geodiversitas

2025 • 47 • 23

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art. 47 (23) — Published on 18 December 2025
www.geodiversitas.com

PUBLICATIONS SCIENTIFIQUES

MUSÉUM NAL HIST NATURELLE

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Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

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Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

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

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Submitted on 31 December 2024 | accepted on 10 March 2025 | published on 18 December 2025

urn:lsid:zoobank.org:pub:5EE9ED75-B90C-4AD2-AF4C-3557CD066F05

Weis R., Mariotti N., Pignatti J. & Delsate D. 2025. — *Lotharingibelus* n. gen., a new belemnite genus from the upper Toarcian Minette ironstones of the NE Paris Basin. *Geodiversitas* 47 (23): 767-781. https://doi.org/10.5252/geodiversitas2025v47a23. http://geodiversitas.com/47/23

ABSTRACT
Jurassic belemnites have been widely studied by pioneering paleontologists in the early to late 19th century; it is therefore not surprising that most taxa still valid today were originally erected during that century. However, the standards for description and figuration having considerably evolved since then, many "historical" taxa have been repeatedly the subject of diverging taxonomic interpretation. It is therefore of great importance to revise these taxa and provide more detailed descriptions and illustrations of the type material. Herein, we restudy abundant material of *Belemnites meta* Blainville, 1827 and *Belemnites subgiganteus* Branco, 1879, two characteristic belemnite taxa of the Minette-type ironstones of Lorraine (France, Region Grand-Est, departments Moselle and Meurthe-et-Moselle), southern Luxembourg and Gaume (Southeast Belgium). Over the years, the taxonomic interpretation and species boundaries of these two taxa have remained unclear, with diverging opinions. We therefore maintain that for the purposes of a precise application of these nominal species and to clarify their stratigraphic position, systematic characters, and phylogenetic relationship, a typification is necessary. Herein, we designate a neotype for *B. subgiganteus*, illustrate the types of both species, and provide details about their type localities and stratigraphic occurrence. Their peculiar morphological characters also lead us to introduce a new genus, *Lotharingibelus* n. gen., with *Belemnites meta* Blainville as a type species. *Lotharingibelus* n. gen. is a megateuthidid with a relatively short stratigraphical range (upper Toarcian) that had its dispersal center in the north-eastern Paris Basin. The occurrence of specimens with or without an epirostrum allows us to discuss aspects of their ontogeny and the long-debated issue of a possible sexual dimorphism in belemnites.

KEY WORDS
Belemnitida,
Cephalopoda,
Jurassic,
neotypification,
new genus,
new combinations.

RÉSUMÉ
Lotharingibelus *n. gen., un nouveau genre de bélemnites du minerai de fer de la Minette du Toarcien supérieur du NE du bassin parisien.*
Les bélemnites du Jurassique ont été abondamment étudiées par les paléontologues pionniers du début à la fin du 19e siècle ; il n'est donc pas surprenant que la plupart des taxons encore valides aujourd'hui aient été érigés à l'origine au cours de ce siècle. Cependant, les standards de description et de figuration ayant considérablement évolué depuis lors, de nombreux taxons « historiques » ont fait l'objet d'interprétations taxonomiques divergentes au fil du temps. Il est donc d'une grande importance de réviser ces taxons et de fournir des descriptions et des illustrations plus détaillées du matériel type. Nous avons ici réétudié de nombreux spécimens de *Belemnites meta* Blainville, 1827 et *Belemnites subgiganteus* Branco, 1879, deux taxons caractéristiques parmi les bélemnites présentes dans les roches du type Minette en Lorraine (France, région Grand-Est, départements de la Moselle et de la Meurthe-et-Moselle), dans le sud du Luxembourg et en Gaume (sud-est de la Belgique). Au fil des ans, l'interprétation taxonomique et les délimitations de ces deux taxons sont restées floues, suscitant des opinions divergentes. Nous soutenons donc qu'une caractérisation est nécessaire pour une identification précise de ces espèces nominales et pour clarifier leur position stratigraphique, leurs caractères systématiques et leur relation phylogénétique. Nous désignons ici un néotype pour *B. subgiganteus*, illustrons les types des deux espèces et fournissons des détails sur leurs localités types et leur occurrence stratigraphique. Leurs caractères morphologiques particuliers nous ont également amenés à introduire un nouveau genre, *Lotharingibelus* n. gen., avec *Belemnites meta* Blainville, 1827 comme espèce type. *Lotharingibelus* n. gen. est un mégatéuthididé dont l'intervalle stratigraphique est relativement restreint (Toarcien supérieur) et dont le centre de dispersion se situait dans le nord-est du bassin parisien. La présence de spécimens avec ou sans épirostre nous permet d'aborder certains aspects de leur ontogénie et la question, longtemps débattue, d'un éventuel dimorphisme sexuel chez les bélemnites.

MOTS CLÉS
Systématique, Belemnitida, Céphalopodes, Jurassique, néotypification, genre nouveau, combinaisons nouvelles.

INTRODUCTION

Belemnites of the Minette-type ironstones of Lorraine and Luxembourg have been extensively treated in early monographs by Blainville (1827), Voltz (1830), Branco (1879), and Benecke (1898, 1905). However, the descriptions and illustrations of these belemnites lack sufficient detail, and their stratigraphic distribution is often not known in detail, leading to diverging interpretations. Moreover, part of the original specimens, kept in collections in Strasbourg, cannot currently be retrieved and were most likely destroyed in a fire in 1967. Therefore, a redescription and the designation of a neotype become necessary.

The extensive belemnite collections from the Minette formation of Lorraine, Belgium and Luxembourg comprise nine genera with 14 species from the late Toarcian and four genera with five species from the Aalenian. An updated faunal list of belemnites from the Minette ironstones is given in Table 1. As yet, only the species from Luxembourg have been restudied by Weis (1999) and Weis & Mariotti (2008). Here, we focus on the taxonomic, stratigraphic, and paleobiogeographic revision of two related species, *Belemnites meta* Blainville, 1827 and *Belemnites subgiganteus* Branco, 1879, two taxa that are widely found in the Minette ironstones, and whose taxonomic attribution has long been unclear. We furthermore discuss aspects of their ontogeny (Bandel & Spaeth 1988) and a possible sexual dimorphism.

GEOLOGICAL SETTING

The informally named Minette ironstone formation corresponds to ferruginous oolites, which cover an area of about 1000 km² from the southern part of the Grand Duchy of Luxembourg and Belgium in the north towards the surroundings of Nancy (Meurthe-et-Moselle, France) in the south (Fig. 1). We use here the name Minette ironstone formation, as it is used in the Grand Duchy of Luxembourg (Lucius 1945). In France, the corresponding deposits are termed Formation ferrugineuse (Mégnien 1980). In Belgium the ferruginous deposits are included in the Mont-Saint-Martin Formation (Boulvain *et al.* 2001).

The formation is characterized by oolitic ironstones at several horizons of up to 15 detrital coarsening upward cycles, with a total thickness of 10-65 m. The deposit is subdivided into several basins and sub-basins: the Nancy basin in the southern part, and, in the northern part, the Briey basin, which is subdivided into the Ars, Orne, Ottange-Esch/Alzette and Longwy-Differdange sub-basins. Important regional and vertical facies variations can be observed: in the lower part of the deposits, silicate ores are dominant, while in the upper parts calcareous goethitic ores prevail. The ironstone facies consists mainly of cross-bedded iron oolites and biocalcarenitic limestone of a high energy environment. Intercalated, bioturbated mud- and siltstone facies

indicate a lower energy environment. The alternation of the two facies builds up a sequence of shallowing-upward cycles. The Minette sediments were deposited in a nearshore shallow marine environment in the subsiding gulf of Luxembourg, surrounded by the lowlands of the Hercynian Rhenish Massif (Siehl & Thein 1989).

Numerous ammonite findings have contributed to the establishment of the stratigraphic extension of the Minette ironstones (Di Cencio & Weis 2020 and references therein). In 1962, at the Colloque du Jurassique de Luxembourg it was decided that the Toarcian/Aalenian boundary corresponds to the boundary of the *Pleydellia aalensis*/*Leioceras opalinum* Zones (Lecompte 1963), as later ratified with the recognition of the GSSP of the Toarcian-Aalenian Boundary (Cresta *et al.* 2001). Maubeuge (1947, 1961) reattributed the ammonites identified as (Aalenian) *Leioceras* Hyatt, 1867 by numerous former scholars to *Pleydellia buckmani* Maubeuge, 1947 and related taxa of late Toarcian age (Di Cencio & Weis 2020). In the main, the Minette ironstone formation is upper Toarcian; the material investigated herein ranges from the Dispansum Zone to the Aalensis Zone (Mactra subzone). However, the stratigraphic extension of the ironstone varies regionally, ranging from the upper Toarcian Dispansum Zone to the upper Aalenian Concavum Zone, with a distinctive stratigraphic gap in the lower Aalenian (Opalinum Zone) (Maubeuge 1947; Di Cencio & Weis 2020).

Fig. 1. — Geographical extension of the Minette ironstones (red color) in France, Luxembourg and Belgium: **1**, Oberkorn, type locality of *L. subgiganteus n. comb.*; **2**, surroundings of Nancy, type locality of *L. meta* (Blainville, 1827) n. comb. Author: Marianne Kayser (MNHNL).

MATERIAL AND METHODS

This study is based on 146 belemnite rostra (130 assigned to *L. meta* n. comb. and 16 assigned to *L. subgiganteus* n. comb.); the specimens originate from several localities in France, Luxembourg and Belgium. The studied material belongs to collections that have been mostly gathered between the early 19th century and the 1980's, during the active period of the iron ore mining.

Abbreviations

Repositories

MAN	Paleontological collections of the Muséum-Aquarium de Nancy, France;
MNHNL	Paleontological collections of the Musée national d'histoire naturelle de Luxembourg;
UCBL-EM	Invertebrate Paleontological Collection of Paris Mines School, University Claude Bernard Lyon 1, Villeurbanne, France.

Shell terminology

The total length of the preserved rostrum is generally subdivided into descriptive size categories, defined herein as follows: very small (< 30 mm), small 30-60 mm, medium (61-100 mm), large (101-150 mm), and very large (> 150 mm).

Standard measurements (expressed in mm) and ratios are defined as follows (see also Fig. 2) and summarized in Table 2:

TL	Total length of the preserved rostrum (rostrum cavum and rostrum solidum);
PAL	post-alveolar length, distance between the position of the protoconch and the tip of the apex;
SD	sagittal (or dorso-ventral) diameter measured at the protoconch level;
LD	lateral diameter, measured at the protoconch level;
Compression Index	ratio SD/LD; an index of < 1.00 indicates a (dorso-ventrally) depressed rostrum, and index of > 1.00 indicates a (dorso-ventrally) compressed rostrum;
Elongation Index	ratio SD/PAL, gives an indication on the growth pattern (slender or stout) of the rostrum solidum.

Methods

To create the images of the belemnite specimens, we employed the "digital whitening" technique as described by Kiselev (2021), an approach more convenient than traditional chemical bleaching methods. This digital method enhances the contrast and clarity of fossil structures by processing multiple images taken from the same point of view under different lighting angles into a single composite image, without applying substances to the specimen. Initial images were captured using a Canon EOS R7 digital mirrorless camera and illuminated with a Rotolight Neo 2 LED light, allowing the repositioning of the light source between shots.

For each final image, a series of seven to ten photographs of a fossil were taken and subsequently combined using

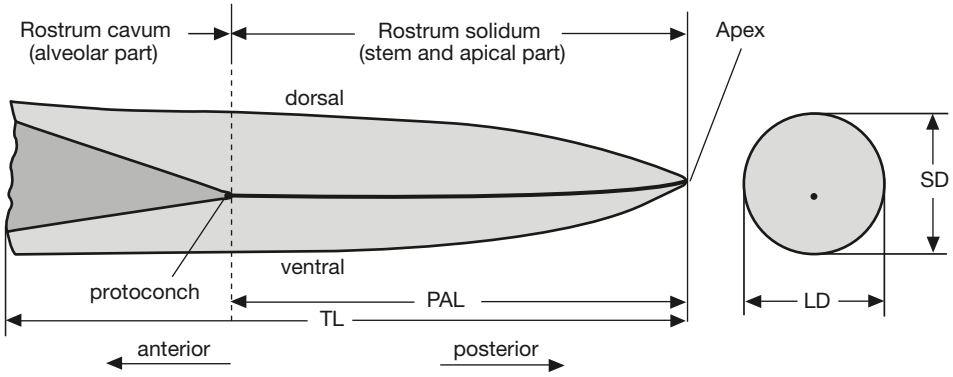

FIG. 2. — Morphological terms and measurements employed in a belemnite rostrum after Weis *et al.* (2017). Author: Marianne Kayser (MNHNL).

TABLE 1. — Updated faunal list of belemnites described from the Minette ironstones (upper Toarcian Dispansum Zone to upper Aalenian Concavum Zone) of Lorraine (France), Gaume (Belgium) and Luxembourg.

Species	Family	References	Chronostratigraphy (Zone)
Brevibelus breviformis (Voltz, 1830)	Megateuthididae	Benecke (1898, 1905); Weis (1999); Weis & Mariotti (2008) (also as *Brevibelus subbreviformis* (Lissajous, 1927))	upper Toarcian (Pseudoradiosa-Aalensis); Aalenian (Murchisonae-Concavum)
Megateuthis athletica (Simpson, 1855)	Megateuthididae	Benecke (1905) (as *Belemnites inornatus* and *B. rhenanus*); Weis (1999) (as *Mesoteuthis rhenana*)	upper Toarcian (Pseudoradiosa-Aalensis)
Megateuthis beneckei (Schwegler, 1938)	Megateuthididae	Weis & Mariotti (2008)	Aalenian (Murchisonae)
Homaloteuthis murielae Weis & Mariotti, 2008	Megateuthididae	Weis & Mariotti (2008)	Aalenian (Concavum)
Homaloteuthis spinata (Quenstedt, 1848)	Megateuthididae	Weis & Mariotti (2008)	Aalenian (Murchisonae)
Acrocoelites oxyconus (Hehl *in* Zieten, 1831)	Megateuthididae	Weis (1999)	upper Toarcian (Aalensis)
Acrocoelites quenstedti (Oppel, 1856)	Megateuthididae	Benecke (1905) (as *Belemnites tripartitus*); Weis (1999)	upper Toarcian (Dispansum-Aalensis)
Acrocoelites conoideus (Oppel, 1856)	Megateuthididae	Benecke (1898)	upper Toarcian (Dispansum)
Odontobelus pyramidalis (Münster *in* Zieten, 1831)	Megateuthididae	Weis (1999)	upper Toarcian (Pseudoradiosa)
Odontobelus brevirostris (d'Orbigny, 1842)	Megateuthididae	Benecke (1905) (as *Belemnites incurvatus*); Weis (1999) (as *Acrocoelites* (*Odontobelus*) *curtus* (d'Orbigny, 1842) and *A.* (*O.*) *subvulgaris* Weis, 1999	upper Toarcian (Pseudoradiosa-Aalensis)
Dactyloteuthis similis (von Seebach, 1864)	Megateuthididae	Benecke (1898) (as *Belemnites irregularis*)	upper Toarcian (Dispansum)
Lotharingibelus meta (Blainville, 1827) n. comb.	Megateuthididae	Benecke (1898); Weis (1999) (also: *Arcobelus lucilinburhucensis* Weis, 1999)	upper Toarcian (Dispansum-Aalensis)
Lotharingibelus subgiganteus (Branco, 1879) n. comb.	Megateuthididae	Branco (1879); Benecke (1905); Weis (1999) (also: *Dactyloteuthis crossotela*)	upper Toarcian
Parabrachybelus subaduncatus (Voltz, 1830)	Megateuthididae	Weis (1999) (as *Catateuthis* sp.)	upper Toarcian (Pseudoradiosa)
Salpingoteuthis longisulcata (Voltz, 1830)	Salpingoteuthididae	Benecke (1898); Weis (1999)	upper Toarcian (Dispansum)
Hastites subclavatus (Voltz, 1830)	Hastitidae	Benecke (1905); Weis (1999)	upper Toarcian (Pseudoradiosa-Aalensis)
Hastites compactus (Kolb, 1942)	Hastitidae	Weis (1999)	upper Toarcian
Holcobelus blainvillii (Voltz, 1830)	Holcobelidae	Weis & Mariotti (2008)	Aalenian (Murchisonae-Concavum)

Adobe Photoshop. The workflow involves importing the images as layers into a Photoshop file, followed by removing the background in each. Subsequently, one of the images is chosen as the base layer and is not processed further. All other layers are inverted into a negative state and their transparency reduced to under 10%. In the final step, the entire stack of layers is converted to grayscale and adjustments to brightness and contrast are made until the specimen features are adequately depicted, this result is then exported as a raster image file.

TABLE 2. — Measurements of *Lotharingibelus meta* (Blainville, 1827) n. comb. and *Lotharingibelus subgiganteus* (Branco, 1879) n. comb. Values in brackets represent estimates. Abbreviations: **OR**, orthorostrum; **ER**, epirostrum-bearing specimen; **CI**, compression index; **EI**, elongation index; **AA**, alveolar angle.

No.	Taxon	Collection number	TL	PAL	SD	LD	CI	EI	AA	Locality	Notes
***Lotharingibelus meta* n. comb.**											
1	–	UCBL-EM 75009	89	33	26	22	(1.25 at alveolus end)	0.79		near Nancy	Lectotype
2	–	MAN 2023.0.168	74	34	24	19	1.26	0.71	–	Lay-Saint-Christophe	Joly collection
3	–	MNHNL DOU989b	65	29	21	–	–	0.72	32°	Halanzy-Musson	–
4	–	MNHNL DOU989a	75	30	24	–	–	0.8	31°	Halanzy-Musson	–
5	–	MNHNL DOU989aa	66	31	-	18	–	–	–	Halanzy-Musson	–
6	–	MNHNL DOU989ac	62	26	23	19	1.21	0.88	–	Halanzy-Musson	–
7	–	MNHNL DOU989ae	62	30	24	19	1.26	0.8	–	Halanzy-Musson	–
8	–	MNHNL DOU989ad	62	27	21	17	1.24	0.78	–	Halanzy-Musson	–
9	–	MNHNL DOU989af	46	16	16	14	1.14	1.00	–	Halanzy-Musson	–
10	–	MNHNL DOU989ag	66	27	19	17	1.12	0.7	–	Halanzy-Musson	–
11	–	MNHNL DOU989ah	55	25	20	17	1.18	0.8	–	Halanzy-Musson	–
12	–	MNHNL DOU989ai	50	25	21	18	1.17	0.84	–	Halanzy-Musson	–
13	–	MNHNL DOU989ab	60	25	22	19	1.16	0.88	–	Halanzy-Musson	–
14	–	MNHNL DOU989f	64	24	21	19	1.10	0.88	30°	Halanzy-Musson	–
15	–	MNHNL DOU989g	72	26.5	20	16	1.25	0.75	29°	Halanzy-Musson	–
16	–	Benecke (1898: pl. 2 fig. 8)	–	–	–	–	–	0.7	(28°)	Algringen	–
***Lotharingibelus subgiganteus* n. comb.**											
17	[ER]	MNHNL TO265	240	(155)	(19)	(17)	(1.12)	(0.12)	–	Kiemerchen	Neotype
18	[OR]	MNHNL LG101	80	35	22	19	1.16	0.63	–	Rumelange	–
19	[OR]	MNHNL DOT505a	105	45	22	–	–	0.49	30°	Thil	TL with ER: 177 mm
20	[OR]	MNHNL DOT511b	103	43	18	14	1.11	0.42	28°	Kiemerchen	
21	[OR]	Branco (1879: pl. 6, fig. 2e)	(67)	(55)	(18)	–	–	(0.33)	(33°)	Ars-sur-Moselle	TL with ER: (120) mm
22	[ER]	Branco (1879: pl. 6, fig. 2a-d)	(172)	–	–	–	–	–	–	Ars-sur-Moselle	–
23	[ER]	MAN 2023.0.166	158	(72)	(17)	–	–	(0.24)	–	Ludres	–

SYSTEMATIC PALEONTOLOGY

Class CEPHALOPODA Cuvier, 1795
Order BELEMNITIDA Haeckel, 1866
Suborder BELEMNITINA Zittel, 1895
Family MEGATEUTHIDIDAE Sachs & Nalnjaeva, 1967

Genus *Lotharingibelus* n. gen.

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TYPE SPECIES. — *Belemnites meta* Blainville, 1827 (synonym of *Belemnites brevis* var. C Blainville, 1827).

ETYMOLOGY. — Named after Lotharingia, a medieval kingdom comprising present-day Lorraine (France), Luxembourg, Saarland (Germany), Netherlands, most of Belgium, and Germany west of the Rhine, and corresponding roughly to the main geographic distribution of the taxa herein included.

INCLUDED SPECIES. — *Belemnites meta* Blainville, 1827; *Belemnites subgiganteus* Branco, 1879.

OCCURRENCE. — Late Toarcian (Dispansum to Aalensis zones) of NE France (Lorraine), Luxembourg, SE Belgium (Gaume), Northern Germany.

DIAGNOSIS. — Megateuthidid possessing a conical to cylindroconical orthorostrum with a short and obtuse apical part, and a small cavity on the tip of the apex. Apical grooves absent; a shallow dorsolateral depression on each flank. Alveolus deeply penetrating and eccentric. Alveolar angle 28-32°. Epirostrum rudimentary or well-developed.

REMARKS

The taxa included herein in *Lotharingibelus* n. gen. have been attributed in the past to the genera *Dactyloteuthis* Bayle, 1878, *Arcobelus* Sachs *in* Sachs & Nalnjaeva, 1967, *Brevibelus* Doyle, 1991 (synonym of *Brachybelus* Naef, 1922), *Homaloteuthis* Stolley, 1919, *Megateuthis* Lissajous, 1915, and *Mesoteuthis* Lissajous, 1915. *Lotharingibelus* n. gen. is distinguished from the similarly shaped *Dactyloteuthis* by its more conical profile, the deeper penetrating alveolus and the absence of apical grooves on the orthorostrum. It is distinguished from the Boreal-Arctic genus *Arcobelus* by the presence of epirostral development and a lower alveolar angle. The genus *Megateuthis* (synonym of *Mesoteuthis*) differs from *Lotharingibelus* n. gen. by the presence of two dorsolateral apical grooves and a shallower alveolus. The coeval genus *Brevibelus* is distinguished from *Lotharingibelus* n. gen. by the shorter and more slender, cylindrical rostrum, a typically mucronate apex and the absence of an epirostral development.

Lotharingibelus meta (Blainville, 1827) n. comb.
(Figs 3A-E; 4A-D)

Belemnites meta [also cited as *Belemnites brevis* var. C] Blainville, 1827: 87, pl. 3, fig. 3. — Deshayes 1830: 131. — d'Orbigny 1846a: pl. 77, figs 8, 9; 1846b: pl. 37, figs 8, 9; 1846c: 566, pl. 77, figs 8, 9; 1855: 357, pl. 77, figs 8, 9. — Giebel 1852: 114. — Hébert 1865: 203. — Benecke 1898: 36, pl. 2, figs 5, 8, 9; 1905: 299. — Schwegler 1938: 473; 1969: 191, fig. 76a, b.

Belemnites meta var. *compressa* – Benecke 1898: 39, pl. 2, figs 6, 6a, 7, 7a (correct identification: *Arcobelus lucilinburhucensis* Weis, 1999).

non Belemnites meta – Janensch 1902: 111, pl. 12, figs 4, 4a. — Werner 1912: 138, pl. 12, figs 5-7 (correct identification: *Dactyloteuthis levidensis* (Simpson, 1855), *fide* Schlegelmilch [1998]).

non Belemnites cf. *meta* – Janensch 1902: 112, pl. 12, figs 3, 3a (correct identification: *Dactyloteuthis levidensis* (Simpson, 1855), *fide* Schlegelmilch [1998]).

Homaloteuthis meta – Bülow-Trummer 1920: 123.

Brachybelus meta – Naef 1922: 241.

Belemnites (?*Homaloteuthis*) *meta* – Ernst 1924: 81; pl. 6, figs 6a, 6b.

Dactyloteuthis meta – Lissajous 1925: 27, 109. — Sturz 1958: 54, pl. 6, fig. 4; pl. 7, fig. 1. — Schirardin 1961: 114.

Dactyloteuthis cf. *meta* – Kolb 1942: 155, pl. 7, figs 8a, 8b.

non Dactyloteuthis aff. *meta* – Nutsubidze 1966: 156, pl. 37, figs 5, 6 (correct identification: *Acrocoelites conoideus* (Oppel, 1856) *fide* Dzyuba *et al.* [2015]).

non Acrocoelites (*Toarcibelus*) *meta* – Riegraf *et al.* 1984: 154, fig. 48g (correct identification: *Acrocoelites levidensis* (Simpson, 1855)).

Brevibelus cf. *gingensis* – Doyle 1992: 63, pl. 24, fig. 6.

Catateuthis meta – Riegraf 1995: 32.

Arcobelus meta – Schlegelmilch 1998: 68, pl. 11, fig. 5. — Riegraf *et al.* 1998: 66, 211. — Weis 1999: 220, fig. 36. — Neige *et al.* 2021: appendix S3 (taxonomical dataset).

Arcobelus lucilinburhucensis Weis, 1999: 221, fig. 35 (compressed variety).

Type material and locus typicum. — **Lectotype. France** • Paris Basin, surroundings of Nancy, designated by Hébert (1865) as 'type' of the species; UCBL-EM 75009 (Deshayes coll.) (Fig. 3A).

Additional material. — **France** • 1 specimen; Paris Basin, Meurthe-et-Moselle, Lay-Saint-Christophe near Nancy; "Aalénien" (nowadays upper Toarcian); MAN 2023.0.168 (Fig. 3B) • 1 specimen; Paris Basin, Meurthe-et-Moselle, Moulins, Bouxières-aux-Chênes; "Aalénien (zone du minerai)" (= upper Toarcian); MAN 2023.0.165 (Fig. 4B). **Belgium** • 125 specimens; Paris Basin, Halanzy and Musson, Mont-Saint-Martin Formation, old mining heaps; upper Toarcian; Dominique Delsate leg.; MNHNL DOU989a-h (Figs 3D, E; 4C-E). **Luxembourg** • 1 specimen; Paris Basin, Esch-sur-Alzette; ironstones; upper Toarcian; MNHNL DOU882 (Fig. 3C) • 1 specimen, Paris Basin, Differdange; Mactra subzone, Aalensis Zone; MNHNL DOT500 (Fig. 4A).

Occurrence. — Upper Toarcian. Dispansum Zone (common): Luxembourg; Gaume, Belgium; Lorraine, France. — Dispansum Zone (very rare): Dehmen, Northern Germany; Blea Wyke Point, North Yorkshire, United Kingdom; ?Mistelgau, Franconia, Southern Germany (Kolb 1942). — Pseudoradiosa and Aalensis (Mactra subzone) zones (occasionally present): Luxembourg; Gaume, Belgium; Lorraine, France.

Description

Medium-sized, stout, conical rostrum (elongation index between 0.7 and 1; Table 2). The profile is ventrally asymmetrical, conical. The outline is symmetrical and cylindriconical. Orthorostrum without grooves. Cross section elliptical, strongly compressed (compression index between 1.12 and 1.26; Table 2). Apical region smooth, sometimes with shallow dorsolateral depressions that extend laterally towards the rostrum cavum. The tip of the apical region shows often a looser calcification resulting in a navel-shaped cavity, which is indicative of a very short epirostral stage. The flanks are more or less flattened. The alveolus occupies approximately two third of the rostrum and is ventrally displaced. The apical line is weakly goniolineate. Alveolar angle 29-32°.

Remarks

Lotharingibelus meta n. comb. is distinguished from the taxa assigned to *Dactyloteuthis* by its more conical profile, the deeply penetrating alveolus and the absence of a ventral apical groove. '*Dactyloteuthis*' *crossotela* (Blake *in* Tate & Blake, 1876) from the United Kingdom is a slightly younger species, that bears some resemblance with *L. meta* n. comb. (see also Doyle 1992); it is however distinguished from the latter by its more cylindrical profile and the presence of an epirostrum. Further investigation of the type material of *D. crossotela* is needed to investigate the question whether *D. crossotela* could represent an early taxon of *Lotharingibelus* n. gen. rather than *Dactyloteuthis*. *Lotharingibelus meta* n. comb. is chiefly distinguished from *L. subgigantea* by the presence of a well-developed epirostrum and a more conical orthorostrum in the latter.

Taxonomic history

In his monograph on the belemnites, Blainville (1827) established *Belemnites brevis* and distinguished three varieties, A, B, and C; for the latter, he proposed conditionally the name *Belemnites meta*. According to Article 15.1 of the ICZN (1999), "A new name or nomenclatural act proposed conditionally and published before 1961 may be available". Thus, the valid name for variety C of *Belemnites brevis* is *Belemnites meta*. This nominal species-group taxon was based on syntypes: a single specimen of the Deshayes collection from the "Oolithe ferrugineuse" (Minette ironstones) from the surroundings of Nancy (Meurthe-et-Moselle; Fig. 1), and an unspecified number of specimens from the d'Orbigny collection from the vicinity of L'Aiguillon-la-Presqu'île, Vendée department, in the Pays de la Loire region in Western France. Deshayes (1830) considered that "pour éviter toute méprise, nous conservons le nom de *Belemnites brevis* à la variété C". He thus designated as (lecto)type for *Belemnites brevis* the specimen of var. C figured in Blainville (1827: pl. 3, figs 3, 3a) and thus *B. brevis* and *B. meta* would have the same type and would become synonyms. However, this nomenclatural act is to be considered invalid, because Blainville (1827) introducing the name *B. meta* for var. C, restricted the syntypes of *B. brevis* to the specimens included in his varieties A and B. The nomenclatural act by Deshayes (1830) of chosing as lectotype for *B. brevis* a specimen attributed by Blainville (1827) to another species-group taxon (*B. meta*), corresponds to the proviso of Art. 74.2 of the ICZN (1999): "Lectotype found not to have been a syntype. If it is demonstrated that

Fig. 3. — *Lotharingibelus meta* (Blainville, 1827) n. comb.: **A**, lectotype, "Oolithe ferrugineuse", upper Toarcian, from the surroundings of Nancy, Lorraine, France, UCBL-EM 75009; **A1**, lateral view; **A2**, ventral view; **B**, (sub)adult, complete specimen, "Aalénien" (= upper Toarcian) of Lay-Saint Christophe, Lorraine, France, MAN 2023.0.168; **B1**, lateral view; **B2**, ventral view; **B3**, cross section at alveolus; **C**, incomplete adult specimen, alveolar part only partially preserved, Minette formation, upper Toarcian, Esch-sur-Alzette, Luxembourg, MNHNL DOU882; **C1**, lateral view; **C2**, ventral view; **D**, longitudinal section of an adult specimen, Mont-Saint-Martin Formation, upper Toarcian, old mining heaps of Halanzy-Musson, Gaume, Belgium, MNHNL DOU989a; **E**, longitudinal section of an adult specimen, Mont-Saint-Martin Formation, upper Toarcian, old mining heaps of Halanzy-Musson, Gaume, Belgium, MNHNL DOU989b. Scale bars: 1 cm. Photos: Paul Braun (MNHNL).

a specimen designated as a lectotype was not a syntype, it loses its status of lectotype". This issue was solved by Hébert (1865), who recognized the three varieties of Blainville (1827) as distinct species and indicated as (lecto)type for *B. meta* the specimen of var. C figured in Blainville (1827).

The generic attribution of *Belemnites meta* has varied. Earlier authors (Bülow-Trummer 1920; Naef 1922) attributed it to *Homaloteuthis*, or to *Brachybelus* (synonym of *Brevibelus*). Lissajous (1925) was the first to attribute it to the genus *Dactyloteuthis* due to its stout rostrum and blunt

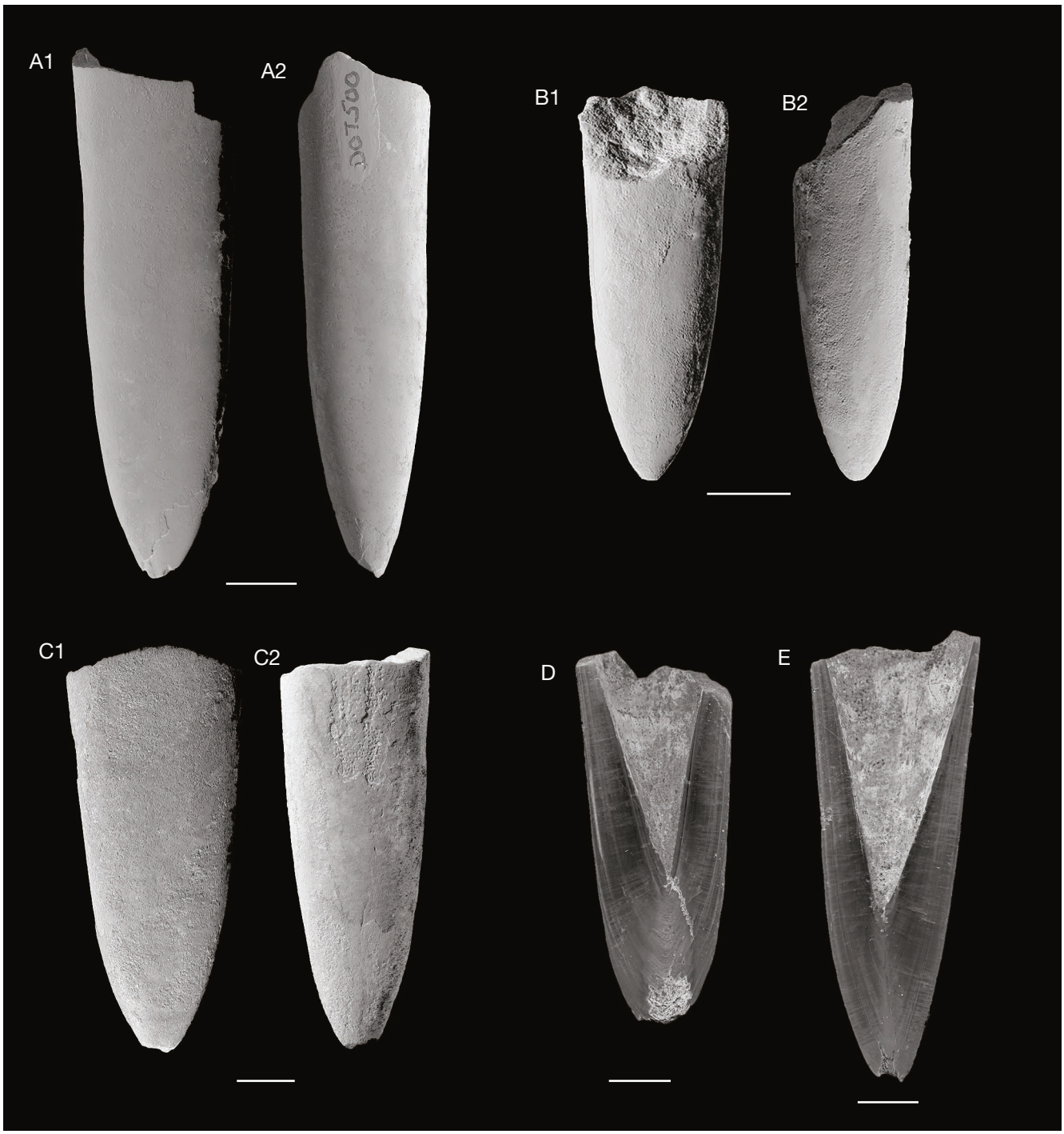

Fig. 4. — *Lotharingibelus meta* (Blainville, 1827) n. comb.: **A**, particularly elongated adult specimen, "base du calcaire supérieur", Minette formation, Aalensis Zone, upper Toarcian of Differdange, MNHNL DOT500; **A1**, lateral view; **A2**, ventral view; **B**, subadult, complete specimen, "Aalénien, zone du minerai" (upper Toarcian) of Moulins nearby Bouxières-aux-Dames, Lorraine, France, MAN 2023.0.165; **B1**, lateral view; **B2**, ventral view; **C**, stout adult specimen, Mont-Saint-Martin Formation..., upper Toarcian, old mining heaps of Halanzy-Musson, Gaume, Belgium, MNHNL DOU989d; **C1**, lateral view; **C2**, ventral view; **D**, longitudinal section of an adult specimen, Mont-Saint-Martin Formation, upper Toarcian, old mining heaps of Halanzy-Musson, Gaume, Belgium, MNHNL DOU989f; **E**: longitudinal section of a subadult specimen, Mont-Saint-Martin Formation, upper Toarcian, Halanzy-Musson, Gaume, Belgium, MNHNL DOU989g. Scale bars: 1 cm. Photos: Paul Braun (MNHNL).

apex. This attribution was followed by Kolb (1942) and Sturz (1958). Schlegelmilch (1998) instead attributed it to the genus *Arcobelus sensu* Doyle, 1994, previously known only from northern Siberia and the Russian Far East (Sachs & Nalnjaeva 1970). The latter attribution was maintained by Weis (1999) and Neige *et al.* (2021).

FIG. 5. — *Lotharingibelus subgiganteus* (Branco, 1879) n. comb.: **A**, neotype designated herein with fully developed epirostrum, upper Toarcian, Pseudoradiosa Zone, Minette formation, "couche grise" of Kiemerchen, Oberkorn, Luxembourg, MNHNL TO265; **A1**, lateral view; **A2**, ventral view; **B**, adult specimen with not yet fully developed epirostrum, upper Toarcian, Pseudoradiosa Zone, Minette formation, "couche grise" of Kiemerchen, Oberkorn, Luxembourg, MNHNL DOT511a; **B1**, lateral view; **B2**, ventral view; **C**, longitudinal section, upper Toarcian, Minette formation of Thil, Lorraine, France, MNHNL DOT505a. Scale bars: 1 cm. Photos: Paul Braun (MNHNL).

Lotharingibelus subgiganteus (Branco, 1879) n. comb.
(Figs 5A-C; 6A-E)

Belemnites subgiganteus Branco, 1879: 101, pl. 6, figs 2, 2a-e. — de Roebe 1881: 549. — Benecke 1905: 292, pl. 27, figs 1-4. — Hof 1994: pl. 2, fig. 3 (specimen to the right).

Belemnites sp. – Benecke 1898: 48-49, pl. 4, figs 10-13 (orthorostra).

Mesoteuthis subgiganteus – Schirardin 1961: 115.

Megateuthis subgigantea – Riegraf 1995: 54. — Weis 1999: 232, figs 11, 39-40. — Neige *et al.* 2021: Appendix S3 (taxonomical dataset).

Dactyloteuthis crossotela (Blake) – Weis 1999: 219, figs 33-34 (orthorostra).

TYPE MATERIAL. — **Neotype. Luxembourg** • Paris Basin, Differdange, Oberkorn, Kiemerchen; 49°30'16"N, 5°53'07"E; "couche grise" (Pseudoradiosa Zone); upper Toarcian; MNHNL TO265 (Fig. 5A).

ADDITIONAL MATERIAL. — **France** • 3 specimens; Paris Basin, Meurthe-et-Moselle, Thil; upper Toarcian; MNHNL DOT505a, DOT505b, DOT505c (Fig. 5C) • 1 specimen (with epirostrum); Paris Basin, Meurthe-et-Moselle, south of Nancy, Ludres; upper Toarcian; MAN 2023.0.166 (Fig. 6A) • 1 specimen (orthorostrum); Paris Basin, Meurthe-et-Moselle, Maxéville near Nancy; upper Toarcian; MAN 2023.0.163 (Fig. 6C).
Luxembourg • 2 specimens; Paris Basin, Differdange, Oberkorn, Kiemerchen; "couche grise"; Pseudoradiosa Zone, upper Toarcian; MNHNL DOT511a, DOT511b (Figs 5B; 6E) • 1 specimen (orthorostrum); Paris Basin, Niederkorn; upper Toarcian; MNHNL DOU997 • 1 specimen (orthorostrum); Paris Basin, Rumelange; "couche grise"; upper Toarcian; MNHNL LG101 (Fig. 6B) • 4 specimens (with epirostrum); Paris Basin, Esch-sur-Alzette; "couche noire"; upper Toarcian; MNHNL DOU514, DOU559a-c • 1 specimen (orthorostrum); Paris Basin, Differdange; upper Toarcian; MNHNL DOT470 (Fig. 6D) • 1 specimen (with incomplete epirostrum); Paris Basin, Differdange; "base du calcaire supérieur" (Mactra subzone); upper Toarcian; MNHNL DOT499.

TYPE HORIZON. — "Couche grise de Differdange", Minette ironstone formation (Pseudoradiosa Zone) (Maubeuge 1947; Di Cencio & Weis 2020).

TYPE LOCALITY. — Luxembourg, Paris Basin, Differdange, Oberkorn, Kiemerchen, a former mining site, nowadays a protected area (Weis 2022).

OCCURRENCE. — Paris Basin (France, Luxembourg, and Belgium), upper Toarcian (Dispansum Zone to Mactra subzone, Aalensis Zone).

DESCRIPTION

Large to very large sized, elongate-conical rostrum with epirostral development. The profile and the outline of the orthorostrum are symmetrical and conical. The profile of the epirostrum is slightly asymmetrical, conical to cylindriconical, its outline is symmetrical and cylindriconical. The apex of the orthorostrum is striated but bears no grooves. The epirostrum bears two long and incised dorsolateral grooves and several, irregular dorsal and ventral striae. The cross section is elliptical, compressed (compression index between 1.16 and 1.24; Table 2). The alveolus occupies one third to one fifth of the total rostrum length and one half of the sole orthostrum length. The alveolus is slightly displaced towards the venter. The apical line is goniolineate. Alveolar angle 28-30°.

REMARKS

Branco (1879) reported the species from his "Oberregion der Schichten mit Trigonia navis", currently uppermost Toarcian, Pseudoradiosa Zone (Maubeuge 1947; Di Cencio & Weis 2020) from three localities: Ars, St.-Quentin near Metz, and Villerupt. The type material (syntypes) described by Branco (1879), originally housed in the collections of the Geologische Landessammlung von Elsass-Lothringen in Strasbourg, was destroyed in a fire in 1967 (Jean-Claude Gall, pers. comm. 1998) and has to be considered as definitely lost (Kévin Janneau, pers. comm. 2022). We herein select as the neotype specimen MNHNL TO265 from the "Couche grise de Differdange" of the Minette ironstone formation in the Kiemerchen section (southwest of Oberkorn, Luxembourg) (Fig. 5A). This locality, a former mining site, nowadays a protected area (Weis 2022), is situated 4 km away from the town of Villerupt and is located in the same geological sub-basin of Differdange-Longwy (Fig. 1); the neotype is from the same geological horizon and formation of the syntypes. The designation of a neotype is considered necessary in order to clarify the taxonomic status of *Belemnites subgiganteus* and in particular its differential characters in respect to *Belemnites meta*.

L. subgiganteus n. comb. bears some resemblance with the epirostrum-bearing specimens of *Dactyloteuthis crossotela*. However, the orthorostrum of *L. subgiganteus* n. comb. differs from that of *D. crossotela* by the stronger conical profile of the former. Moreover, the epirostrum of *L. subgiganteus* n. comb. bears two strongly incised dorsolateral grooves. Due to this feature, *L. subgiganteus* n. comb. has been formerly attributed to the genus *Megateuthis*. However, *L. subgiganteus* n. comb. differs from *Megateuthis* by the shape and features of its orthorostrum, which bears no grooves. The similarity of the orthorostra of *L. meta* n. comb. and *L. subgiganteus* n. comb. demonstrates their close affinities and their inclusion into a single genus.

A POSSIBLE SEXUAL DIMORPHISM IN *LOTHARINGIBELUS* N. GEN.

Belemnites are supposed to show some degree of sexual dimorphism given that dimorphic traits are well documented in other cephalopods, such as ammonites and living coleoids (Davis *et al.* 1996; Wilkin 2022). An example of a possible sexual dimorphism in belemnites has been described by Doyle (1985) from the Toarcian of Yorkshire. In that case the presence of an epirostrum has been interpreted as a sexual adaptation. This idea had already been advanced by earlier workers (d'Orbigny 1842-1851; Lissajous 1925). Schlegelmilch (1998) comments that it is "tempting to interpret these results as a sexual dimorphism but not necessarily so" and suggests studying further potentially dimorphic pairs, such as *Dactyloteuthis similis* and *D. semistriata.* Stevens *et al.* (2017) studied in detail the Cretaceous epirostrum-bearing belemnite *Neohibolites minimus* (Miller, 1826) (see also Spaeth 1971) and concluded that the interpretation of the epirostrum as a sexually selected character remains plausible. In a recent paper about the anatomy of the giant belemnite genus *Megateuthis*, Klug *et al.* (2024) conclude that "there is no hard evidence for sexual dimorphism in belemnites yet. Concerning the two large forms *Megateuthis suevica* and *M. elliptica*, their widely overlapping occurrence and their similar morphologies are remarkable. Such species pairs evoke the question for sexual dimorphism, which has been discussed for belemnites a few times […]".

On the other hand, dimorphism in belemnites could also have been expressed in other ways than solely by differences in rostrum size and shape. For example, biometric methods

Fig. 6. — *Lotharingibelus subgiganteus* (Branco, 1879) n. comb.: **A**, specimen with epirostrum, "Aalénien" (=upper Toarcian) of Ludres, Lorraine, France, MAN 2023.0166; **A1**, lateral view; **A2**, ventral view; **B**, orthostrum without epirostrum, "couche grise", Minette formation, upper Toarcian of Rumelange-Langengrund, Luxembourg, MNHNL LG101; **B1**, lateral view; **B2**, ventral view; **C**, adult orthorostrum without epirostrum, "Aalénien, zone du minerai" (= upper Toarcian) of Maxéville, Lorraine, France, MAN 2023.0.163; **C1**, lateral view; **C2**, ventral view; **D**, orthorostrum with traces of broken epirostrum, Minette formation, upper Toarcian of Differdange, Luxembourg, MNHNL DOT470; **E**, longitudinal cut of an orthorostrum with traces of the broken epirostrum, "couche grise", Minette formation, Pseudoradiosa Zone, upper Toarcian of Oberkorn-Kiemerchen, MNHNL DOT511b. Scale bars: 1 cm. Photos: Paul Braun (MNHNL).

were used by Delattre (1956) in Toarcian *Odontobelus* Naef, 1922 and Ippolitov (2006) in Middle and Late Jurassic *Hibolithes* Montfort, 1808, in which the epirostrum is seldom present (e.g., *H. duperroni* Combémorel, 1988). Geochemical methods were used by McArthur *et al.* (2007), who showed significant differences within two types of rostra attributed to a single species. In Recent squids, Arkhipkin *et al.* (2015) evidenced an elongate structure, the "tail", which facilitates

TABLE 3. — Overview on some dimorphic belemnite pairs described in the literature. Abbreviations: **OR**, orthorostrum; **ER**, epirostrum-bearing specimen.

Epirostrum-bearing taxa	Taxa with orthorostrum only	Stratigraphic distribution	References
Cuspiteuthis tubularis (Young & Bird, 1822)	*Cuspiteuthis simpsoni* (Mayer-Eymar, 1883)	lower Toarcian	Doyle (1985, 1992)
Dactyloteuthis similis (von Seebach, 1864)	*Dactyloteuthis semistriata* (Münster, 1830)	upper Toarcian	Schlegelmilch (1998: 18)
Dactyloteuthis ventricosa (Quenstedt, 1848)	*Dactyloteuthis digitalis* (Blainville, 1827)	lower Toarcian (Bifrons Zone) to upper Toarcian (Levesquei Zone)	Doyle (1992)
Dactyloteuthis crossotela (Blake *in* Tate & Blake, 1876) [ER]	*Dactyloteuthis crossotela* (Blake *in* Tate & Blake, 1876) [OR]	lower Toarcian (Bifrons Zone) to upper Toarcian (Variabilis Zone)	Doyle (1992)
Pleurobelus compressus (Stahl, 1824)	*Pleurobelus* aff. *compressus* (Stahl, 1824)	upper Pliensbachian	Pinard *et al.* (2014)
Pleurobelus subirregularis (Lissajous, 1927)	*Pleurobelus lagenaeformis* (Hartmann in von Zieten, 1832)	upper Pliensbachian	Pinard *et al.* (2014)
Calabribelus tetramerus (Eudes-Deslongchamps, 1878)	*Calabribelus tetramerus* (Eudes-Deslongchamps, 1878)	lower Bajocian	Weis *et al.* (2017)
Megateuthis glaber (Simpson, 1855)	*Megateuthis rhenana* (Oppel, 1856)	lower Toarcian (Bifrons Zone, Fibulatum subzone) to upper Toarcian (Levesquei Zone)	Doyle (1992)

the development of a more mobile adult phase in these coleoids; by analogy, the elongate epirostrum in extinct coleoids like the belemnites could have played a similar role. However, in some groups like *Onykia* spp., the elongation of the body occurs within both males and females, but in other groups, *Lycoteuthis* Pfeffer, 1900 for instance, it occurs only amongst males. The dimorphic vs. adaptive nature of the epirostrum remains therefore still a question open to debate (see also Bandel & Spaeth 1988; Stevens *et al.* 2017). Another hypothesis was advanced based on well preserved soft-part belemnites from the German Posidonia shale; one specimen shows an enlarged (> 5 mm) hook (mega-onychites) at the base of the arm crown which was interpreted as sexual dimorphism (Hauff 1985; Schlegelmilch 1998; Wilkin 2022). This hypothesis has been discarded by some workers (Riegraf 1996), who argued that in recent coleoids large hooks would occur in both the females and the males. Opposed to this view, Stevens (2010) reported that in modern squids large hooks are developed during maturity and that their presence in males only hints at a reproductive rather predatory function, so it seems likely that fossil mega-hooks fulfilled a similar role. It is important, however, to note that such mega-hooks are known only in Jurassic belemnites (Klug *et al.* 2024).

Regarding *Lotharingibelus meta* n. comb. and *L. subgiganteus* n. comb., we are undoubtedly in presence of a "dimorphic pair" similar to the one identified by Doyle (1985) for the genus *Youngibelus* (synonym of *Cuspiteuthis*). Similar pairs have since then been identified in Early and early Middle Jurassic belemnites (Pliensbachian to Bajocian) (Table 3). In none of those pairs was a sexual dimorphism proven, though the possibility cannot be ruled out. In the case of *Lotharingibelus* n. gen., it can further be noted that the ratio of rostra of *L. meta* n. comb. to *L. subgiganteus* n. comb. is *c.* 10 to 1. These data are based on the rostra that are currently present in public collections and need to be taken with great care as it is likely that there is a collection bias. For *Cuspiteuthis*, Doyle (1985) gave ratios of 1.1 and 1.2 for two localities. Given the data at hand, it is therefore difficult to draw a conclusion about the sexual dimorphism in *Lotharingibelus* n. gen. Further studies on the "dimorphic pairs" known so far (Table 3) are needed to corroborate the hypothesis of sexual dimorphism, either linked with the development of an epirostrum or reflected by differences in size and form of the rostrum (Ippolitov 2006).

Acknowledgements
We would like to express our gratitude to Paul Braun (MnhnL) and Emmanuel Robert (UCBL-EM) for their assistance with the photography. Thibaut Keinerknecht and Aurélie Braxenthaler (MAN Nancy) provided valuable assistance with the loan of collection material. RW thanks Jean-Claude Gall, emeritus professor, and Kévin Janneau, collection manager at the Jardin des Sciences (Université de Strasbourg), for information on the historical collections of Strasbourg. Simon Philippo (MnhnL) and Domenico Mannetta (Sapienza University) prepared the longitudinal sections. We are grateful to the referees, Dr Oksana Dzyuba and Prof. Pascal Neige, who contributed to enhance the manuscript with their constructive remarks.

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Submitted on 31 December 2024;
accepted on 10 March 2025;
published on 18 December 2025.