

TAXONOMICAL DIVERSITY AND PALAEOBIOGEOGRAPHICAL AFFINITY OF BELEMNITES FROM THE PLIENSBACHIAN–TOARCICAN GSSP (LUSITANIAN BASIN, PORTUGAL)

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Typescript received 25 May 2020; accepted in revised form 26 August 2020

Abstract: High-resolution analysis of the late Pliensbachian – early Toarcian belemnite assemblages from the Peniche section (Lusitanian Basin) has enabled, for the first time, recognition of eight taxa of the suborder Belemnitina, previously reported from contemporaneous north-west Tethyan and Arctic sections. The presence of *Bairistowius amaliae* sp. nov. in the late Pliensbachian (*emaciatum* Zone) represents a novelty given that hitherto the genus *Bairistowius* was known only from late Sinemurian and early Pliensbachian deposits. Additionally, the replacement of *Bairistowius amaliae* by *Catateuthis longiforma*, during the latest Pliensbachian, suggests an evolutionary relationship between the two taxa. This relationship suggests a new scenario for the subsequent development of endemic Toarcian Boreal–Arctic faunas, characterized by the occurrence of *Catateuthis*. Comparison of the Peniche belemnite fauna with coeval faunas from the Mediterranean/Submediterranean and Euro-Boreal domains indicates taxonomic uniformity during the late

Pliensbachian and early Toarcian (*emaciatum* and *polymorphum* Zones), in the north-west Tethys. Despite the lack of a marked taxonomic turnover, the Pliensbachian–Toarcian boundary corresponds to a slight decrease in diversity observed not only in the Lusitanian Basin but also in coeval north-western European basins. Ordination and cluster analyses indicate that the largest changes in belemnite diversity and palaeogeographical distribution occurred rather during the Toarcian Oceanic Anoxic Event (base of the *levisoni* Zone). This event is marked by the extinction of taxa, affecting more severely the Mediterranean/Submediterranean domain and resulting in a more pronounced provincial differentiation among north-western European and Arctic belemnite faunas.

Key words: belemnite, diversity, palaeobiogeography, Pliensbachian–Toarcian boundary, Toarcian Oceanic Anoxic Event, Lusitanian Basin.

BELEMNITES are coleoid cephalopods that originated in the Late Triassic (Iba *et al.* 2012), rapidly radiated in the Early Jurassic and subsequently played a key role in marine ecosystems (Weis & Delsate 2006; Dera *et al.* 2016; Hoffmann & Stevens 2019). The Pliensbachian–Toarcian interval (Early Jurassic) is considered a major bottleneck in belemnite early evolutionary history (Dera *et al.* 2016), probably related to major palaeoenvironmental and palaeogeographical changes during the Toarcian. However, the study of belemnite diversity during this time-interval has been hampered by a variety of factors, including the poor stratigraphic representation of the Pliensbachian–Toarcian boundary in many European sections (Morard

et al. 2003; Pinard *et al.* 2014), and the lack of high-resolution (ammonoid subzone) analysis of the belemnite assemblages in particular localities (Choffat 1880; Riegraf 1980; Mousterde *et al.* 1983; Schlegelmilch 1998). Additionally, many studies on Toarcian belemnites are focused on the Euro-Boreal basins (Riegraf *et al.* 1984; Doyle 1990, 1992; Little 1995; Schlegelmilch 1998; Morten & Twitchett 2009; Caswell & Coe 2014; Xu *et al.* 2018), whereas little is known from the Mediterranean/Submediterranean domain (Lissajous 1927; Combémorrel in Rulleau *et al.* 1998; Sanders *et al.* 2015; Weis *et al.* 2015). Therefore, palaeobiogeographical patterns, diversification patterns and evolutionary trends of Early Jurassic

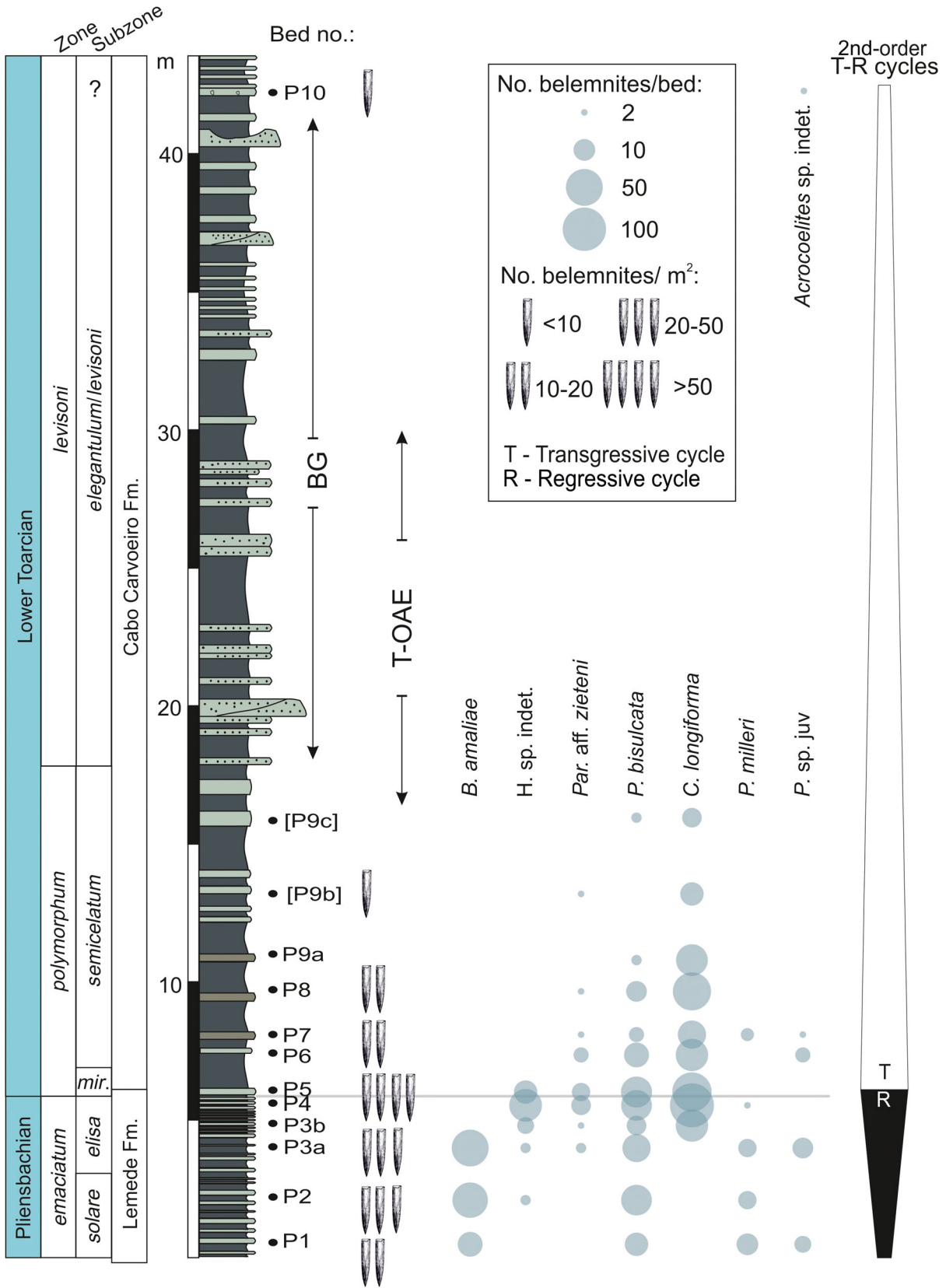


FIG. 1. Stratigraphic distribution and absolute abundance of belemnite species (per bed and per m²) in the Peniche section (Lusitanian Basin, Portugal). Fewer than two occurrences per bed are not represented (see Rita *et al.* 2020, tables S1–S2 for the full dataset). The Pliensbachian–Toarcian boundary event and the Toarcian Oceanic Anoxic Event (T-OAE) are highlighted and were positioned based on Rocha *et al.* (2016) and Duarte *et al.* (2018). Sequence stratigraphy according to Duarte (2007). The bed numbers in square brackets correspond to merged beds due to sample size constraints, regarding the Peniche diversity analysis, and follow Rita *et al.* (2019). Stratigraphic log based on Rita *et al.* (2019). Ammonite zonation and subzonation from Mouterde (1955) and Rocha *et al.* (2016), respectively. Lithostratigraphy from Hesselbo *et al.* (2007). Bed numbers from Rita *et al.* (2019). *Abbreviations:* BG, belemnite gap; *elisa*, *elisa/hawskerense* Subzone; *mir.*, *mirabile/paltum* Subzone; *solare*, *solare/apyrenum* Subzone.

belemnites, in the north-west Tethys, remain poorly constrained and some aspects of their provincialism remain speculative (Doyle 1994).

During the Pliensbachian, the north-west Tethys was characterized by a homogeneous European belemnite fauna (Doyle *et al.* 1994; Weis & Thuy 2015). However, the early Toarcian, characterized by palaeoenvironmental changes and the second-order mass extinction (Toarcian Oceanic Anoxic Event, T-OAE), represents an important period of taxonomic and geographical changes in belemnite assemblages, leading to a Boreal/Tethyan provincialism (Doyle 1994; Dera *et al.* 2016). In the Euro-Boreal basins, belemnites recovered and experienced a radiation during the middle–late Toarcian (Dera *et al.* 2016), despite the effects of the T-OAE during the early Toarcian, which caused a reduction in belemnite abundance (Caswell & Coe 2014). The belemnite stratigraphic record in the Mediterranean/Submediterranean domain basins (Italy, Portugal and Morocco) displays a severe reduction in belemnite abundance, or total absence of belemnites, during the T-OAE (latest *polymorphum* – early *levisoni* Zones; Sanders *et al.* 2015; Weis *et al.* 2015; Ait-Itto *et al.* 2017; Rita *et al.* 2019). Moreover, the Toarcian marks the beginning of the endemism of Arctic faunas, probably related to northward migrations of north-west Tethyan groups (Doyle 1987; Doyle *et al.* 1994), which survived regionally during the early Toarcian crisis, and their rapid evolution into new endemic genera (Sachs & Nalnjaeva 1975; Meledina *et al.* 2005; Dzyuba *et al.* 2015).

In this study we present for the first time a detailed systematic description of the Lusitanian Basin belemnite fauna from the late Pliensbachian to the early Toarcian, and a diversity analysis. This study is based on a high-resolution stratigraphic analysis of more than 900 specimens collected in the Toarcian GSSP Peniche section. The excellent outcrop conditions, and the abundant belemnite fauna of the Peniche section, enable, on the one hand, a detailed analysis of intraspecific and ontogenetic variation of belemnite taxa in individual samples and, on the other hand, a high-resolution (subzone) study of the belemnite diversity during the late Pliensbachian and early Toarcian. The diversity analysis

of the Iberian margin belemnite fauna allows, for the first time, a comparison of diversity patterns at an ammonite zone and subzone scale across the Mediterranean/Submediterranean and Euro-Boreal domains. This comparative approach permits an assessment of the impact of the Pliensbachian–Toarcian crisis on belemnite diversity and a better understanding of the palaeobiogeographical belemnite dynamics during the Early Jurassic of the north-west Tethys.

GEOLOGICAL SETTING

The Peniche section corresponds to the Toarcian GSSP (Rocha *et al.* 2016) and it is well constrained in terms of ammonite zonation (Duarte & Soares 2002; Duarte *et al.* 2018). It is located in the Lusitanian Basin, a Mesozoic sedimentary basin developed in the Iberian Western Margin during the North Atlantic Ocean and Occidental Tethyan opening, as a consequence of the Pangea fragmentation (Thierry *et al.* 2000; Kullberg *et al.* 2013). The first sedimentary cycle (Wilson *et al.* 1989) corresponds to extension and rifting episodes and occurred during the Late Triassic – Middle Jurassic (Callovia). It led to the deposition, among others, of a marly limestone succession related to the large opening of the carbonate ramp to the marine environment (Duarte & Soares 2002; Azerêdo *et al.* 2003; Azerêdo *et al.* 2014).

The studied section corresponds to a marly limestone succession, 45 m thick, assigned to the upper Pliensbachian – lower Toarcian interval, corresponding to an outer ramp environment in an epicontinental sea (Duarte & Soares 2002; Duarte 2007; Duarte *et al.* 2018; Fig. 1). The end of the Pliensbachian, represented by the Lemedo Formation, corresponds to an alternation of decimetric marly limestones and centimetric marls, 11.2 m thick. The next *c.* 11 m of the succession, belonging to the Toarcian (*polymorphum* Zone), corresponds to the first member of the Cabo Carvoeiro Formation (CC1) and consists of an alternation of bioturbated marls, with marly limestones (Fig. 1). The majority of this member is highly fossiliferous, containing, among others, belemnites, pyritized ammonites, brachiopods and bivalves (Duarte &

	Euro-Boreal		Submediterranean/ Mediterranean		T-OAE
	Zones	Subzones	Zones	Subzones	
Early Toarcian	<i>falciferum/serpentinum</i>	<i>falciferum</i>	<i>levisoni</i>	<i>falciferum</i>	
		<i>exaratum</i>		<i>elegantulum/levisoni</i>	
	<i>tenuicostatum</i>	<i>Semicelatum tenuicostatum Clevendicum</i>	<i>polymorphum</i>	<i>semicelatum</i>	
		<i>paltum</i>		<i>mirabile/paltum</i>	
Late Pliensb.	<i>spinatum</i>	<i>hawskerense</i>	<i>emaciatum</i>	<i>elisa/hawskerense</i>	
		<i>apyrenum</i>		<i>solare/apyrenum</i>	

FIG. 2. Ammonite biostratigraphical scheme adopted in this paper (partially after Cecca & Macchioni 2004 and Duarte *et al.* 2018) correlating the Euro-Boreal and Mediterranean/Submediterranean domains at both the zone and subzone levels. The position of the Toarcian Oceanic Anoxic Event (T-OAE) follows McArthur *et al.* (2020).

Soares 2002). The upper 25 m of the studied succession belongs to the second member of the Cabo Carvoeiro Formation (CC2, *levisoni* Zone; Fig. 1). This part of the succession is represented by siliciclastic-rich marls, interbedded with sandy marly limestones and rare carbonated sandstones and microconglomerates, clearly associated with turbiditic deposition (see Wright & Wilson 1984; Duarte 1997). For that reason, the occurrence of benthic macrofauna in these horizons is rare (some horizons with brachiopods), and both benthic and planktonic organisms become scarcer upwards in the sedimentary succession (Comas-Rengifo *et al.* 2015; Rita *et al.* 2016; Correia *et al.* 2017). Ammonites occur in the whole CC2 member. The *levisoni* Zone corresponds to a barren interval for belemnites (Rita *et al.* 2019), except for one single horizon, where 11 poorly preserved specimens were found (only two specimens could be identified to the genus level; Fig. 1). This level is not well-defined biostratigraphically at the subzone scale, but recent strontium isotopic data on belemnites and brachiopods seem to indicate the uppermost *exaratum* Subzone (= *elegantulum/levisoni*; McArthur *et al.* 2020) rather than the base of the *falciferum* Subzone. This means that belemnites are missing for almost an entire subzone in the Peniche section.

Figure 2 summarizes the ammonoid zones and subzones covered by the present study and how they correlate with biostratigraphical schemes from coeval oceanic domains. As indicated in Figure 1, in the *solare/apyrenum* Subzone, beds P1 and P2 were sampled; in the *elisa/*

hawskerense Subzone, beds P3a, P3b and P4 were sampled; in the *mirabile/paltum* Subzone, bed P5 was sampled; in the *semicelatum* Subzone, beds P6, P7, P8, P9a, P9b and P9c were sampled; and in the *elegantulum/levisoni* Subzone, bed 10 was sampled.

MATERIAL AND METHOD

Systematics

A total of 931 specimens were collected from 13 beds from upper Pliensbachian to lower Toarcian sediments (*emaciatum–levisoni* ammonite zones: *c.* 2.7 Ma according to Ogg *et al.* 2016; Fig. 1; Rita *et al.* 2020, tables S1–S2).

We focused on quantitatively collecting belemnites from well-exposed bedding planes. The belemnite rostra were collected by (1) sampling all specimens in 14 1 m² areas; and (2) collecting at least 30 complete specimens (with at least the alveolus preserved) in the remaining bed area, i.e. outside of the quadrats, when possible. This first sampling method allowed the calculation of absolute abundance, considering both fragmented and complete specimens. The whole dataset, regardless of the sampling method, was used for the taxonomic and diversity analyses and for the calculation of the relative abundance of taxa.

Prior to identification, the collected specimens were mechanically prepared with a sand blaster and an air scribe. The photographed specimens were coated with heated ammonium chloride powder. Belemnite species identification was based on the analysis of traditional features, such as shape (outline and profile) and the presence of grooves in the apical region. The transverse section, the depth of penetration of the phragmocone and the apical line were observed on micro-computed tomography (μ CT) using our in-house μ CT phoenix v|tome|x s 240 (Research Edition) scanner (Rita *et al.* 2019, 2020, table S3) but also in longitudinally cut and polished specimens. All these features were afterwards compared with published descriptions and figures (Riegraf *et al.* 1984; Doyle 1990, 1992; Schlegelmilch 1998; Pinard *et al.* 2014; Sanders *et al.* 2015; Weis *et al.* 2018). This method allowed us to recognize the features of each ontogenetic stage, due to the observation of epirostra and growth lines. It was possible to distinguish between adult (ephebic–gerontic *sensu* Doyle 1990), neanic (*sensu* Doyle 1990) and juvenile (nepionic *sensu* Doyle 1990) specimens.

Systematic descriptions include size measurements of well-preserved specimens, taking into account the following metrics: total preserved length (L); length of the rostrum solidum (apical length, l); alveolar angle (AA); dorsoventral diameter (Dv), lateral diameter (Dl) at the

protoconch level; cross-sectional distance from protoconch to ventral side (Rv) or to dorsal side (Rd); and width (W) and height (H) at the aperture level (Fig. 3), following the terminology of Doyle (1990) and Dera *et al.* (2016). A total of 277 specimens were CT-scanned to allow the acquisition of all the metrics, given that the alveolus was filled with sediment. In addition, 654 specimens were measured with a digital calliper. The rostrum shape was assessed by calculating the robustness (L/H), compression (Dv/Dl) and elongation (Dv/l) indices. The robustness index (Rob.) discriminates stocky (*c.* 2), robust (*c.* 2–*c.* 10), or slender specimens (>10). The compression index (CI) indicates the general shape of the alveolar aperture and/or cross-sections. The calculated values may be lower than, equal to or greater than 1, and refer to depressed, regular, or compressed shapes, respectively. The elongation index (EI) discriminates elongated (higher values) from short forms (lower values). The eccentricity ($E = Rd - Rv/Dv \cdot 100\%$) of the protoconch indicates if the protoconch is deviated towards the ventral or to the dorsal side of the rostrum.

The size categories used in systematic descriptions were previously defined by Weis *et al.* (2018) and refer to the maximum total preserved length of the rostrum (L) of the adult specimens (when ontogenetic stages were possible to identify) as follows: very small (<30 mm), small (30–60 mm), medium (61–100 mm) and large (101–150 mm; Fig. 4).

Diversity analysis

For the diversity analysis of the Peniche data the species richness (no. species; S), rarefied species richness (sample size-based rarefaction) and Shannon–Wiener index (Shannon & Weaver 1949) were calculated. The data were analysed at the bed scale but, due to sample size constraints (e.g. poor outcrop conditions), the data from beds P9b

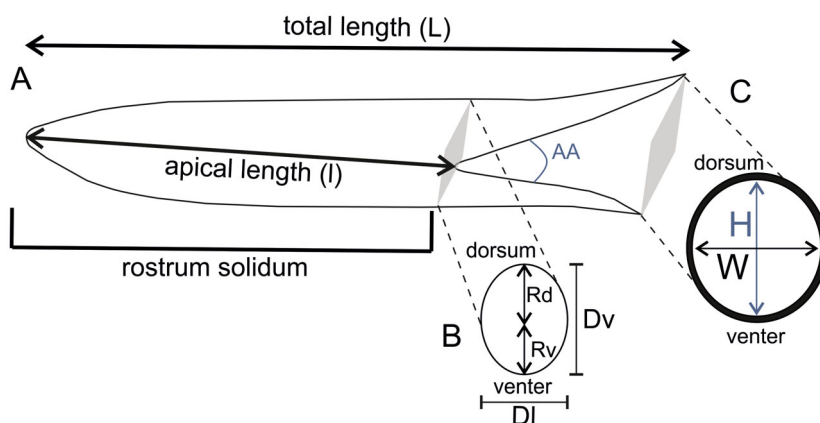
and P9c were merged. Sample P10 was not considered for the rarefied species richness because only two specimens were able to be identified at the genus level. Rarefied species richness was calculated using the function *rarefy* from the *vegan* package (Oksanen *et al.* 2018) in R (R Core Team 2018), which corrects for the sample size by using a subsampling method. Shannon–Wiener diversity index was calculated with the function *diversity*. *Passaloteuthis* sp. juv. was not included in this analysis due to the presence of *P. milleri* and *P. bisulcata* in the levels where it is represented. Hastitidae sp. indet. and *Acrocoelites* sp. indet. were included in the analysis.

In order to compare belemnite diversity of the Lusitanian Basin with coeval Tethyan basins, ammonite zone and subzone scales were used. When abundance data were not available to allow rarefied species richness to be calculated, presence/absence data were used and raw species diversity S was calculated.

Belemnite fauna from Peniche were compared with data from: (1) Asturian Basin (Rodiles section, northern Spain; authors' prelim. data, 209 specimens; Rita *et al.* 2020, table S4); (2) Western Paris Basin (Fresney-le-Puceux and Feugueroles-sur-Orne sections, Normandy, France; Weis *et al.* 2018 and supplemented with authors' unpub. abundance data; Rita *et al.* 2020, table S5); (3) Cleveland Basin (UK; Doyle 1990; Caswell & Coe 2014; Rita *et al.* 2020, table S6); (4) Swabo-Franconian Basin (Germany; Schlegelmilch 1998; Riegraf *et al.* 1984; Rita *et al.* 2020, table S6); (5) Causses Basin (Tournadous section, southern France; Pinard *et al.* 2014 and supplemented with authors' unpub. abundance data; Rita *et al.* 2020, table S6); and (6) South Riffian Basin (Morocco; Sanders *et al.* 2015; Fig. 5). It should be noted that only specimens classified to the species level (except for Hastitidae indet. in Lusitanian and Asturian basins) were included in the diversity analysis and only ammonite zones with 20 or more specimens were considered.

The published data on the belemnite assemblages from the Swabo-Franconian Basin (Schlegelmilch 1998; Riegraf

FIG. 3. Longitudinal view (A) and transverse cross-section of a belemnite at the protoconch (B) and aperture (C) levels of a belemnite rostrum, with the measured parameters indicated: alveolar angle (AA), dorsoventral diameter (Dv), lateral diameter (Dl), height (H), apical length (l), total preserved length (L), cross-sectional distance from protoconch to ventral side (Rv) and cross-sectional distance from protoconch to dorsal side (Rd) and width (W).



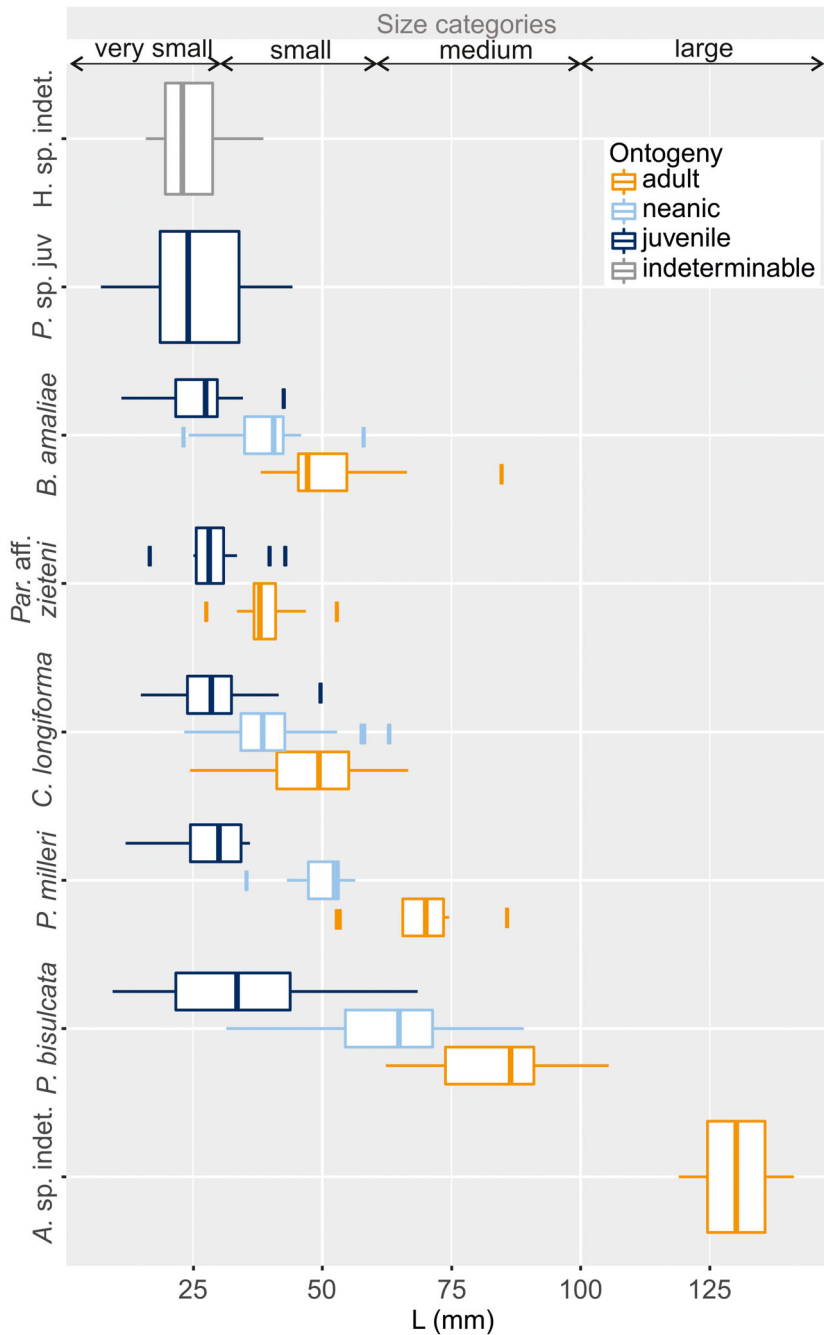


FIG. 4. Box and whisker plot indicating the size categories of the different belemnite taxa comprising the late Pliensbachian – early Toarcian fauna from Peniche with emphasis on the ontogeny. The box indicates the upper and lower quartiles and the median of the total length (L) of the rostra. The whiskers indicate the maximum and minimum of the distribution.

et al. 1984) at the zone and subzone level do not include highly resolved abundance data. Additionally, South Riffian Basin data (Morocco; Sanders *et al.* 2015) are limited to the *polymorphum* Zone (lower Toarcian). Therefore, presence/absence data were used to perform the non-metric multidimensional scaling (nMDS) based on Bray–Curtis distances and cluster analyses, in order to allow a comparison between all the north-west Tethyan belemnite faunas described as hitherto belonging to the late Pliensbachian – early Toarcian (*emaciatum*–*levisoni* zones) interval. Analysis of similarities (ANOSIM) was used to

determine whether the different clusters identified in the nMDS analysis differed significantly (Heaven & Scrosati 2008). This was done using the function `anosim` from the `vegan` package (Oksanen *et al.* 2018) in R (R Core Team 2018).

In this study, we considered the Lusitanian and South Riffian basins as part of the Mediterranean/Submediterranean domain and the remaining studied basins (Cleveland, Asturian, Causses and Swabo-Franconian) as part of the Euro-Boreal domain, except for Russia (northern Siberia and Russian Far East), which is included in the

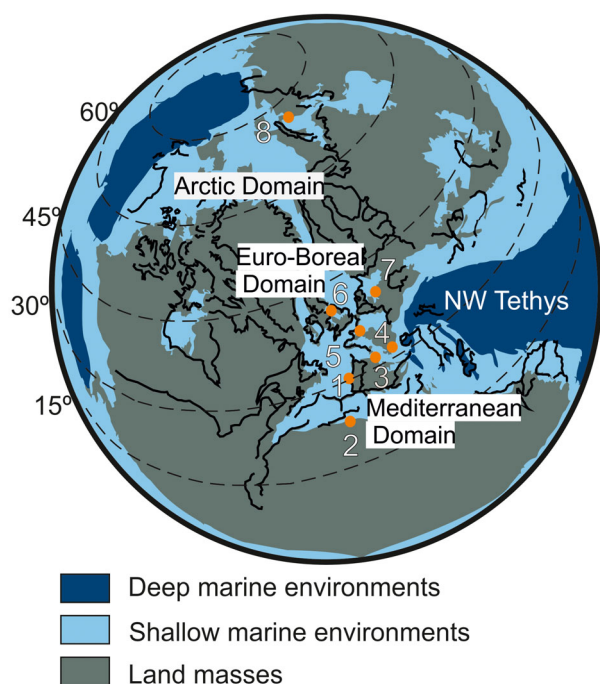


FIG. 5. Palaeogeographical context of the north-western Tethyan and Arctic domains. Palaeogeography based on Paleoglobe image for the Toarcian, 180 Ma (Scotese & Dreher 2012). The studied areas are: 1, Lusitanian Basin (Portugal); 2, South Riffian Basin (Morocco); 3, Asturian Basin (northern Spain); 4, Causses Basin (southern France); 5, Western Paris Basin (Normandy, France); 6, Cleveland Basin (UK); 7, Swabo-Franconian Basin (Germany); 8, Russia (northern Siberia and Russia Far East).

Arctic domain (mainly following Dera *et al.* 2011; see also Page 2008; McArthur *et al.* 2020 for alternative approaches).

Institutional abbreviation. MCUC, Museu da Ciência da Universidade de Coimbra.

SYSTEMATIC PALAEOLOGY

The belemnite classification used herein follows previous studies on Early Jurassic belemnites (Riegraf *et al.* 1984; Doyle 1990, 1992; Schlegelmilch 1998; Pinard *et al.* 2014; Sanders *et al.* 2015; Weis *et al.* 2015, 2018). Terminology follows Doyle & Kelly (1988) as well as Doyle (1990), and the synonymy lists follow Matthews (1973). The studied material will be deposited in MCUC 2018.10 collection of the Museu da Ciência da Universidade of Coimbra (Portugal). The synonymy lists follow the recommendations by Matthews (1973).

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

Type genus. *Hastites* Mayer-Eymar, 1883.

Other included genera. *Bairstowius* Jeletzky in Doyle *et al.*, 1994; *Parahastites* Nalnjaeva, 1968; *Rhabdobelus* Naef, 1922; *Sachsibelus* Gustomesov, 1966; *Subhastites* Gustomesov, 1977.

Occurrence. Lower – Middle Jurassic, ?Hettangian or Sinemurian–Bajocian of Europe, Turkey and northern Russia.

Remarks. Some authors applied an enlarged family concept, including other genera with double lateral lines and hastate earlier ontogenetic stages such as *Pleurobelus* (Jeletzky 1966; Doyle *et al.* 1994; Pinard *et al.* 2014), *Gastrobilus* (Doyle *et al.* 1994; Doyle 2010) and *Pseudohastites* (Riegraf *et al.* 1998; Schlegelmilch 1998) in the Hastitidae family. Further work is needed in order to disentangle the phylogenetic relationships between these genera, commonly included into Passaloteuthididae and Hastitidae s.s.

Genus BAIRSTOWIUS Jeletzky in Doyle *et al.*, 1994

Type species. *Belemnites junceus* Phillips, 1867.

Remarks. The genus *Bairstowius* was originally included in Hastitidae family rather than Passaloteuthididae, based on the ‘*Hastites*-like pattern of lateral furrows, its compressed rostrum, and absence of apical grooves’ (Doyle *et al.* 1994, p. 12). Subsequent publications (Doyle 1994, 2003, 2010; Riegraf *et al.* 1998, ‘Subhastitidae’; Schlegelmilch 1998) maintained this classification without further discussion. Further morphological analysis as demonstrated by Bolton (1982) and hereafter (Peniche) call for a slight emendation of the original diagnosis. In fact, short dorsolateral apical grooves are commonly developed in both *Bairstowius longissimus* (Bolton 1982) and *B. amaliae*, although they always remain weak, compared with Passaloteuthididae. The presence of weakly developed dorsolateral grooves in some individuals can be interpreted as an atavistic character, given that *Bairstowius* is commonly considered the phylogenetical link between passaloteuthidids and hastitids (Schwegler 1962; Schumann 1974; Bolton 1982). The development of an epirostrum has been noted by Bolton (1982) and it is confirmed by our material. Epirostra are not known for the genera *Subhastites*, *Hastites*, *Rhabdobelus*, *Parahastites* or *Sachsibelus* but are commonly developed in *Pleurobelus*, a genus included into Hastitidae by some authors (Jeletzky 1966; Doyle 1994; Pinard *et al.* 2014). However, according to Doyle (1990, p. 14), the presence or absence of an epirostrum cannot be considered as a valuable taxonomic criterion for differentiation of genera. Consequently, the presence/absence of an epirostrum is not considered here a diagnostic character retained at the genus level.

Occurrence. Upper Sinemurian – upper Pliensbachian of England, France, Germany, Italy and Portugal.

Bairstowius amaliae sp. nov.

Figure 6A–I

LSID. urn:lsid:zoobank.org:act:3DA0AB3C-F8FB-40BE-8D17-681F7B28FE96

Derivation of name. Amália Rodrigues (1920–1999) was a famous Portuguese *Fado* singer considered to be one of the most significant ambassadors of the Portuguese culture and language around the world.

Type material. Specimen MCUC 2018.10.887 (bed P2; Fig. 6F) is hereby designated as the holotype. Paratypes: MCUC

2018.10.931, MCUC 2018.10.914, MCUC 2018.10.722, MCUC 2018.10.911, MCUC 2018.10.843, MCUC 2018.10.819, MCUC 2018.10.809 and MCUC 2018.10.700.

Additional material. 98 specimens from Lemedé Fm. (upper Pliensbachian, *emaciatum* Zone, *solare/apyrenum–elisa/hawskerense* Subzones, beds P1–P3a; Fig. 1).

Diagnosis. Spicular and elongated rostrum with asymmetrical and hastate profile; and subhastate to cylindrical symmetrical outline. Cross-section compressed, pyriform to quadrate. Grooves are developed as triple lateral lines in ventrolateral, mediolateral and dorsolateral position, respectively; ventrolateral line developed on the stem and alveolar region as a deep groove;

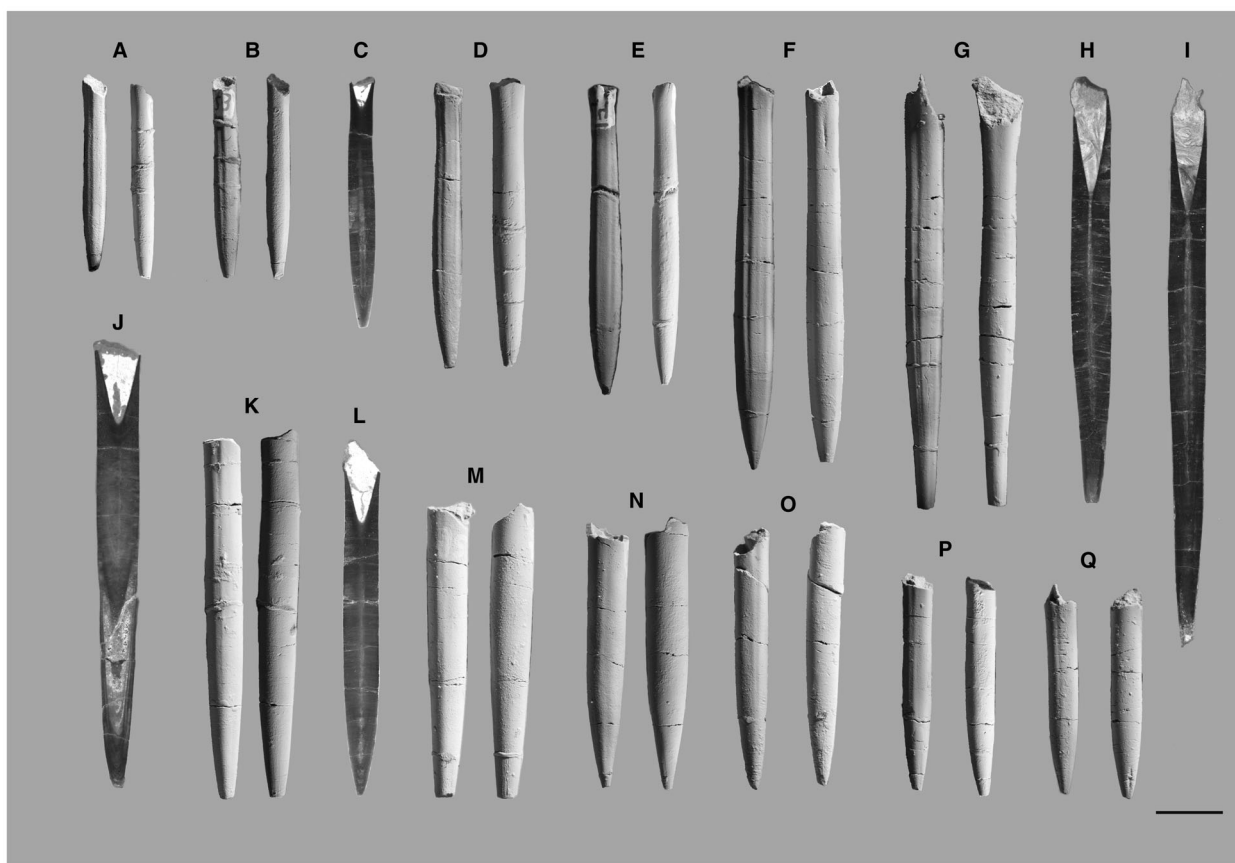


FIG. 6. Late Pliensbachian – early Toarcian belemnites from the Peniche section. A–I, *Bairstowius amaliae*: A, juvenile, specimen MCUC 2018.10.914, bed P1; B, juvenile, specimen MCUC 2018.10.819, bed P2; C, longitudinal cross-section of neanic specimen, MCUC 2018.10.700, bed P3a; D, neanic, specimen MCUC 2018.10.911, bed P1; E, neanic, specimen MCUC 2018.10.722, bed P3a; F, holotype, adult without epirostrum, specimen MCUC 2018.10.887, bed P2; G, adult with epirostrum, specimen MCUC 2018.10.931, bed P1; H, longitudinal cross-section of an adult specimen with epirostrum, specimen MCUC 2018.10.843, bed P2; I, longitudinal cross-section of an adult specimen with epirostrum, specimen MCUC 2018.10.809, bed P2. J–Q, *Catateuthis longiforma*: J, longitudinal cross-section of an adult specimen with epirostrum, specimen MCUC 2018.10.497, bed P4; K, adult with epirostrum, specimen MCUC 2018.10.519, bed P4; L, longitudinal cross-section of an adult specimen without epirostrum, specimen MCUC 2018.10.511, bed P4; M, adult with fragmented epirostrum, specimen MCUC 2018.10.451, bed P4; N, neanic, specimen MCUC 2018.10.217, bed P6; O, neanic, specimen MCUC 2018.10.460, bed P4; P, juvenile, specimen MCUC 2018.10.459, bed P4; Q, juvenile, specimen MCUC 2018.10.501, bed P4. Left side corresponds to lateral view and right side corresponds to ventral or dorsal view. Scale bar represents 1 cm.

mediolateral line weakly developed in the stem region only; dorsolateral line extending from the apical to the stem region, fading out on the alveolar region (Fig. 7). Epirostrum commonly developed and the apical line ortholineate. The alveolus occupies c. one-quarter to one-fifth of the orthorostrum.

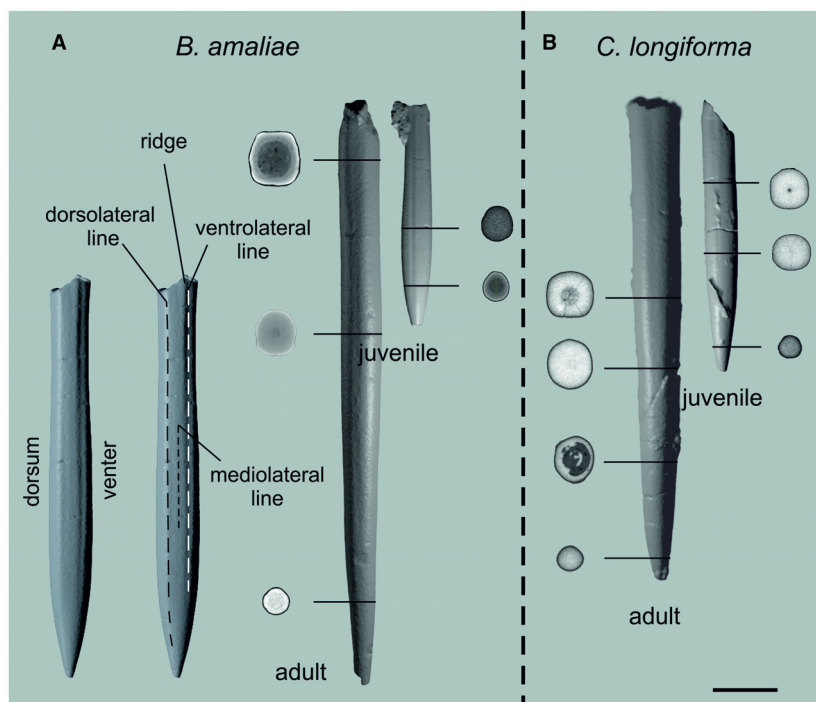
Differential diagnosis. The morphology of *B. amaliae* can be placed between the stouter *Bairstowius charmouthensis* (Mayer 1864) and the more gracile elongate *B. junceus* (Phillips 1867) and *B. longissimus* (Miller 1826). The latter taxa are stratigraphically older than *B. amaliae* (early Pliensbachian, *jamesoni* and *ibex* Zones). *B. junceus* and *B. longissimus* differ by their longer, more elongated rostra, the cylindrical profile and the subcircular cross-section. *B. charmouthensis* is the species that most resembles *B. amaliae* by its hastate to subhastate profile and outline, and its compressed cross-section. However, it differs by the absence of epirostrum and dorsolateral apical grooves, and by a deeper penetration of the alveolus (c. one-third of total rostrum). *B. amaliae* is morphologically and stratigraphically replaced by *Catateuthis longiforma* at the Pliensbachian–Toarcian boundary in the Peniche section. The species *C. longiforma* differs from *B. amaliae* by a cylindrical outline and profile, a more eccentric protoconch, a different pattern of lateral lines (Fig. 7), a stouter (lower Rob.) and less elongated rostrum, and a higher compression of the rostrum (Fig. 8).

Description. The small-to-medium-sized, spicular elongated rostrum shows an asymmetrical hastate profile and a symmetrical subhastate to cylindrical outline. The apex is needle-like and some specimens bear two very weak dorsolateral apical grooves in the continuation of the lateral lines. This is, however, not a stable feature. A pattern of three parallel lateral

lines is observed (Fig. 7A): in a ventrolateral position a deep, broad and well-defined groove can be observed; this main lateral line/groove has a ‘Doppellinien’ pattern. It is separated by a weak ridge from the lesser incised second lateral line, which is developed as a shallow depression only in the stem region, in a mediolateral position. The third lateral line is positioned in a dorsolateral position, extending from the apex to the alveolar region, fading out on the latter (Fig. 7A). The cross-section is compressed, being pyriform in the apical region and quadrate in the stem and alveolar areas (Figs 7A, 9A). The dorsal alveolar area is characterized by a flattening. The phragmocone occupies one-quarter to one-fifth of the orthorostrum. The alveolar angle varies between c. 19° and 23° (Rita et al. 2020, table S7). A cylindrical epirostrum is sometimes developed in the larger specimens (8 specimens out of a total of 107), in combination with an attenuated and striated apex. The cross-section of the epirostrum is subcircular to slightly pyriform. The transition between epirostrum and orthorostrum is extremely gradual from an external point of view and can be readily observed only in longitudinally sectioned specimens (Fig. 6I).

Remarks. Measurements and morphometric parameters can be found in Rita et al. (2020). *Bairstowius amaliae* represents one of the most abundant taxa in the Peniche assemblage during the end of the *emaciatum* Zone (beds P1–P3a). Previously, the genus *Bairstowius* was known only from the uppermost Sinemurian (*raricostatum* Zone) to the lower Pliensbachian (*ibex* Zone; Bolton 1982; Doyle et al. 1994; Schlegelmilch 1998; Doyle 2010; Weis et al. 2015). This new record from Peniche extends the stratigraphic range of this genus towards the upper Pliensbachian (*emaciatum* Zone).

FIG. 7. Comparison of morphological details of two belemnite species from the Peniche section with emphasis on the differences between the transverse cross-section. A, *Bairstowius amaliae* (left, MCUC 2018.10.887; middle, MCUC 2018.10.809; right, MCUC 2018.10.703). B, *Catateuthis longiforma* (left, MCUC 2018.10.497; right, MCUC 2018.10.292). Scale bar represents 1 cm.



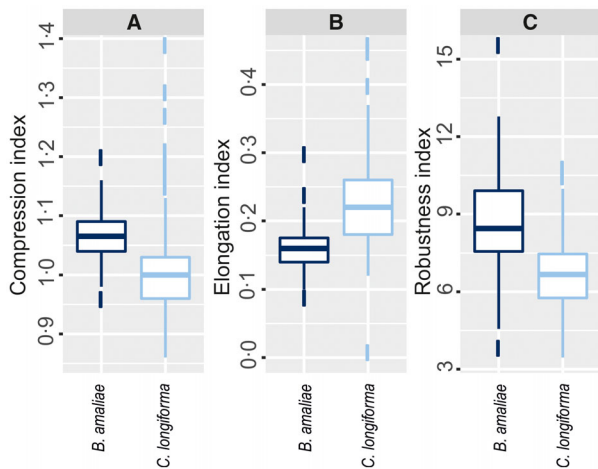


FIG. 8. Box and whisker plots illustrating the morphometric differences between *Catateuthis longiforma* and *Bairstowius amaliae* from the late Pliensbachian to early Toarcian belemnite fauna of Peniche (Lusitanian Basin), with emphasis on the ontogeny. The boxes indicate the upper and lower quartiles of the distribution and the bar in the middle of the boxes indicates the median of the elongation, compression and robustness indices of the rostra. The whiskers indicate the maximum and minimum of the distribution. A, compression index (dorsoventral diameter/lateral diameter). B, elongation index (dorsoventral diameter/rostrum solidum length). C, robustness index (total preserved length/height).

Occurrence. Upper Pliensbachian (*emaciatum* Zone, *solare/apyreum–elisa/hawskerense* Subzones, beds P1–P3a) of Peniche.

Type locality and stratum. Peniche section, Portugal; beds P1–P3a; Lemedo Fm., upper Pliensbachian, *emaciatum* Zone, *solare/apyreum–elisa/hawskerense* Subzones.

Ontogeny. The CI and Rob. increase during ontogeny while the EI decreases (Fig. 9A).

HASTITIDAE indet.

Figure 10G–I

Material. 56 specimens from Lemedo Fm. (upper Pliensbachian, *emaciatum* Zone, *elisa/hawskerense* Subzone, beds P2–P4) and Cabo Carvoeiro Fm. (lower Toarcian, base of *polymorphum* Zone, *mirabile/paltum* Subzone, bed P5; Fig. 1).

Description. The very small to small-sized rostra are characterized by a subhastate to cylindrical profile and outline and an obtuse, smooth apex. Two closely placed, parallel lateral lines ('Doppellinien' *sensu* Stolley 1919) can be recognized in the alveolar region: the lower line, in ventrolateral position, is more strongly expressed than the upper one, and it extends from the alveolar to the apical region. The upper lateral line, in

dorsolateral position, is restricted to the alveolar and stem regions. A third, weakly developed lateral line is sometimes found in the alveolar region. The cross-section is depressed (CI: 0.93–0.85; Rita *et al.* 2020, table S8), varying from circular, in the apical region, to quadrate in the alveolar region. The phragmocone penetrates *c.* one-third to one-quarter of the rostrum. The apical line is ortholineate. The alveolar angle varies between 19° and 25° (Rita *et al.* 2020, table S8).

Remarks. The small size of the rostrum and the poorly developed diagnostic characters could indicate that these specimens represent juveniles of Hastitidae. It is, however, not possible to assign these specimens to a genus with certainty, due to the lack of diagnostic characters. We can exclude the juvenile forms of *Bairstowius amaliae* or *Catateuthis longiforma* because they have a blunt apex. Additionally, the stratigraphic distribution of Hastitidae sp. indet. differs from the range of *B. amaliae* or *C. longiforma* (Fig. 1).

Occurrence. Upper Pliensbachian and lowermost Toarcian of Peniche (*emaciatum–polymorphum* Zones, *elisa/hawskerense–mirabile/paltum* Subzones; beds P1, P2, P3a, P3b, P4 and P5).

Family PASSALOTEUTHIDIDAE Naef, 1922

Type genus. *Passaloteuthis* Lissajous, 1915.

Included genera. *Angeloteuthis* Lang *et al.*, 1928; *Catateuthis* Sachs & Nalnjajeva, 1967; *Coeloteuthis* Lissajous, 1906; *Gastrobelus* Naef, 1922; *Micropassaloteuthis* Riegraf *et al.*, 1984; *Nannobelus* Pavlov, 1914; *Parapassaloteuthis* Riegraf, 1980; *Pleurobelus* Naef, 1922; *Pseudohastites* Naef, 1922; *Schwegleria* Riegraf, 1980.

Occurrence. Lower – Middle Jurassic (Hettangian–Aalenian) of Europe, East Greenland, Russia, South America and North Africa.

Genus CATATEUTHIS Sachs & Nalnjajeva, 1967

Type species. *Catateuthis atrica* Nalnjajeva in Sachs & Nalnjajeva, 1967

Remarks. Doyle (1990, 2003) considered the Boreal–Arctic genus *Catateuthis* as a synonym of *Pseudohastites*, but elsewhere the same author considers this attribution questionable: '...other taxa such as *Passaloteuthis*, *Hastites* and *Catateuthis* (= ? *Pseudohastites*) are recorded much beyond their stratigraphic range in Europe... and retain differences which suggest generic autonomy from their European counterparts' (Doyle 1994, p. 114). We follow here the view of Riegraf *et al.* (1984), Doyle *et al.* (1994), Riegraf *et al.* (1998) and Meledina *et al.* (2005) who considered *Catateuthis* as a valid, independent genus. The genus *Catateuthis* is chiefly distributed in the Boreal–Arctic (Spitsbergen, northern Siberia and Russian Far East) from the lower Toarcian (*antiquum* Zone ? and/

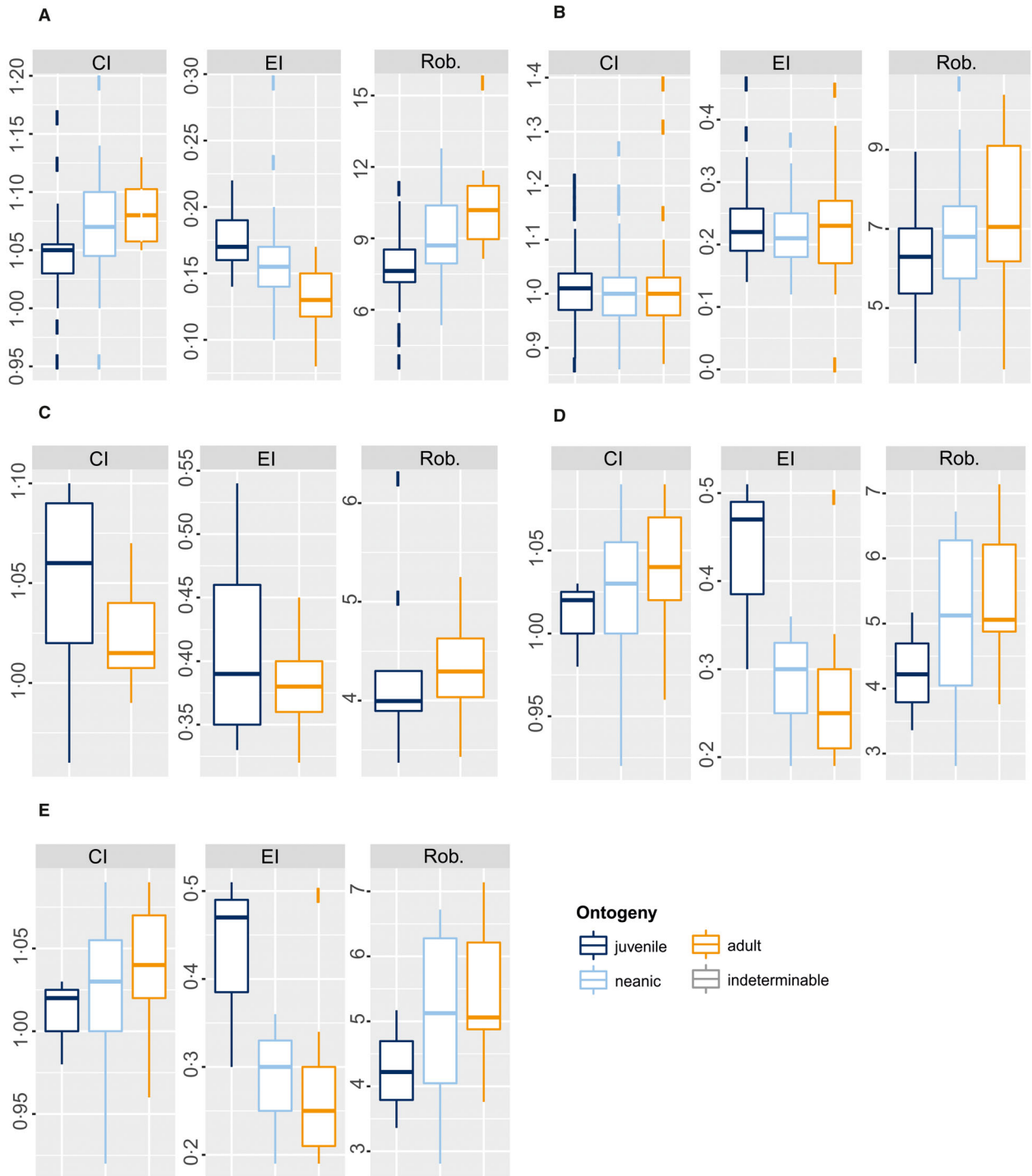


FIG. 9. Box and whisker plot emphasizing the morphometric variation of the late Pliensbachian – early Toarcian belemnite species of Peniche (Lusitanian Basin), according to ontogeny. The boxes indicate the upper and lower quartiles of the distribution and the bar in the middle of the boxes indicates the median value of the elongation index (EI; dorsoventral diameter/rostrum solidum length), compression index (CI; dorsoventral diameter/lateral diameter) and robustness index (Rob.; total preserved length/height) of the rostra. The whiskers indicate the maximum and minimum of the distribution. A, *Bairstowius amaliae*. B, *Catateuthis longiforma*. C, *Parasaloteuthis* aff. *Zieteni*. D, *Passaloteuthis bisulcata*. E, *Passaloteuthis milleri*.

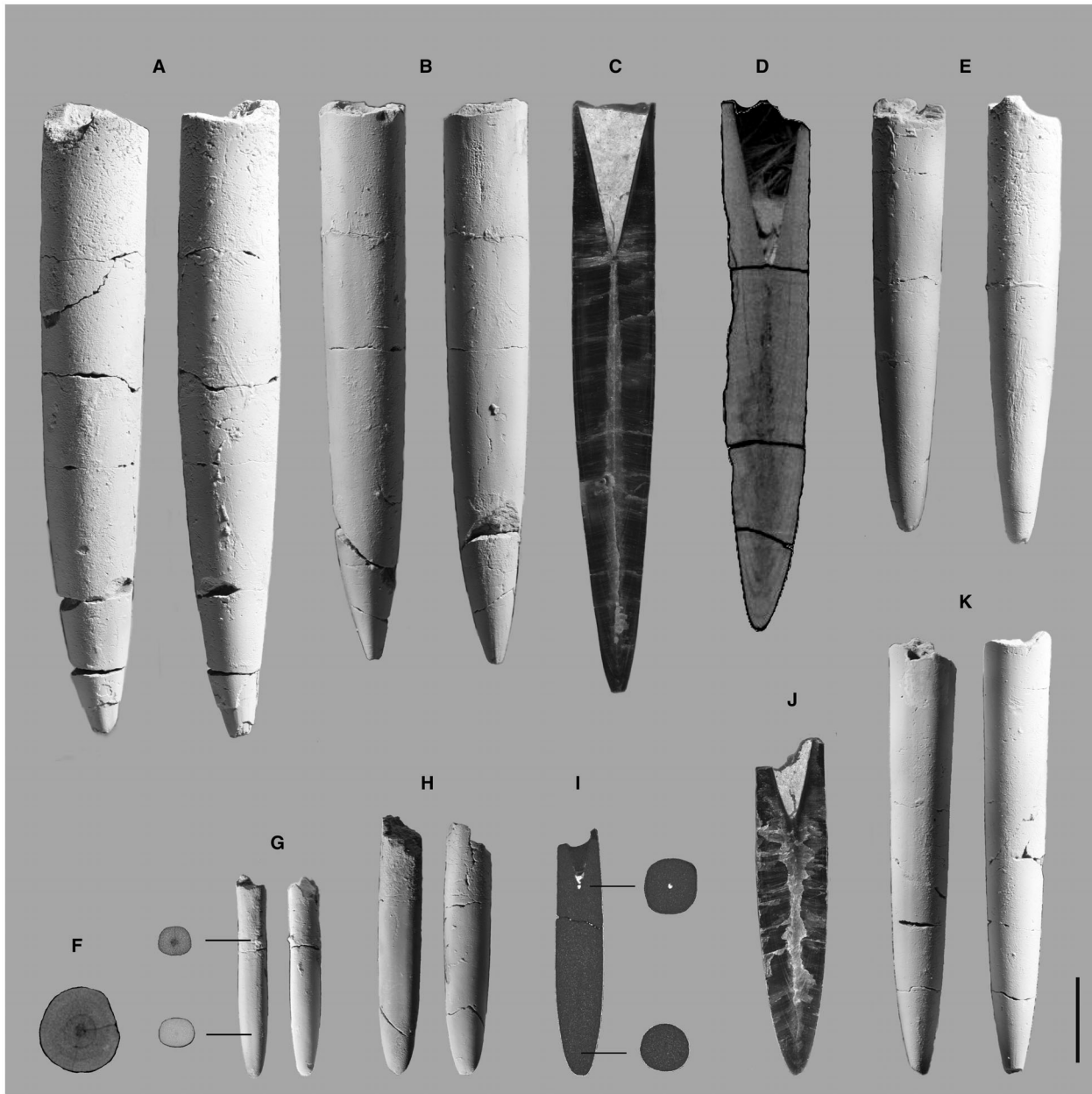


FIG. 10. Late Pliensbachian – early Toarcian belemnites from the Peniche section. A, *Passaloteuthis milleri* (adult, specimen MCUC 2018.10.799, bed P2). B, *P. milleri* (adult, specimen MCUC 2018.10.801, bed P2). C, *P. milleri* (longitudinal cross-section of an adult specimen, specimen MCUC 2018.10.511, bed P4). D, *P. milleri* (longitudinal cross-section of an adult specimen, specimen MCUC 2018.10.898, bed P1). E, *P. milleri* (neanic, specimen MCUC 2018.10.810, bed P2). F, *P. milleri* (transverse cross-section of the stem region of an adult specimen, specimen MCUC 2018.10.898, bed P1). G, Hastitidae sp. indet. (lateral view, ventral/dorsal view and transverse cross-section of the alveolar and apical regions, specimen MCUC 2018.10.277, bed P5). H, Hastitidae sp. indet. (specimen MCUC 2018.10.283, bed P5). I, Hastitidae sp. indet. (lateral view, ventral/dorsal view and transverse cross-section of the alveolar and apical regions, specimen MCUC 2018.10.291, bed P5). J, *P. milleri* (longitudinal cross-section of a neanic specimen, specimen MCUC 2018.10.904, bed P1). K, *P. milleri* (neanic, specimen MCUC 2018.10.811, bed P2). Left side corresponds to lateral view and right side corresponds to ventral or dorsal view. Scale bar represents 1 cm.

or *falciferum* Zone) to the lower Aalenian (Sachs & Naljaeva 1970; Meledina *et al.* 2005). The presence of the Boreal–Arctic species *Catateuthis subinaudita* (Voronets 1962) has also been

reported in the Middle Toarcian (*bifrons* Zone) of southern Germany (Riegraf *et al.* 1984; Schlegelmilch 1998; Dzyuba *et al.* 2015).

Occurrence. Spitsbergen and Russia (northern Siberia and Russian Far East) from the lower Toarcian (Falciferum Zone) to the lower Aalenian. Middle Toarcian (*bifrons* Zone) of southern Germany. Upper Pliensbachian (*margaritatus* Zone) – lower Toarcian (*polymorphum* Zone) of the UK, France (Causse and Normandy), Spain (?), Morocco and Italy.

Catateuthis longiforma comb. nov.

(Blake in Tate & Blake, 1876)

Figure 6J–Q

- 1876 *Belemnites longiformis* Blake, p. 320, pl. 4, fig. 8.
 1990 *Pseudohastites longiformis* (Blake); Doyle, p. 24, pl. 3, figs 5–9 (cum syn.)
 2003 *Bairstowius longiforma* (Blake); Doyle, p. 82.
 2015 *Pseudohastites longiformis* (Blake); Sanders *et al.*, p. 57, fig. 7F, G.
 2015 *Pseudohastites longiformis* (Blake); Weis *et al.*, p. 738, fig. 2 h–m.
 2018 *Pseudohastites longiformis* (Blake); Weis *et al.*, p. 108, fig. 13D.
 2019 *Pseudohastites longiformis* (Blake); Rita *et al.*, suppl. mat., figs S1 B1–B3.

Material. 359 specimens from Lemede Fm. (upper Pliensbachian, *emaciatum* Zone, *elisa/hawskerense* Subzone, beds P3b–P4) and Cabo Carvoeiro Fm. (lower Toarcian, *polymorphum* Zone, *mirabile/paltum*–*semicelatum* Subzones, beds P5–P9c; Fig. 1).

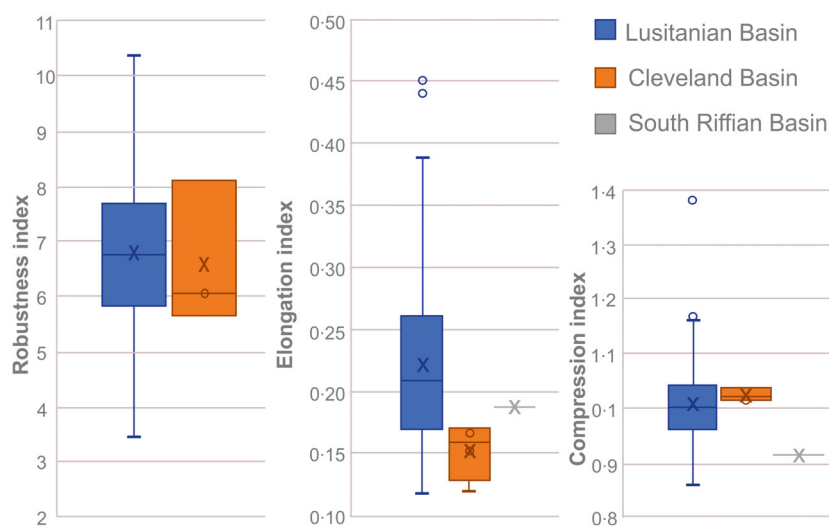
Description. Small to medium-sized slender forms with an acute apex bent towards the dorsal side. The outline is elongated, cylindrical and symmetrical, the profile differing only by its slight asymmetry. The profile can be subhastate, especially in the juvenile forms. Two dorsolateral grooves can be observed: they are short and weakly developed in the juvenile and neanic specimens, but become more pronounced in the adults. A pattern of

two lateral lines is observed. The upper one, located in the dorsolateral area, extends from the stem to the apex with a variable length and is connected to the apical dorsolateral groove. The lower lateral line, located in the ventrolateral area, is better developed in the alveolar region, extending to the stem. Rarely, a dorsal groove in the alveolar region (probably pathological) can be observed. The cross-section is compressed, circular/sub-circular in the apical region and quadrate in the alveolar region (Fig. 7B). A flat area is developed in the dorsal part. The phragmocone occupies one-third to one-quarter of the orthorostrum and the apical line is ortholineate. A depressed section can occur in some individuals (Rita *et al.* 2020, table S9; specimen 2018.10.136). An epirostrum is sometimes developed (47 out of 359 specimens) in larger specimens ($L = 23.4$ – 67.7 mm). The boundary between epirostrum and orthorostrum is visible only in longitudinal section (Fig. 6). The epirostrum is elongated and acute, bearing abundant striae. If the phragmocone is not considered, the solid orthorostrum/epirostrum ratio is 1.82–1.86 (Rita *et al.* 2020, table S9).

Remarks. The specimens from Peniche differ from those described in the literature (Doyle 1990; Sanders *et al.* 2015; Weis *et al.* 2015, 2018) by the occasional development of an epirostrum. Additionally, the specimens described herein are slightly more slender and more elongated than those described by Doyle (1990; Fig. 11). These differences are, however, insufficient to consider these specimens as a new taxon. The single specimen shown in longitudinal section by Doyle (1990, pl. 3, fig. 9) does not show an epirostrum, but its size and ontogenetical development indicate that it might not be a fully grown specimen, and the epirostral development is considered a feature of the later (adult) growth stages (Müller-Stoll 1936; Arkhipkin *et al.* 2015). Peter Doyle (pers. comm. 2019) stated that no epirostra were found within the set of specimens from the Cleveland Basin he analysed.

Taxonomic remark. The genus attribution of *Belemnites longiformis* is revised herein based on the extensive material from Peniche. Doyle (1990) included it in the genus *Pseudohastites*

FIG. 11. Morphometric comparison of the belemnites species *Catateuthis longiforma*, from the Peniche section (Lusitanian Basin), and *Pseudohastites longiformis*, from the Cleveland Basin (Doyle 1990) and South Riffian Basin (Sanders *et al.* 2015). The line in the middle of the boxes indicates the median. The upper and lower limits of the boxes indicate the 75th and the 25th percentiles, respectively. Whiskers indicate the maximum and minimum values of the distribution.



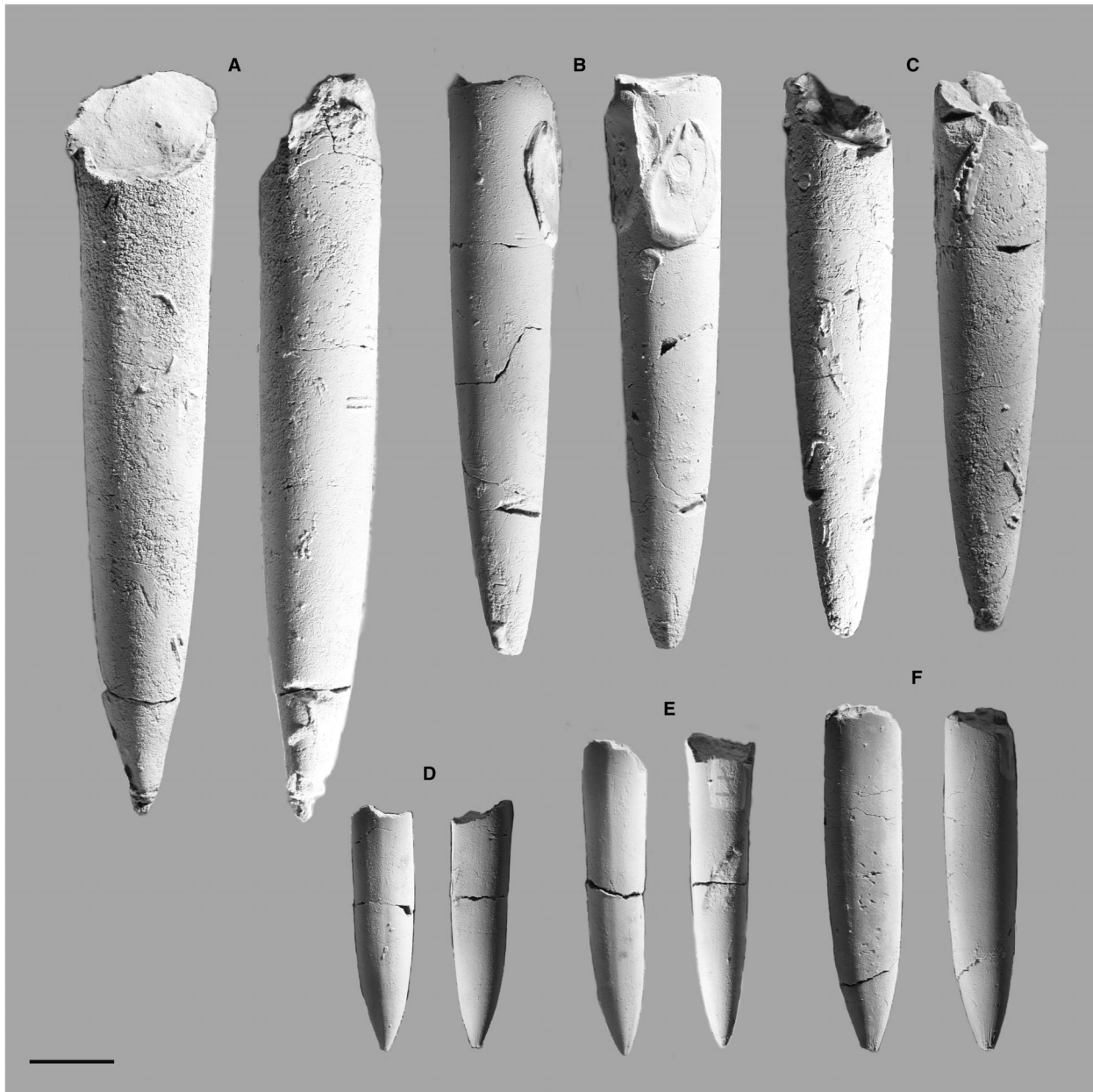


FIG. 12. Late Pliensbachian – early Toarcian belemnites from the Peniche section. A, *Passaloteuthis bisulcata* (adult, specimen MCUC 2018.10.261, bed P5). B, *P. bisulcata* (neanic, specimen MCUC 2018.10.864, bed P2). C, *P. bisulcata* (neanic, specimen MCUC 2018.10.262, bed P5). D, *Parapassaloteuthis* aff. *zieteni* (juvenile, specimen MCUC 2018.10.660, bed P3b). E, *Passaloteuthis* sp. juv. (specimen MCUC 2018.10.893, bed P1). F, *Par.* aff. *zieteni* (adult, specimen MCUC 2018.10.662, bed 3b). Left side corresponds to lateral view and right side corresponds to ventral or dorsal view. Scale bar represents 1 cm.

(type species *Belemnites scabrosus* Simpson, 1866), widely distributed in the lower Pliensbachian of the UK (Doyle 2010). Subsequently, Doyle (2003) referred the species to *Bairstowius*. Schlegelmilch (1998), Riegraf (1995), Sanders *et al.* (2015) and Weis *et al.* (2015) followed the original attribution of Doyle (1990). However, contrary to some of the previously cited works, we herein consider *Catateuthis* as an independent genus and not a subjective synonym of *Pseudohastites* (see remarks above, under ‘Genus *Catateuthis*’), considering the comparison

between the type material and representative species of *Catateuthis* (type: *C. atrica* Sachs & Nalnjajeva, 1967) and *Pseudohastites* (type: *Ps. scabrosus* (Simpson, 1866)); and other species such *Ps. apicicurvatus* (Blainville, 1827) and *Ps. turris* (Simpson, 1866). The species attributed to *Pseudohastites* are confined stratigraphically to the lower Pliensbachian and are characterized by strongly developed dorsolateral apical grooves. On the other side, *Catateuthis* is confined to the Toarcian and lower Aalenian; *C. atrica* and related taxa of *Catateuthis* are characterized by



FIG. 13. Details of a *Parapassaloteuthis* aff. *zietenii* specimen (MCUC 2018.10.155, bed P7, *polymorphum* Zone, *semicelatum* Subzone). The interrupted line indicates an early development of an epirostrum. Scale bar represents 1 cm.

short, and weakly developed dorsolateral apical grooves. The apical line is commonly ortholineate in *Catateuthis* taxa (Sachs & Naljaeva 1970), but goniolineate (eccentricity: 19–23%) in *Ps. apicicurvatus* (Schlegelmilch 1998). Additionally, the ontogeny of *Catateuthis* and *Pseudohastites* differs substantially. The ontogeny of *Ps. apicicurvatus* shows short conical early juvenile stages (Schlegelmilch 1998, pl. 2, fig. 10). Meanwhile, *Catateuthis* taxa have slender, elongated, cylindrical to cylindriconeal early juvenile stages (Sachs & Naljaeva 1970). Considering the morphological similarity of *Belemnites longiformis* with the Toarcian taxa of *Catateuthis* from the Boreal–Arctic domain, we attribute this species to *Catateuthis* rather than to *Pseudohastites*.

Combining the morphological and stratigraphic information from Peniche with literature data, we outline the possibility of a lineage *Bairstowius*–*Catateuthis*, with *Bairstowius amaliae* and *Catateuthis longiformis* as connecting taxa between both genera. This morphological affinity had already been acknowledged by Doyle (2003), who included *Belemnites longiformis* into *Bairstowius* genus.

Occurrence. Upper Pliensbachian – lower Toarcian (*emaciatum*–*polymorphum* Zones, *elisa/hawskerense*–*semicelatum* Subzones) of Peniche. *Catateuthis longiformis* is also present in the upper Pliensbachian and lower Toarcian (*spinatum* = *emaciatum* and *tenuicostatum* = *polymorphum* Zones) of England (Cleveland,

Yorkshire), Germany (Swabia), Luxembourg, France (Normandy), Italy (Central Apennines), Bulgaria, Spain (?) and Morocco (South Riffian Basin).

Ontogeny. The CI slightly decreases during ontogeny while the EI remains constant. Rob. increases with ontogeny (Fig. 9B).

Genus PARAPASSALOTEUTHIS Riegraf, 1980

Type species. *Belemnites zietenii* Mayer-Eymar, 1884, by original designation.

Occurrence. Lower Toarcian (*polymorphum* Zone) of the South Riffian Basin of Morocco, upper Pliensbachian – lowermost Toarcian (*tenuicostatum* = *polymorphum* Zone) of the UK and mainland Europe.

Parapassaloteuthis aff. *zietenii* (Mayer-Eymar, 1884)

Figure 12D, F

aff. 1884 *Belemnites zietenii* Mayer-Eymar, p. 47.

aff. 1990 *Parapassaloteuthis zietenii* (Mayer-Eymar); Doyle, p. 25, pl. 4, figs 2, 3, 5, 7–9 (cum syn.)

aff. 1998 *Parapassaloteuthis zietenii* (Mayer-Eymar); Schlegelmilch, p. 55, pl. 4, figs 8, 9.

non aff. *Parapassaloteuthis* sp. A; Sanders, p. 57, 2015 fig. 8a–i.

Material. 28 specimens from Lemedé Fm. (upper Pliensbachian, *emaciatum* Zone, *elisa/hawskerense* Subzone, beds P3a–P4) and Cabo Carvoeiro Fm. (lower Toarcian, *polymorphum* Zone, *mirabile/paltum*–*semicelatum* Subzones, beds P5–P9b; Fig. 1).

Description. Very small to small rostra with a characteristic short apical region. The profile is asymmetrical and cylindrical-conical, the outline symmetrical, cylindrical to subhastate. The apex is mucronate and bent towards the dorsal side. The development of apical striae is common. Two weakly developed, short dorsolateral grooves are observed. Two lateral lines, represented as shallow depressions, separated by a weak ridge, can be recognized: a medio-dorsolateral line (broader and better developed) and a ventrolateral line (weakly developed). Both extend from the alveolar region to the stem, not reaching the apical region. The cross-section is subcircular to slightly pyriform in the alveolar region and subquadrate in the apical region, due to the lateral depressions. The phragmocone penetrates one-half to one-third of the rostrum and is slightly ventrally displaced. The apical line is goniolineate to slightly cyrtolineate. Alveolar angle varies between *c.* 21° and 24° (Rita et al. 2020, table S10). A small epirostrum can be seen (Fig. 13).

Remarks. Some differences can be established between these specimens and *Parapassaloteuthis zietenii*. In the latter, the

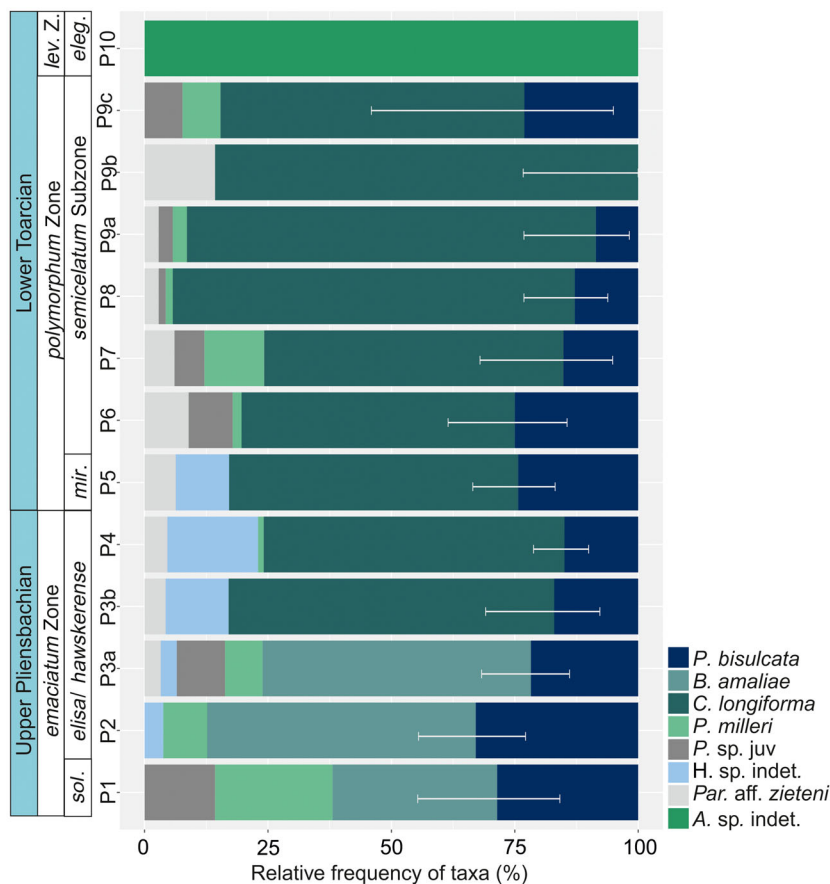


FIG. 14. Relative abundance of belemnite taxa during the late Pliensbachian and early Toarcian in the Peniche section. The error bars correspond to the 95% confidence interval of the relative frequency of the most abundant taxa (*C. longiforma*/*B. amaliae* and *P. bisulcata*). Ammonite zonation and subzonation from Mouterde (1955) and Rocha *et al.* (2016), respectively and bed numbers from Duarte *et al.* (2018). Abbreviations: *eleg.*, *elegantulum/levisoni* Subzone; *lev. Z.*, *levisoni* Zone; *mir.*, *mirabile/paltum* Subzone; *sol.*, *solare/apyrenum* Subzone.

upper lateral line extends from the stem to the apical region and the lower one is developed only in the stem region (not in the apical region). It is also possible to observe a continuity between the upper line and the apical groove. *Par. zietenii* is depressed with a cyrtolineate apical line and an eccentric phragmocone, in contrast to our specimens. Our specimens differ from *Parapassaloteuthis* sp. A from Morocco (South Rifian Basin; see Sanders *et al.* 2015) by the recurved apex and the smaller size.

Occurrence. Upper Pliensbachian – lower Toarcian (*emaciatum*–*polymorphum* zones) of Peniche. The nominal species *Par. zietenii* is known from the uppermost Pliensbachian and lowermost Toarcian of England (Yorkshire), Germany (Swabo-Franconian Basin), Luxembourg and north-east France (Paris Basin), Bulgaria, and Morocco (South Rifian Basin).

Ontogeny. The CI and EI decrease during ontogeny. In contrast, the Rob. of the rostra increases throughout ontogeny (Fig. 9C).

Genus PASSALOTEUTHIS Lissajous, 1915

Type species. *Belemnites bruguierianus* d'Orbigny, 1842.

Occurrence. Lower Toarcian (*polymorphum* Zone) of South Rifian Basin of Morocco. Upper Pliensbachian – lower Toarcian (*tenuicostatum* = *polymorphum* zone) of the UK, mainland Europe and Russia.

Passaloteuthis bisulcata (Blainville, 1827)

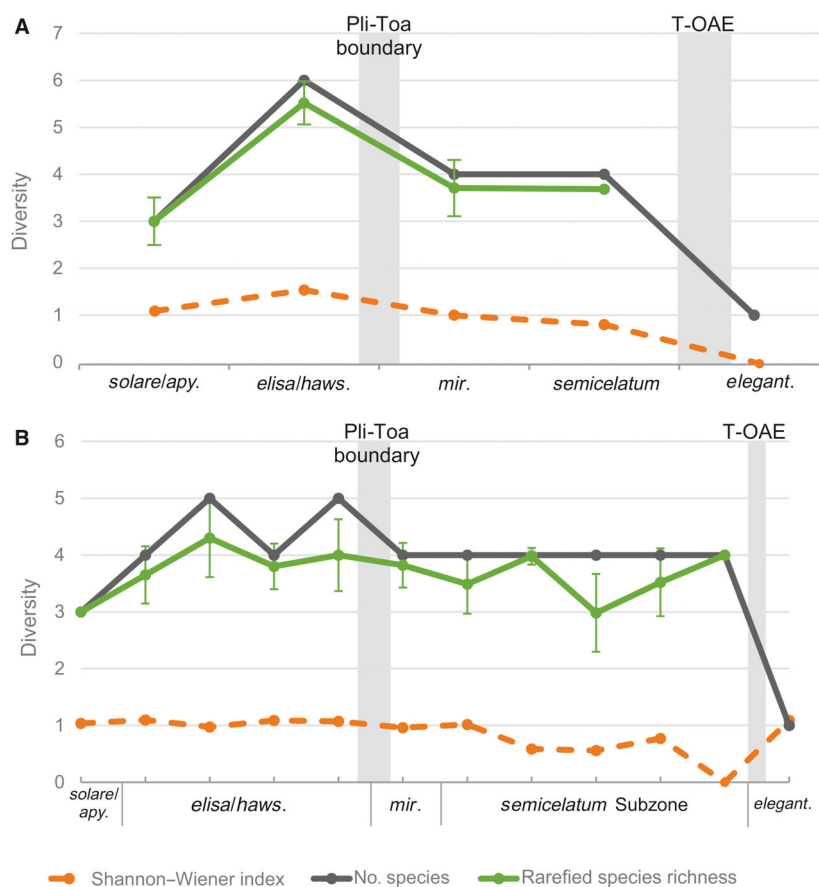
Figure 12A–C

1827 *Belemnites bisulcatus* Blainville, p. 79, pl. 2, fig. 7.

1831 *Belemnites laevigatus* Zieten, p. 29, pl. 21, fig. 12.

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

FIG. 15. Diversity indices (Shannon–Wiener index, S and rarefied species richness) of the Peniche belemnite assemblage of the upper Pliensbachian – lower Toarcian interval. A, subzone scale. B, bed scale (note the vertical marks on the horizontal axis). Note that beds P9c and P9b were merged due to sample size constraints. The Toarcian Oceanic Anoxic Event (T-OAE) corresponds to a belemnite gap. Error bars represent 95% confidence interval of the rarefied species richness. Abbreviations: *elegant.*, *elegantulum/levisoni* Subzone; *elisa/haws.*, *elisa/hawskerense* Subzone; *mir.*, *mirabile/paltum* Subzone; Pli-Toa, Pliensbachian–Toarcian; *solare/apy.*, *solare/apyrenum* Subzone.



- 1990 *Passaloteuthis bisulcata* (Blainville); Doyle, p. 19, pl. 1, fig. 1–8; pl. 2, fig. 1–4; pl. 3, fig. 1–4 (cum syn.)
- 1998 *Passaloteuthis bisulcata* (Blainville); Schlegelmilch, p. 51, pl. 2, figs 6, 7.
- 1998 *Passaloteuthis laevigata* (Zieten); Schlegelmilch, 1998, p. 51, pl. 2, fig. 8.
- 2014 *Passaloteuthis laevigata* (Zieten); Pinard *et al.*, p. 172, fig. 8D.
- 2015 *Passaloteuthis bisulcata* (Blainville); Sanders *et al.*, p. 55, figs 5B, 7E.
- 2015 *Passaloteuthis laevigata* (Zieten); Weis *et al.*, p. 737, fig. 2i–k.
- 2018 *Passaloteuthis laevigata* (Zieten); Weis *et al.*, p. 106, fig. 12F, G.

Material. 153 specimens from Lemedo Fm. (upper Pliensbachian, *emaciatum* Zone, *solare/apyrenum*–*elisa/hawskerense* Subzones, beds P1–P4) and Cabo Carvoeiro Fm. (lower Toarcian, *polymorphum* Zone, *mirabile/paltum*–*semicelatum* Subzones, beds P5–P9a and P9c; Fig. 1).

Description. The medium to large-sized robust specimens show a symmetrical and conical to cylindrical profile and outline. The apex is acute and bears two dorsolateral grooves weakly developed in most individuals. The cross-section is

circular to pyriform in the apical region and subquadrate in the stem and alveolar regions, sometimes slightly compressed. The phragmocone is slightly eccentric, penetrating one-third of the rostrum, except for some specimens, where higher values of penetration can be observed. The apical line is goniolineate. The alveolar angle ranges between c. 20° and 24° (Rita *et al.* 2020, table S11).

Occurrence. Upper Pliensbachian (*margaritatus* Zone) – lowermost Toarcian (*tenuicostatum/levisoni* Zone) of Europe (Cleveland Basin, Swabo-Franconian Basin, Lusitanian Basin, Luxembourg, France, Italy, Slovakia, Bulgaria and Spain) and northern Morocco (South Riffian Basin).

Ontogeny. The CI and Rob. increase during ontogeny while the EI decreases (Fig. 9D).

Passaloteuthis milleri (Phillips, 1867)
Figure 10A–F

- 1867 *Belemnites milleri* Phillips, p. 54, pl. 8, fig. 19.
- 1990 *Passaloteuthis milleri* (Phillips); Doyle, p. 22, pl. 2, figs 5–9 (cum syn.)

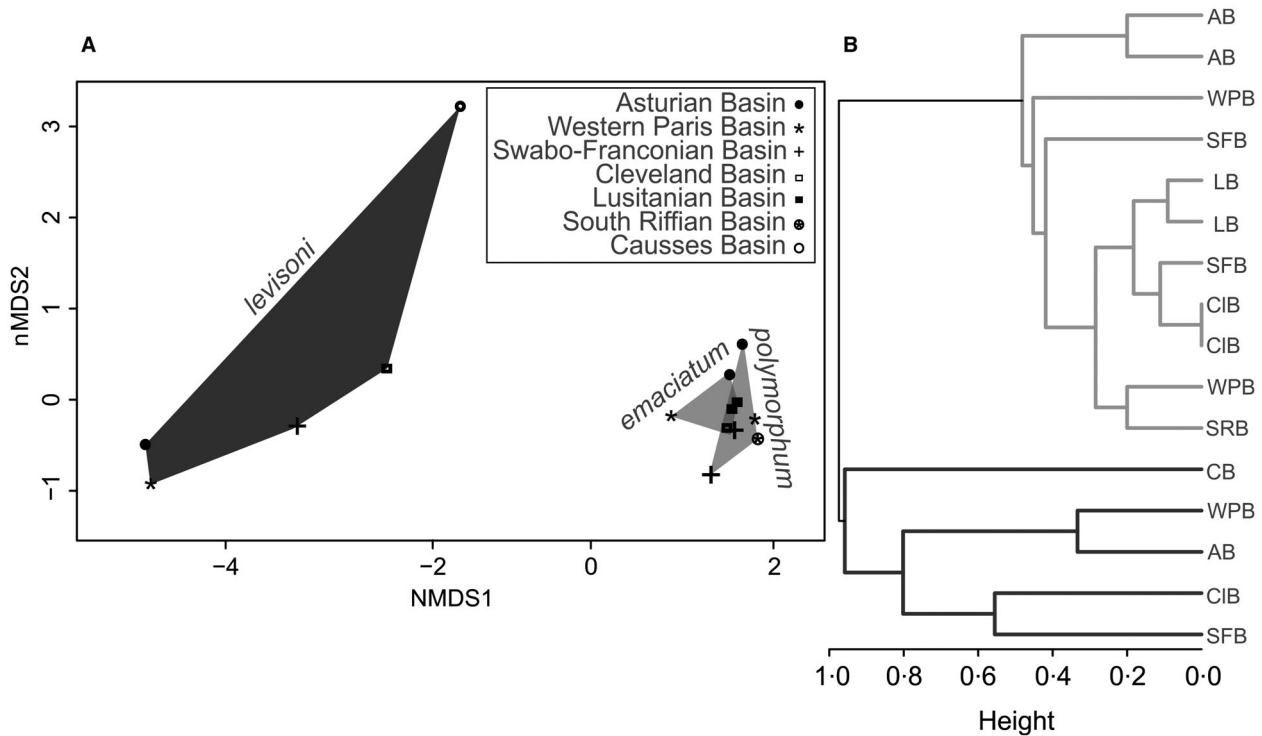


FIG. 16. Faunal similarities among north-west Tethys sites during the late Pliensbachian and early Toarcian (*emaciatum*–*levisoni* zones) regarding belemnite species composition. A, non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis distances (stress = 0.24, $n = 16$). B, cluster dendrogram using the average linkage method (UPGMA); two main assemblage clusters are identified by different shades of grey. *Abbreviations:* AB, Asturian Basin; CB, Causses Basin; CIB, Cleveland Basin; LB, Lusitanian Basin; SFB, Swabo-Franconian Basin; SRB, South Riffian Basin; WPB, Western Paris Basin.

1998 *Passaloteuthis milleri* (Phillips); Schlegelmilch, p. 52, pl. 3, figs 4, 7.

2014 *Passaloteuthis milleri* (Phillips); Pinard *et al.*, p. 172, fig. 8E.

2018 *Passaloteuthis milleri* (Phillips); Weis *et al.*, p. 106, fig. 13A.

Material. 34 specimens from Lemedé Fm. (upper Pliensbachian, *emaciatum* Zone, *solare/apyrenum-elisa/hawskerense* Subzones, beds P1–P3a and P4) and Cabo Carvoeiro Fm. (lower Toarcian, *polymorphum* Zone, *semicelatum* Subzone, beds P6–P9c; Fig. 1).

Description. The medium-sized, elongated rostrum is characterized by a cylindrical to cylindrical profile. The outline is cylindrical to subhastate. The apex is moderately acute, occasionally with striae developed only in the ventral area; dorsolateral grooves are developed as well-defined depressions. The cross-section is slightly compressed, subquadrate to subcircular in the alveolar region but pyriform in the apical area. A lateral flattening is present in the alveolar region. The apical line is ortholineate to slightly goniolineate, and the phragmocone occupies one-quarter to one-third of the rostrum (Rita *et al.* 2020, table S12).

Occurrence. Upper Pliensbachian – lowermost Toarcian (*margaritatus*–*tenuicostatum* = *polymorphum* zones) of England

(Yorkshire, Northampton, Dorset), France (Normandy, Rhône Valley, Causses), Germany (Swabo-Franconian Basin), Luxembourg, Bulgaria and Portugal (Peniche).

Ontogeny. The CI and Rob. increase during ontogeny, while the EI decreases (Fig. 9E).

Passaloteuthis sp. juv.

Figure 12E

Material. 29 specimens from Lemedé Fm. (upper Pliensbachian, *emaciatum* Zone, *solare/apyrenum-elisa/hawskerense* Subzones, beds P1 and P3a) and Cabo Carvoeiro Fm. (lower Toarcian, *polymorphum* Zone, *mirabile/paltum-semicelatum* Subzones, beds P5–P9a and P9c; Fig. 1).

Description. Very small to small rostra with a conical symmetrical profile and outline and acute apex. The cross-section is quadrate to circular in the alveolar region but pyriform in the apical region. The phragmocone penetrates one-half to one-third of the rostrum (Rita *et al.* 2020, table S13). The apical line is ortholineate or slightly goniolineate.

Remarks. These specimens can be assigned only as juveniles of *Passaloteuthis* due to the main features described above.

However, the absence of other taxonomically relevant features such as lateral lines and apical grooves, which usually develop later in ontogeny, does not allow a species-level classification. These specimens are, however, probably juvenile forms of the most common taxa *P. bisulcata* or the rarer *P. milleri*.

Occurrence. Upper Pliensbachian – lowermost Toarcian (*emaciatum*–*polymorphum* Zones, *solare/apyrenum*–*semicelatum* Subzones; beds P1, P3a, P5–P9a and P9c) of Peniche.

Family MEGATEUTHIDIDAE Sachs & Nalnjaeva, 1967

Type genus. *Megateuthis* Bayle, 1878.

Other included genera. *Acrocoelites* Lissajous, 1915; *Arcobelus* Sachs in Sachs & Nalnjaeva, 1967; *Brevibelus* Doyle, 1992; *Cuspi-teuthis* Abel, 1916; *Dactyloteuthis* Bayle, 1878; *Eocylindroteuthis* Riegraf, 1980; *Homaloteuthis* Stolley, 1919; *Odontobelus* Naef, 1922; *Parabrachybelus* Riegraf, 1980; *Paramegateuthis* Gustomov, 1960; *Rarobelus* Nalnjaeva in Dzyuba et al., 2015; *Simpsonibelus* Doyle, 1992.

Occurrence. Lower Jurassic (Pliensbachian) – Middle Jurassic (Bathonian) of Europe, Turkey and northern Russia (Siberia and Russian Far East), Japan, North America (Alaska, Canada, Greenland), South America (Argentina) and possibly West Antarctica, New Zealand and New Caledonia.

Genus ACROCOELITES Lissajous, 1915

Type species. *Belemnites oxyconus* Hehl in Zieten (1831).

Occurrence. Uppermost Pliensbachian – lower Aalenian of Europe, Siberia, and probably North and South America and Japan.

ACROCOELITES sp. indet.

Material. 2 specimens (MCUC 2018.10.002; MCUC 2018.10.001) from Cabo Carvoeiro Fm. (lower Toarcian, *levisoni* Zone, bed P10; Fig. 1).

Description. The specimen MCUC 2018.10.002 corresponds to a large, slender rostra with a cylindrical symmetrical profile and outline. The apical region is very elongated, and the apex is acute. The cross-section is subcircular in the alveolar region but pyriform in the apical region. The phragmocone penetrates one-third of the rostrum (Rita et al. 2020, table S14). A ventral apical groove occupies one-third of the whole rostrum and two weak dorsolateral grooves are observed in the apical region. The apex bears long striae. The specimen MCUC 2018.10.001 is a large, stout rostrum with a conical symmetrical profile and acute apex.

Remarks. The specimens were embedded in calciclastic sediment, which precluded a non-destructive preparation process. The preparation allowed only one side to be observed in one of the specimens (MCUC 2018.10.001) and the surface of both specimens could not be properly cleaned. Therefore, several taxonomically relevant features could not be measured or analysed, such as penetration of the phragmocone, apical line, cross-section and the presence of grooves and lateral lines. The absence of these taxonomically relevant features hampers a species-level classification. Other authors also report only *Acrocoelites* sp. indet. from these beds (McArthur et al. 2020).

Occurrence. Lower Toarcian (*levisoni* Zone, bed P10) of Peniche.

RESULTS

The Peniche section

Composition of belemnite assemblages. During the early Pliensbachian (*emaciatum* Zone, beds P1–P3a), the belemnite assemblage is dominated by *B. amaliae* (37–50%) and *P. bisulcata* (25–30%), while Hastitidae sp. indet., *P. milleri* and *Passaloteuthis* sp. juv. represent a minor proportion (Fig. 14). Belemnite absolute abundance is high (10–50 specimens per m²) during this interval (Fig. 1).

From the latest Pliensbachian (*emaciatum* Zone, *elisa/hawskerense* Subzone, bed P3b) to the lowermost Toarcian (*polymorphum* Zone, *mirabile/paltum* Subzone, bed P5), *B. amaliae* is replaced by *C. longiforma*. Therefore, the assemblage is dominated by *C. longiforma* (58–66%), *P. bisulcata* (15–24%) and Hastitidae sp. indet. (11–18%). The species *P. milleri* and *Par. aff. zieteni* are poorly represented (Fig. 14). The absolute abundance from bed P3b to bed P5 is the highest of the studied interval (>50 specimens per m², Fig. 1), which can be related to the slight condensation associated with this interval (Pittet et al. 2014; Rita et al. 2016; Rocha et al. 2016).

During the early Toarcian (*polymorphum* Zone, *semicelatum* Subzone, beds P6–P9c), the belemnite fauna consists only of passaloteuthids. The species *P. bisulcata* (9–25%) and *C. longiforma* (56–86%) dominate the assemblage and the species *Par. aff. zieteni*, *P. milleri* and *Passaloteuthis* sp. juv. represent only a minor proportion of the assemblage (Fig. 14). The belemnite absolute abundance decreases dramatically from more than 50 specimens per m² in bed P5 (*mirabile/paltum* Subzone) to less than 10 specimens per m² in bed P9b (*semicelatum* Subzone, Fig. 1).

The *levisoni* Zone (latest *elegantulum/levisoni* Subzone; early Toarcian) corresponds to a belemnite gap (interval where no belemnites are found, Hesselbo et al. 2007), interrupted by the occurrence of two specimens of

Acrocoelites sp. indet. and nine indeterminable specimens in bed P10 (Fig. 1). Belemnites reappear in the Lusitanian Basin only in the late Toarcian (*bonarelli* Zone; Duarte 1997).

Biodiversity patterns. At the bed scale, belemnite diversity is not constant during the late Pliensbachian – early Toarcian interval in the Peniche section, according to S, Shannon–Wiener index and rarefied species richness (Fig. 15). Due to the observed sample size oscillations (ranging from 2 to 174 in 13 beds, see Rita *et al.* 2020, table S1), rarefied species diversity might be the more reliable measurement of the diversity in the Peniche belemnite fauna. This approach standardizes samples by size, drawing down samples to equal numbers of specimens, normalizing richness to a standard sample size (Sanders 1968; Zhao *et al.* 2014). This is particularly important due to the nature of the sedimentary record, which does not allow a uniform sampling because of facies preservation, outcrop conditions or taphonomy (preservation probability), for example Smith & McGowan (2011).

An increase in the diversity (S, Shannon–Wiener index and rarefied species richness) is observed during the upper Pliensbachian (*emaciatum* Zone, beds P1–P3a). The interval ranging from P3a to P8 corresponds to a diversity drop, followed by an increase until the end of the *polymorphum* Zone (Shannon–Wiener index and rarefied species richness). Diversity dramatically decreases (Shannon–Wiener index and S) from the *polymorphum*–*levisoni* zonal boundary (beginning of the T-OAE) until bed P10 (Fig. 15B).

At the subzone scale (Fig. 15B), diversity increases from the *solare/apyrenum* Subzone to the *elisa/hawskerense* Subzone, followed by a decrease at the Pliensbachian–Toarcian boundary (rarefied species richness, Shannon–Wiener index and S) in the Lusitanian Basin.

During the T-OAE (latest *semicelatum* – *elegantulum/levisoni* Subzone), a decrease in belemnite diversity is observed in the Lusitanian Basin (Shannon–Wiener index and S; Fig. 15B).

Comparison with coeval basins

Composition of belemnite assemblages. The passaloteuthid and hastitid genera (*Catateuthis*, Hastitidae sp. indet., *Parapassaloteuthis* and *Passaloteuthis*) present in the late Pliensbachian and early Toarcian belemnite assemblage of Peniche, according to our results, are comparable with the data from contemporaneous Arctic and Tethyan sections (e.g. UK: Doyle 1990, 1992, 2003; Germany: Riegraf *et al.* 1984; Schlegelmilch 1998; Italy: Weis *et al.* 2015; Bulgaria: Stoyanova-Vergilova 1993; Greenland: Doyle 1991; France:

Pinard *et al.* 2014; Weis *et al.* 2018; Morocco: Sanders *et al.* 2015; Siberia: Sachs & Nalnjaeva 1970), revealing a high homogeneity of belemnite fauna in the late Pliensbachian and early Toarcian, with species such as *Passaloteuthis bisulcata*, *Parapassaloteuthis zietenii*, *Passaloteuthis milleri* and *Catateuthis longiforma*.

In the nMDS and cluster analyses (Fig. 16), each point represents a zonal assemblage from one of the seven sites considered (Asturian Basin, Western Paris Basin, Swabo-Franconian Basin, Cleveland Basin, Lusitanian Basin, Causses Basin and South Riffian Basin). According to the results, two groups can be distinguished in terms of faunal similarities. The first group corresponds to the assemblages ranging from the *emaciatum* to the *polymorphum* Zone interval (Asturian, Western Paris, Cleveland, Lusitanian and Swabo-Franconian Basins and Riffian Basin; Fig. 16). The second group consists of all the *levisoni* Zone (lower Toarcian) belemnite assemblages (Causses, Asturian, Western Paris, Cleveland and Swabo-Franconian Basins; Fig. 16). Within the latter, three clusters can be distinguished: Causses Basin (cluster 1); Asturian and Western Paris Basins (cluster 2); and Swabo-Franconian and Cleveland Basins (cluster 3). The clusters are significantly different according to ANOSIM test, which gives an R value of 0.49 and a p-value of 0.001 (Rita *et al.* 2020, fig. S1).

It should be noted that the data from the Lusitanian Basin corresponding to the *levisoni* Zone have not been included in the nMDS analysis due to the lack of specimens determined to the species level (only two *Acrocoelites* sp. indet. were identified). Although McArthur *et al.* (2020) have reported ?*Pleurobelus* sp. A from the *polymorphum* Zone, our samples did not include this genus. Given that the McArthur *et al.* specimens were not described or figured nor the abundance recorded, we did not include them in our diversity or comparative analyses.

Biodiversity patterns. At the subzone scale (Fig. 15B), during the late Pliensbachian, diversity increases from the *solare/apyrenum* to the *elisa/hawskerense* Subzone, followed by a decrease at the Pliensbachian–Toarcian boundary (rarefied species richness, Shannon–Wiener index and S) in the Lusitanian Basin. This trend is comparable with the changes in belemnite diversity observed in the Asturian, Western Paris and Cleveland Basins (Caswell & Coe 2014) at the zone scale (rarefied species richness; Fig. 17A). At the subzone scale it is comparable with Cleveland Basin, where belemnite diversity increases from the *apyrenum* to the *hawskerense* Subzone (see Rita *et al.* 2020, fig. S2).

During the T-OAE (latest *polymorphum* – early *levisoni* Zone), a decrease in belemnite diversity is observed in the Lusitanian Basin (Shannon–Wiener index and S; Fig. 15B).

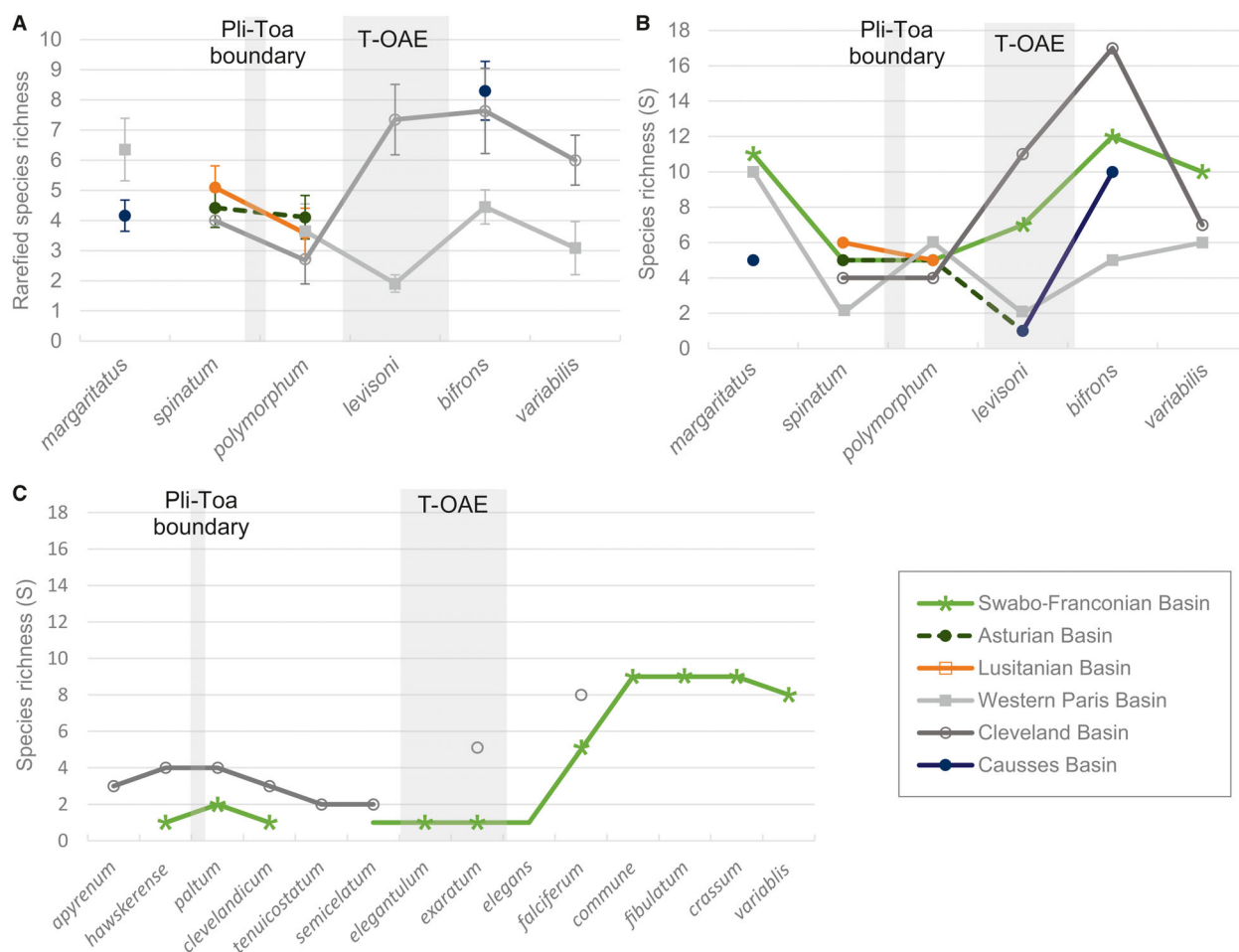


FIG. 17. Diversity patterns of belemnite assemblages during the upper Pliensbachian – middle Toarcian (*margaritatus*–*variabilis* zones) in the north-western Tethys Ocean. A, rarefied species richness at the zone scale (Caswell & Coe 2014; Pinard *et al.* 2014; Weis *et al.* 2018; this work); error bars represent 95% confidence interval of the species richness. B, species richness (S) at the zone scale (Schlegelmilch 1998; Caswell & Coe 2014; Pinard *et al.* 2014; Weis *et al.* 2018; this work). C, species richness at the subzone scale (Riegraf *et al.* 1984; Caswell & Coe 2014). Compare with Ullmann *et al.* (2014), who observed a decrease in diversity within the *exaratum* Subzone. *Abbreviations:* Pli-Toa, Pliensbachian–Toarcian; T-OAE, Toarcian Oceanic Anoxic Event.

This is comparable to the diversity trend observed in the Western Paris (rarefied species richness) at the zone level and in the Asturian (S) Basins at both the zone and subzone scales (Fig. 17). New analyses based on previously published data from the Cleveland and Swabo-Franconian Basins (Riegraf *et al.* 1984; Doyle & Bennett 1995; Little 1995; see Material and Method), in contrast, reveal an increase in belemnite diversity (S) during the T-OAE at the zone scale (Fig. 17B). For instance, after the T-OAE, in the *bifrons* Zone the diversity (S) keeps increasing in the Cleveland and Swabo-Franconian Basins, which is also observed in the Causses Basin. In the *variabilis* Zone, the diversity decreases (S) in the Cleveland and Western Paris Basins (Fig. 17B). At the subzone scale, however, the T-OAE (*exaratum* Subzone) corresponded to a decrease in diversity

(S) for the Swabo-Franconian Basin, while in the Cleveland Basin the diversity (S) increases (Fig. 17C).

DISCUSSION

Macroevolutionary context of the Early Jurassic belemnite assemblages from Peniche

The interpretation of the diversity and of the palaeogeographical distribution patterns of Early Jurassic belemnites in the Tethys Ocean is restricted due to the availability of highly resolved biostratigraphy data, which are biased towards the Euro-Boreal domain. This is related to the lack of belemnite collections resolved to the ammonite

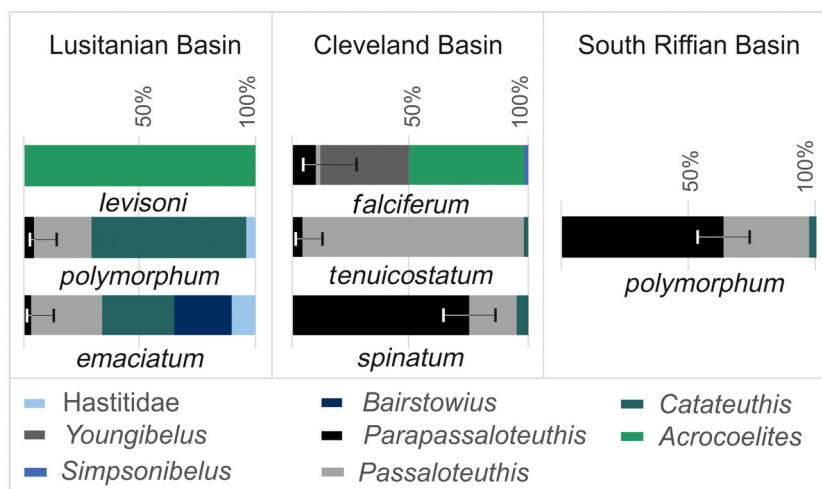


FIG. 18. Comparison of the relative proportions of the taxa comprising the belemnite assemblage from the Cleveland Basin (Doyle 1990), Lusitanian Basin and South Riffian Basin (Sanders *et al.* 2015). The error bars represent the 95% confidence interval of the relative proportion of *Passaloteuthis* and *Parapassaloteuthis* genera. Equivalent ammonite zones from different domains are vertically aligned.

subzone scale, and the gaps observed in the belemnite or stratigraphic record in Mediterranean/Submediterranean sections, such as Morocco (Sanders *et al.* 2015), or from the southern part of the Euro-Boreal domain, such as Causses Basin (Pinard *et al.* 2014). Nonetheless, some progress has been achieved and general outlines of diversity and palaeogeographical distribution may be expanded (Doyle 1987; Challinor 1991, 1992; Doyle *et al.* 1994; Iba *et al.* 2012; Pinard *et al.* 2014; Sanders *et al.* 2015; Weis & Thuy 2015; Weis *et al.* 2018).

Despite the similarities between European belemnite faunas during the late Pliensbachian and earliest Toarcian, the presence of the new species *B. amaliae* in the upper Pliensbachian of Peniche makes the Lusitanian Basin belemnite fauna unique. *Bairstowius* has been hitherto identified only in the upper Sinemurian – lower Pliensbachian of England, Germany, France, Spain, western Turkey, and central Italy (Doyle 1994, 2010; Schlegelmilch 1998; Weis *et al.* 2015). Therefore, the record of *B. amaliae* in the Lusitanian Basin extends the stratigraphic range of the genus *Bairstowius* to the upper Pliensbachian (*emaciatum* Zone) in the north-western Tethys. Additionally, it expands the biogeographical range of the *Bairstowius* genus to the Lusitanian Basin.

Another unique feature of the Lusitanian Basin belemnite fauna is the high relative abundance of the species *C. longiforma* in the assemblage. This taxon was previously identified in Morocco (South Riffian Basin; Sanders *et al.* 2015) and in the Cleveland Basin (Caswell & Coe 2014) where it comprised 1–10% of the assemblage, while in Peniche it comprises 30–65% of the assemblage (Fig. 18). This indicates that this taxon might have a preference for particular environmental conditions present in the Lusitanian Basin, but its exact environmental preferences are currently hard to elucidate. Rita *et al.* (2019) found that this species is particularly sensitive, in terms of body size,

during the Pliensbachian–Toarcian warming event coinciding with a rise in surface seawater temperature, deoxygenation, input of nutrients and various other biotic and abiotic changes.

The stratigraphic replacement of *B. amaliae* by *C. longiforma* in the Peniche assemblage during the uppermost Pliensbachian, together with the morphological features shared by the two taxa (see Systematic Palaeontology section), support the possibility of a lineage *Bairstowius*–*Catateuthis*, with *B. amaliae* and *C. longiforma* connecting both genera (see also Doyle 2003, who included *Belemnites longiformis* into *Bairstowius* genus for this reason). The possible phylogenetic relation between *B. amaliae* and *C. longiforma* offers an evolutionary scenario for the European lowermost Toarcian fauna and the endemic Boreal–Arctic fauna that developed during the *falciferum* Zone in northern Siberia (Dzyuba *et al.* 2015), corroborating the hypothesis of a northward migration during the lower Toarcian from the Mediterranean/Submediterranean domain to the Euro-Boreal domain.

Belemnite diversity patterns across the north-western Tethys

The Early Jurassic has been considered a major bottleneck in belemnite evolution as reflected in the diversity decline from the lower–middle Toarcian (Dera *et al.* 2016). However, the relative contribution of the perturbations at the Pliensbachian–Toarcian boundary event and the T-OAE is often difficult to assess due to lack of availability of high-resolution biostratigraphic data for belemnites with regard to the ammonoid subzones.

The belemnite diversity in the Lusitanian Basin slightly decreases across the Pliensbachian–Toarcian boundary. We cannot entirely rule out the effect of preservation on this pattern, given that rare species

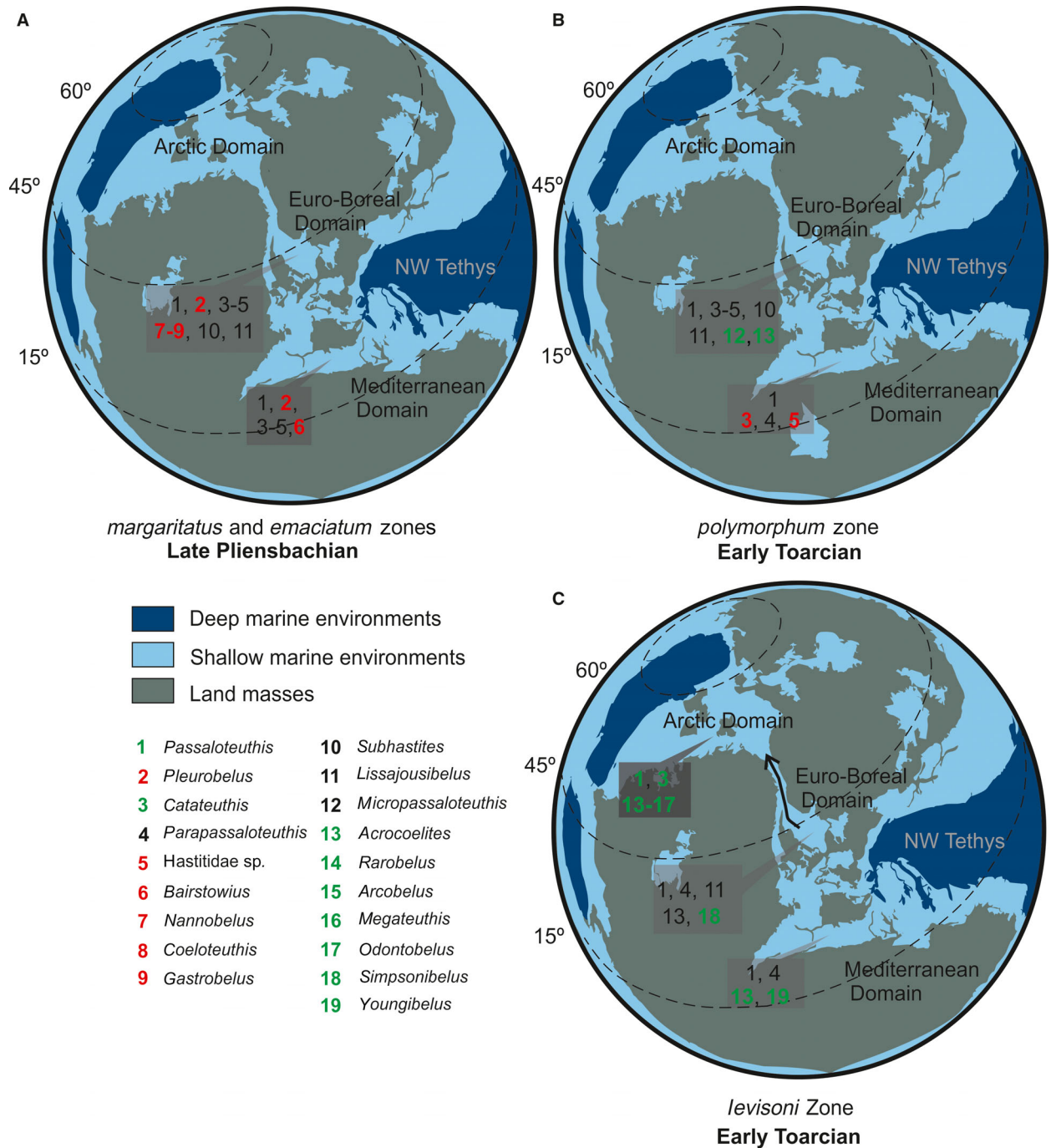


FIG. 19. Graphical representation of the palaeogeographical distributions of the belemnite genera during the late Pliensbachian and early Toarcian (*margaritatus*–*levisoni* zones) in the north-western Tethys (Euro-Boreal and Mediterranean/Submediterranean domains) and Arctic Domain: Russia (northern Siberia; Sachs & Nalnjaeva 1967), Cleveland Basin (Caswell & Coe 2014), Swabo-Franconian Basin (Schlegelmilch 1998; Riegraf *et al.* 1984), Western Paris Basin (Weis *et al.* 2018 and additional unpub. data), Eastern Paris Basin (Luxembourg, Linger section, unpub. data), South Riffian Basin (Sanders *et al.* 2015), Causses Basin (Pinard *et al.* 2014), Italy (Apennines; Weis *et al.* 2015), Lusitanian and Asturias Basins (this work) and Austria (Northern Calcareous Alps; Weis & Thuy 2015). Note that species in red represent extinct/disappeared species at the end of the particular interval and species in green represent species that had originated or appeared during the particular interval. For more details see Rita *et al.* (2020, table S7).

such as *Passaloteuthis milleri* temporarily disappear (Lazarus effect; compare with Twitchett 2007). However, our largest samples are reported from the Pliensbachian–Toarcian boundary interval, what might mean that this is probably a genuine pattern, rather than a sampling artefact. Furthermore, this trend is also observed in the Asturian (herein preliminary results), Swabo-Franconian (Schlegelmilch 1998) and Cleveland (Doyle 1992; Caswell & Coe 2014) Basins. The overall decrease from the late Pliensbachian to the early Toarcian is also comparable with data from the Western Paris Basin, where the diversity decreases (rarefied species richness) from the *margaritatus* Zone (late Pliensbachian) to the *polymorphum* Zone (early Toarcian), although no data are available for the *emaciatum* Zone (Weis *et al.* 2018). In the Causses Basin, the diversity (S) in the *margaritatus* Zone is much higher than in the *serpentinum* Zone (= *levisoni*, early Toarcian). From this basin, no belemnite data are available from the *tenuicostatum* Zone (= *polymorphum*, early Toarcian), hampering analysis of the diversity patterns across the Pliensbachian–Toarcian boundary and the T-OAE (Pinard *et al.* 2014).

The T-OAE, dated from the latest *polymorphum* to early *levisoni* Zone (~ *exaratum* Subzone), corresponds to a severe decrease in belemnite diversity in the Asturian, Western Paris and Lusitanian Basins, in contrast with the increase observed in the Cleveland and in the Swabo-Franconian Basins (at the zone scale). It is, however, noteworthy that the belemnite record is absent or rare in many sections during the early Toarcian, especially in the *levisoni* Zone in the Mediterranean/Submediterranean domain (Weis & Thuy 2015). In fact, in Peniche, the beginning of the T-OAE (early *levisoni* Zone) is almost coincident with a gap in the belemnite record, ranging from the *polymorphum/levisoni* zone boundary to the *bonarelli* Zone (late Toarcian; Duarte 1997). This gap is interrupted by the sparse record of *Acrocoelites* sp. indet., after the T-OAE (middle part of the *levisoni* Zone, bed P10; compare with McArthur *et al.* 2020 for similar observations). The belemnite record in the Causses Basin during the *levisoni* Zone is also scarce and dominated by *Acrocoelites* (Pinard *et al.* 2014). The same is observed in central Italy and in Morocco (South Riffian Basin), where the *levisoni* Zone is characterized by a sparse record of *Cuspiteuthis* (Weis *et al.* 2015) and potentially *Parapassaloteuthis* (Sanders *et al.* 2015; Rita *et al.* 2020, table S15). It is, however, noteworthy that Sanders *et al.* (2015) reported specimens from beds traditionally assigned to the *levisoni* Zone, but those layers do not contain clear indicators of the *levisoni* Zone and might, therefore, rather correspond to the uppermost Polymorphum Zone (Bardin *et al.* 2015).

In contrast, the *levisoni* Zone in the northern part of the Euro-Boreal domain (Swabo-Franconian and Cleveland Basins), is characterized by an increase in belemnite diversity (S), while various genera and species are not reported in the Mediterranean/Submediterranean domain, such as *Youngibelus* and *Simpsonibelus* (Figs 17, 19). However, when diversity (S) is analysed at the subzone scale, this increase seems to be more acute after the T-OAE, in the *falciferum* Subzone (Fig. 17; compare with Riegraf *et al.* 1984 and Caswell & Coe 2014). Additionally, when analysing belemnite data from Cleveland Basin (Caswell & Coe 2014) at the bed scale, a diversity decrease (S) is observed in the aftermath of the T-OAE, in the early *falciferum* Subzone, followed by an increase in the middle/late *falciferum* Subzone. This suggests that the high taxonomic turnover in these (sub)zones might mask the T-OAE extinction, at lower stratigraphic resolution, and might also be responsible for the seemingly high diversity in the *levisoni* Zone, or individual subzones, in these regions. Further high-resolution (bed and/or subzone scale) analysis of standardized species richness is necessary to disentangle the belemnite diversity dynamics and palaeogeographical patterns during the T-OAE, across the north-west Tethys latitudinal gradient.

The results from the nMDS and cluster analyses support the thesis of a belemnite taxonomic uniformity during the latest Pliensbachian – earliest Toarcian (*emaciatum* and *polymorphum* zones) in Europe and adjoining areas. The largest changes in belemnite diversity and palaeogeographical distribution occurred during the T-OAE (*levisoni* Zone), rather than at the Pliensbachian–Toarcian boundary in the north-west Tethyan Ocean. These results seem to differ from the response observed in ammonoids, which have larger differences between Mediterranean and Euro-Boreal faunas across the Pliensbachian–Toarcian boundary and more uniform (cosmopolitan) faunas during the T-OAE (at least at the zone level: compare with Dera *et al.* 2011). Our results also emphasize the marked differences between the northern (Cleveland and Swabo-Franconian Basins) and the southern part (Causses and Asturian Basins) of the Euro-Boreal domain in terms of belemnite taxonomic composition during the *levisoni* Zone, not recognized before that. This, at first glance, also differs from the diversity pattern observed in ammonoids, characterized by marked changes in diversity at the Pliensbachian–Toarcian boundary (Dera *et al.* 2010).

Our quantitative analysis is also consistent with Doyle (1994) and Sanders *et al.* (2015), who suggested that the European (*s.l.*) early Jurassic belemnite faunas had a similar composition until the Toarcian. Consequently, during Toarcian and Aalenian, significant changes took place, with a high diversification and a trend towards endemic Tethyan and Boreal–Arctic belemnite faunas (Doyle 1994;

Weis *et al.* 2018). This provincialism was thought to have been triggered by the biotic crisis and palaeoenvironmental perturbations occurring during the early Toarcian, particularly the T-OAE (Doyle 1987; Doyle 1994). The results of our diversity analysis support this interpretation due to the minor decreases observed across the Pliensbachian–Toarcian boundary and more major changes across the T-OAE in various north-west Tethyan basins during the lower Toarcian, despite some regional differences. Further research is necessary to corroborate and understand the underlying reasons for the discrepancies in diversity and biogeographical patterns in belemnites compared with ammonoids.

CONCLUSION

A detailed palaeontological analysis of the early Jurassic belemnites from the Lusitanian Basin is presented for the first time. The Peniche belemnite assemblage is predominantly composed of well-known taxa of the suborder Belemnitina (*P. bisulcata*, *P. milleri*, *Par. aff. zieteni*, *Hastitidae* sp. indet., *Acrocoelites* sp. indet., *B. amaliae*, *C. longiforma*, *Passaloteuthis* sp. juv.), chiefly distributed in north-western and central Europe.

The presence in the *emaciatum* Zone (= *spinatum*, upper Pliensbachian) of numerous specimens ascribed to the genus *Bairistowius* represents a novelty, together with the high abundance of *Catateuthis longiforma* comb. nov. in younger samples (uppermost *emaciatum* and *polymorphum* zones), in comparison with other European sections. Moreover, the replacement of *Bairistowius amaliae* by *Catateuthis longiforma* during the uppermost Pliensbachian suggests an evolutionary relationship between the two taxa.

Despite the lack of a marked taxonomic turnover, the Pliensbachian–Toarcian boundary might correspond to one of the pulses of the Pliensbachian–Toarcian crisis by a slight decrease in species diversity observed not only in the Lusitanian Basin but also in coeval basins (Cleveland, Swabo-Franconian, Western Paris, Causses and Asturian Basins). However, the biggest changes in the belemnite fauna in the north-western Tethys are observed during the *levisoni* Zone, corresponding to extinction of dominant taxa as well as originations. The extinctions are particularly severe in the Mediterranean/Submediterranean domain and in the southern part of the Euro-Boreal domain, and contribute to a provincial differentiation among north-west European and Arctic belemnite faunas. In Peniche, belemnites are largely absent in the *levisoni* Zone, with the exception of *Acrocoelites* sp. indet. in a single bed after the T-OAE. Our study highlights that, in order to fully disentangle belemnite diversity and palaeogeographical dynamics across the north-western Tethys

latitudinal gradient during the T-OAE, high-resolution abundance data and sample standardized diversity studies (bed or subzone scale) are necessary.

Acknowledgements. We thank Birgit Leipner-Mata for helping in belemnite preparation, and Paulina Nätscher, Christian Schulbert and Martina Schlott for assistance with scanning the specimens. We thank Wolfgang Kiessling for the valuable comments on the methods and Tarquin Bolton (Durham, UK) for information on British Pliensbachian belemnites. We thank Laura Piñuela, Johann Schobert, José Carlos García-Ramos and Pascal Neige for helping with fieldwork in Asturias and Normandy. We thank Peter Doyle and an anonymous reviewer for valuable comments on the manuscript. This is a contribution to the DFG Research Unit FOR 2332 (grant numbers Ba 5148/1-1, Ba 5148/1-2 to KDB) TERSANE and to the IGCP 655 (IUGS–UNESCO).

DATA ARCHIVING STATEMENT

Data and supporting information for this study are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.05qfttf11>); CT scanning data are available in Zenodo (<https://doi.org/10.5281/zenodo.3459233>). This published work and the nomenclatural act it contains have been registered in ZooBank: <http://zoobank.org/Refereces/4FF4B510-1889-47EA-B690-E36E5D74B000>.

Editor. Arnaud Brayard

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