time a comprehensive overview on the morphological characters, thus allowing a comparison with allied taxa such as *Acrocoelites* (Toarcian–Aalenian) and *Pachybelemnopsis* (Bajocian–Callovian). In this respect, the following evolutionary trends at the Aalenian/Bajocian boundary are outlined:

- the rostrum shape changes from stout and conical, with the tendency to an epirostral stage, to elongate and (sub)hastate, without an epirostral stage;
- the apical line evolves from excentric to central;
- the apical grooves are reduced;
- an intermediate ventral groove and subsequently an alveolar ventral canal is developed; the latter is accompanied by a splitting surface;
- the alveolar angle is reduced;
- the phragmocone cameral deposits are reduced;
- the earliest juvenile stage becomes clavirostrid rather than conirostrid;
- the transverse section of the apical region changes from compressed to depressed.

Concerning the phylogenetical relationships between Holcobelidae and their allies, the following conclusions are drawn:

- numerous morphological clues indicate a direct derivation of *Holcobelus* (and subsequently *Calabribelus*) from *Acrocoelites*;
- the present study does not provide support for a direct phylogenetical relationship between Holcobelidae and Cylindroteuthididae, as suggested by previous authors.

As concerns palaeobiogeography, the composition of the holcobelid fauna allows us to distinguish the following faunas:

- a Submediterranean fauna, composed of numerous species of Holcobelidae and other Pachybelemnopseina (*Pachybelemnopsis* and *Hibolithes)* recorded from southern Italy, SE France, western Algeria and central Morocco;
- a Subboreal fauna, composed of numerous representatives of Belemnitina (*Homaloteuthis*, *Brevibelus*, *Eocylindroteuthis*, *Megateuthis*), and the single holcobelid species *H. blainvillii*, recorded from southern Germany, NW Switzerland, NE and central France, Luxembourg;
- a mixed fauna with representatives of both Submediterranean and Subboreal faunas, recorded from western and NW France, SW England, Romania, Bulgaria, Caucasus.

This distribution pattern anticipates the distinction of Boreal and Tethyan faunas in the late Middle and Late Jurassic, based on the distribution of Belemnitina (e. g., cylindroteuthids) in the former and Pachybelemnopseina (e. g., pachybelemnopseids, hibolithids) in the latter.

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Plate 1

Fig. 1. *Holcobelus blainvillii* (Voltz); La Verpillière (Isère, France), Upper Aalenian, Concavum Zone; MNHNL BEL001 (coll. Rulleau). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 2. *Holcobelus blainvillii* (Voltz); Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18035. – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 3. *Holcobelus blainvillii* (Voltz); Balingen (SW Germany), Lower Bajocian, Discites Zone; MNHNL DOT175 (coll. Riegraf). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 4. *Holcobelus blainvillii* (Voltz), apex not preserved; Torcieu (Ain, France), Aalenian, Murchisonae–Discites Zone; UCBL FSL391822 (coll. Juventin). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 5. *Holcobelus blainvillii* (Voltz), transversal thin section at protoconch level; Blumberg-Achdorf, Wutach region (SW Germany), Upper Aalenian, Concavum Zone; MNHNL DOT182 b (coll. Riegraf). – × 3.6.

Fig. 6. *Holcobelus blainvillii* (Voltz), longitudinal thin section; Blumberg-Achdorf, Wutach region (SW Germany), Upper Aalenian, Concavum Zone; MNHNL DOT182 a (coll. Riegraf). – × 1.6.

Fig. 7. *Holcobelus blainvillii* (Voltz), subadult; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18036. – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 8. *Holcobelus blainvillii* (Voltz), compressed specimen; Torcieu (Ain, France), Lower Bajocian; UCBL FSL391824 (coll. Juventin). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 9. *Holcobelus* cf. *blainvillii* (Voltz); Hutberg near Rumelange (Luxembourg), Middle Aalenian, Murchisonae Zone; MNHNL HU209. – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 10. *Holcobelus brevicanalis* (Eudes-Deslongchamps); Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18037 (coll. Harlé). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 11. *Holcobelus* cf. *brevicanalis* (Eudes-Deslongchamps), with short, deformed epirostrum; Caloveto (Calabria, Italy), Aalenian/Bajocian boundary; MUSR NS20/817. – **a**. Lateral view, venter right. **b**. Ventral view. **c**. Longitudinal section.

Fig. 12. *Holcobelus brevicanalis* (Eudes-Deslongchamps); Saint Vigor (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18054 (coll. Harlé). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 13. *Holcobelus brevicanalis* (Eudes-Deslongchamps), epirostrum broken; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18045 (coll. Harlé). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 14. *Holcobelus brevicanalis* (Eudes-Deslongchamps); Feuguerolles-sur-Orne (Calvados, France), Aalenian; MNHNL BEL023 (coll. Chesnier). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 15. *Holcobelus brevicanalis* (Eudes-Deslongchamps), longitudinal thin section; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18039 (coll. Harlé).

Fig. 16. *Holcobelus brevicanalis* (Eudes-Deslongchamps), longitudinally broken; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18040 (coll. Harlé).

Fig. 17. *Holcobelus brevicanalis* (Eudes-Deslongchamps), transversal thin section at protoconch level; Sully (Calvados, France), Bajocian; UCBL FSL391831 (coll. De Riaz). – × 3.6.

Fig. 18. *Holcobelus elmii* n. sp., longitudinal section of an apical fragment, with endofauna; Caloveto (Calabria, Italy), Lower Bajocian; MUSR NS20/1017.

Fig. 19. *Holcobelus elmii* n. sp., apical fragment, paratype; Hassi Bou Lakhal (Algeria), Bajocian; UCBL FSL391834. – **a**. Lateral view, venter left. **b**. Transversal section. **c**. Ventral view.

Fig. 20. *Holcobelus elmii* n. sp., apical fragment, holotype; Lac du Castillon near Castellane (Alpes de Haute Provençe, France); MNHNL BEL006 (coll. Riegraf). – **a**. Lateral view, venter right. **b**. Transversal section. **c**. Ventral view.

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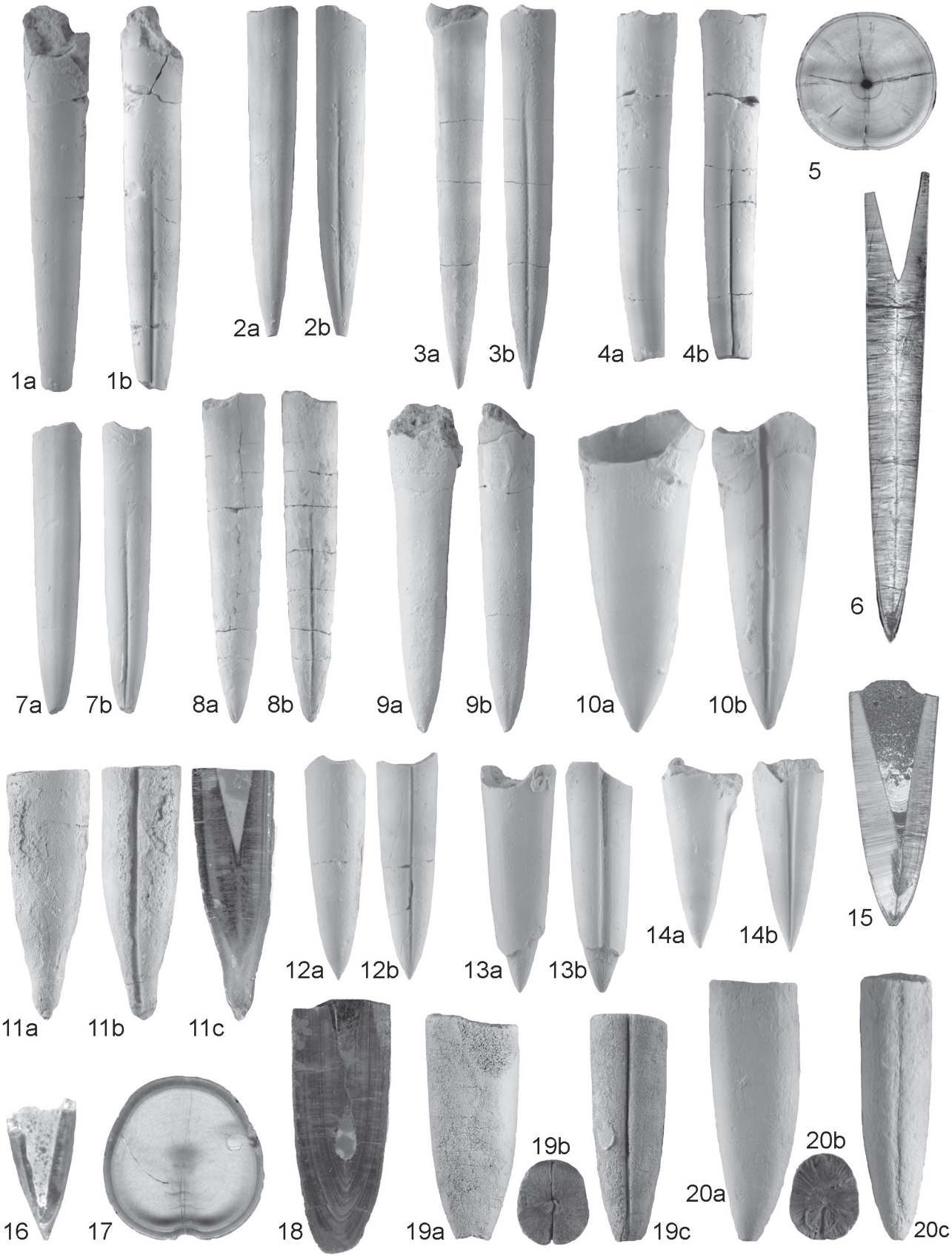
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Plate 2

Fig. 1. *Holcobelus harleyi* (Mayer); Calvados (France), ?Aalenian/Bajocian boundary; UCBL EM18001. – **a**. Lateral view, venter left. **b**. Ventral view. **c**. Longitudinal thin section.

Fig. 2. *Holcobelus harleyi* (Mayer), topotype designated by Lissajous (1927), the alveolar part is missing; Tilly-sur-Seilles (Calvados, France), ?Aalenian/Bajocian boundary (original attribution: "Lias"); FSL27510 (coll. Lissajous).

Fig. 3. *Holcobelus harleyi* (Mayer); Fontenay le Pesnel (Calvados, France), ?Aalenian/Bajocian boundary; UCBL EM18086 (coll. Harlé). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 4. *Holcobelus harleyi* (Mayer), juvenile; Fontenay le Pesnel (Calvados, France), ?Aalenian/Bajocian boundary; UCBL EM18083 (coll. Harlé). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 5. *Holcobelus harleyi* (Mayer); Fontaine-Etoupefour (Calvados, France), ?Aalenian/Bajocian boundary; UCBL EM18076. – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 6. *Holcobelus harleyi* (Mayer), juvenile; Fontenay le Pesnel (Calvados, France), ?Aalenian/Bajocian boundary; UCBL EM18085 (coll. Harlé). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 7. *Holcobelus harleyi* (Mayer), transversal thin section at protoconch level; Calvados (France), Aalenian/Bajocian boundary ("Mâlière"); UCBL EM18078. – × 2.5.

Fig. 8. *Holcobelus munieri* (Eudes-Deslongchamps); Croisilles (Calvados, France), Aalenian/Bajocian boundary; UCBL FSL391828. – **a**. Lateral view, venter left. **b**. Ventral view. **c**. Longitudinal section.

Fig. 9. *Holcobelus munieri* (Eudes-Deslongchamps), orginal to "*Belemnites eduardi* v. Hochstetter, 1897", alveolar part missing; St. Veit near Vienna (Austria), Bajocian; NHMW 1965/614/0000-1. – **a**. Lateral view, venter left. **b**. Transverse section. **c**. Ventral view.

Fig. 10. *Holcobelus munieri* (Eudes-Deslongchamps), neotype; Les Moutiers-en-Cinglais (Calvados, France), Lower Bajocian; MNHN R09426 (coll. Puzos n° EM75010). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 11. *Holcobelus munieri* (Eudes-Deslongchamps), longitudinal thin section, evidencing the epirostrum; Les Moutiers-en-Cinglais (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18034 (coll. Puzos).

Fig. 12. *Holcobelus munieri* (Eudes-Deslongchamps); Les Moutiers-en-Cinglais (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18003 (coll. Puzos). – **a**. Lateral view, venter left. **b**.Ventral view.

Fig. 13. *Holcobelus munieri* (Eudes-Deslongchamps), epirostrum broken; Les Moutiers-en-Cinglais (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18029 (coll. Puzos). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 14. *Holcobelus munieri* (Eudes-Deslongchamps), transversal thin section at the protoconch level; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18101. – × 2.

Fig. 15. *Holcobelus munieri* (Eudes-Deslongchamps), slender morphotype; Feuguerolles-sur-Orne (Calvados, France), "Oolithe de Bayeux", Lower Bajocian, Humphriesianum Zone; MNHNL BEL030. – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 16. *Holcobelus munieri* (Eudes-Deslongchamps), juvenile; Les Moutiers-en-Cinglais (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18020 (coll. Puzos). – **a**. Lateral view, venter right. **b**. Ventral view.

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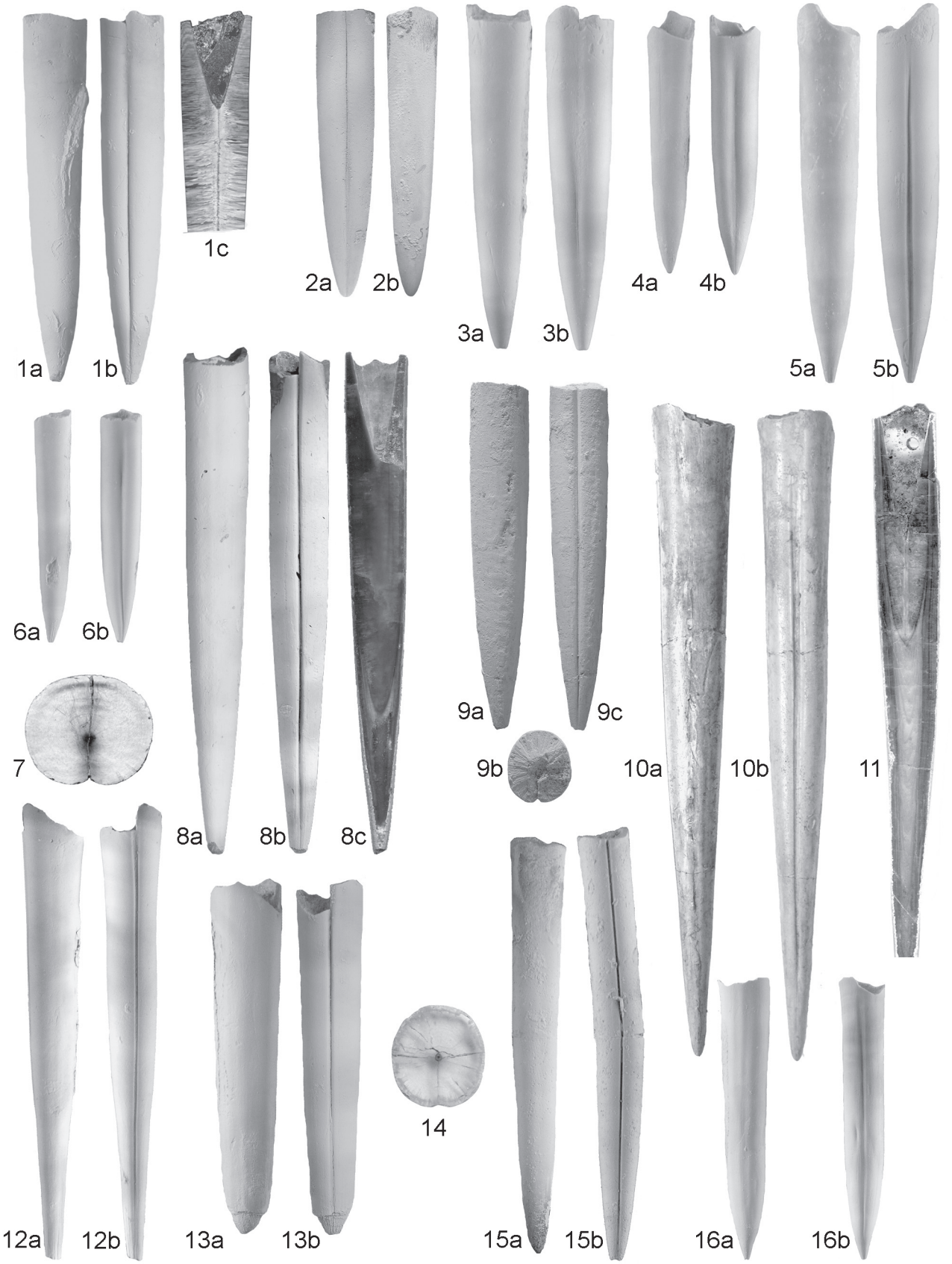
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Plate 3

Fig. 1. *Holcobelus munieri* (Eudes-Deslongchamps), figured in Roger (1952); Croisilles (Calvados, France), Bajocian; MNHN R07132. – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 2. *Holcobelus munieri* (Eudes-Deslongchamps), juvenile; Bayeux (Calvados, France), "Oolithe inférieure", Lower Bajocian; SMNS 66261-2. – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 3. *Holcobelus munieri* (Eudes-Deslongchamps), apical fragment with remnants of dorsolateral grooves; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18028. – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 4. *Holcobelus munieri* (Eudes-Deslongchamps), subadult with evident constriction in the alveolar part; Les Moutiers-en-Cinglais (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18030 (coll. Puzos). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 5. *Holcobelus munieri* (Eudes-Deslongchamps), juvenile, longitudinal section; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18027.

Fig. 6. *Holcobelus munieri* (Eudes-Deslongchamps), juvenile; Les Moutiers-en-Cinglais (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18032 (coll. Puzos). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 7. *Holcobelus munieri* (Eudes-Deslongchamps); Truc de Balduc near Mende (Lozère, France), Upper Aalenian; MNHNL BEL022 (coll. Riegraf). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 8. *Holcobelus munieri* (Eudes-Deslongchamps); Les Moutiers-en-Cinglais (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18004 (coll. Puzos). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 9. *Holcobelus munieri* (Eudes-Deslongchamps); "Côte folle" near Gap (Hautes-Alpes, France), Aalenian; UJFG IG.9000 (coll. Haug). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 10. *Holcobelus munieri* (Eudes-Deslongchamps); Les Moutiers-en-Cinglais (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18006 (coll. Puzos). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 11. *Holcobelus munieri* (Eudes-Deslongchamps), individual with a short ventral groove; Les Moutiers-en-Cinglais (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18007 (coll. Puzos). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 12. *Holcobelus munieri* (Eudes-Deslongchamps), apex broken; Caloveto (Calabria, Italy), Aalenian/Bajocian boundary; MUSR NS20/831. – **a**. Lateral view, venter left. **b**. Ventral view.

All figures in natural size.


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Plate 4

Fig. 1. *Holcobelus tetramerus* (Eudes-Deslongchamps); Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18057 (coll. Harlé). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 2. *Holcobelus tetramerus* (Eudes-Deslongchamps); Feuguerolles-sur-Orne (Calvados, France), Aalenian/Bajocian boundary; MNHNL BEL025. – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 3. *Holcobelus tetramerus* (Eudes-Deslongchamps), subadult; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18063 (coll. Harlé). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 4. *Holcobelus tetramerus* (Eudes-Deslongchamps); Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18002 (coll. Harlé). – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 5. *Holcobelus tetramerus* (Eudes-Deslongchamps), longitudinal thin section; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18067 (coll. Harlé).

Fig. 6. *Holcobelus tetramerus* (Eudes-Deslongchamps), transversal thin section at protoconch level; Feuguerolles-sur-Orne (Calvados, France), Aalenian/Bajocian boundary; MNHNL BEL026. – × 2.

Fig. 7. *Holcobelus tetramerus* (Eudes-Deslongchamps), juvenile; Fontaine-Etoupefour (Calvados, France), Aalenian/Bajocian boundary; UCBL EM18060 (coll. Harlé). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 8. *Holcobelus trauthi* (Stolley), robust adult individual; La Baume near Castellane (Alpes de Haute-Provençe, France), Lower Bajocian, Laeviuscula Zone; RNGHP 010012 (coll. De Baets). – **a**. Lateral view, venter right. **b**. Transversal section. **c**. Ventral view.

Fig. 9. *Holcobelus trauthi* (Stolley), paralectotype herein designated; Bayeux (Calvados, France), Bajocian; NHMW 1868/0011/0016-b. – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 10. *Holcobelus trauthi* (Stolley), lectotype herein designated; Bayeux (Calvados, France), Bajocian; NHMW 1868/0011/0016-a. – **a**. Lateral view, venter right. **b**. Ventral view.

Fig. 11. *Holcobelus tschegemensis* (Krimholz), original to Ooster (1857: pl. 2, figs. 7–8); Sulzgraben, Stockhornkette (Switzerland), Aalenian or Bajocian; NHMB 5015816 (coll. Ooster). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 12. *Calabribelus pallinii* n. gen. n. sp., apical fragment with remnants of dorsolateral grooves; Caloveto (Calabria, Italy), Lower Bajocian; MUSR NS201505. – **a**. Lateral view, venter right. **b**. Transversal section. **c**. Ventral view.

Fig. 13. *Calabribelus pallinii* n. gen. n. sp., paratype, rostrum solidum with eroded apex; Caloveto (Calabria, Italy), Lower Bajocian; MUSR NS20/772. – **a**. Lateral view, venter right. **b**. Ventral view. **c**. Longitudinal thin section, × 1.7.

Fig. 14. *Calabribelus pallinii* n. gen. n. sp., juvenile; Castillon Lake near Castellane (Alpes de Haute-Provençe, France), Lower Bajocian; MNHNL BEL003 b (coll. Riegraf). – **a**. Lateral view, venter left. **b**. Ventral view.

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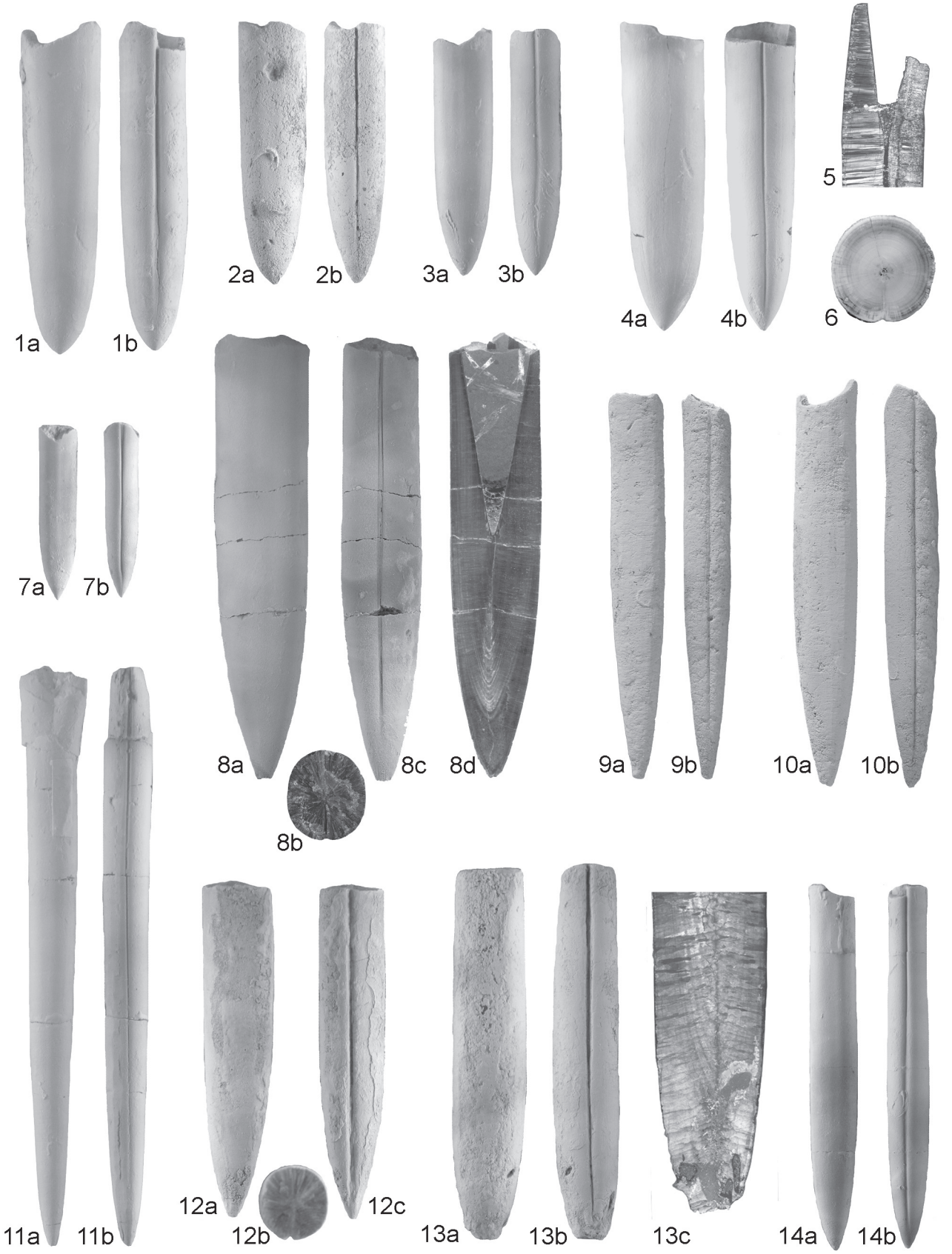
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Plate 5

Fig. 1. *Calabribelus pallinii* n. gen. n. sp., paratype, adult specimen with epirostral tendency; Caloveto (Calabria, Italy), Lower Bajocian; MUSR NS20/1180. – **a**. Lateral view, venter right. **b**. Transversal section. **c**. Ventral view.

Fig. 2. *Calabribelus pallinii* n. gen. n. sp.; Castillon Lake near Castellane (Alpes de Haute-Provençe, France), Lower Bajocian; MNHNL BEL003 a (coll. Riegraf). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 3. *Calabribelus pallinii* n. gen. n. sp., holotype; Caloveto (Calabria, Italy), Lower Bajocian; MUSR NS20/772. – **a**. Lateral view, venter right. **b**. Ventral view. **c**. Longitudinal thin section.

Fig. 4. *Calabribelus pallinii* n. gen. n. sp., paratype, rostrum solidum without alveolar part; Caloveto (Calabria, Italy), Lower Bajocian; MUSR NS20/858. – **a**. Lateral view, venter right. **b**. Ventral view.

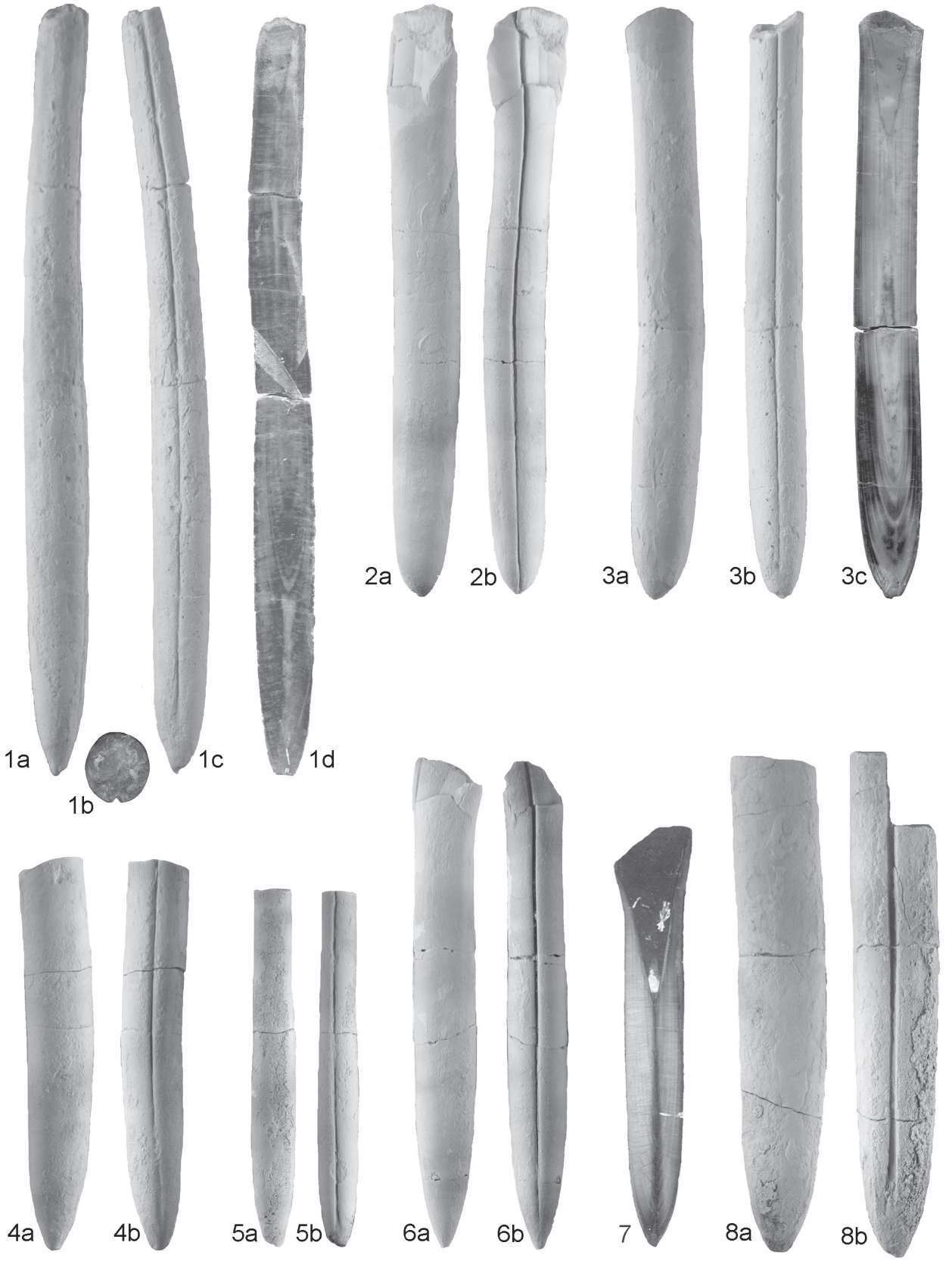
Fig. 5. *Calabribelus pallinii* n. gen. n. sp., paratype, juvenile; Caloveto (Calabria, Italy), Lower Bajocian; MUSR NS20/1175. – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 6. *Calabribelus pallinii* n. gen. n. sp., juvenile or subadult individual; Castillon Lake near Castellane (Alpes de Haute-Provençe, France), Lower Bajocian; MNHNL BEL007 (coll. Riegraf). – **a**. Lateral view, venter left. **b**. Ventral view.

Fig. 7. *Calabribelus pallinii* n. gen. n. sp., longitudinal thin section, of a subadult individual; Castillon Lake near Castellane (Alpes de Haute-Provençe, France), Lower Bajocian, Propinquans Zone; MNHNL BEL045.

Fig. 8. *Calabribelus* aff. *pallinii* n. gen. n. sp.; Caloveto (Calabria, Italy), Lower Bajocian; MUSR NS20/1397. – **a**. Lateral view, venter right. **b**. Ventral view.

All figures in natural size.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