


# The first belemnite of boreal ancestry from the Early Cretaceous (Valanginian) of the western Tethys: implications for belemnite ecology

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**Abstract:** The first occurrence of the belemnite species *Liobelus acrei* (formerly *Acroteuthis acrei*) is reported from the Lower Cretaceous (Valanginian) of the Vocontian Basin (VB; south-east France). This first record of the genus *Liobelus* (Family Cyllindroteuthididae), which is commonly attributed to the latest Jurassic and Early Cretaceous of the Boreal Realm, revises the spatial distribution pattern of boreal belemnites significantly. The Valanginian belemnite assemblages of the VB are dominated by genera of Tethyan ancestry, including both Duvaliidae (*Berriasibelus*, *Castellani-belus*, *Duvalia*, *Pseudobelus*) and Belemnopseidae (*Adiakritobelus*, *Hibolithes*, *Mirabelobelus*, *Vaunagites*). These two groups of Tethyan taxa comprise more than 99.9% of the belemnite-rich assemblages of the Valanginian of the VB. The occurrence of a boreal specimen documents an isolated immigration of belemnites from the north in the early

Valanginian. At the same time most Tethyan belemnite taxa are absent from the Boreal Realm, only *Duvalia*, *Pseudobelus* and *Hibolithes* have been described from North-East Greenland, and *Hibolithes* from Svalbard. Based on these diverging biogeographical patterns of the Tethyan belemnite genera we establish two taxonomically different belemnite faunas: Tethyan Fauna 1 (*Duvalia*, *Pseudobelus*, *Hibolithes*), which has a near global, Tethyan-wide and even boreal distribution, and Tethyan Fauna 2 (*Adiakritobelus*, *Berriasibelus*, *Castellani-belus*, *Mirabelobelus*, *Vaunagites*), which is less widely distributed and is restricted to southern Europe. These different spatial distribution patterns shed light on the ecology, migration patterns and evolution of Early Cretaceous belemnites.

**Key words:** belemnite, Early Cretaceous, palaeobiogeography, migration, ecology.

JURASSIC and Cretaceous cephalopod faunas (ammonites, belemnites) have a distinctive provincialism, which resulted in the recognition of two different biogeographical units, the Tethyan and Boreal Realms. In Europe this faunal provincialism culminated during the latest Jurassic to earliest Cretaceous (late Tithonian, Berriasian), caused by a sealevel lowstand (Ziegler 1990; Haq 2014), which further intensified the segregation of faunas and floras (e.g. Wimbledon *et al.* 2020). The strong provincialism of the latest Jurassic and earliest Cretaceous resulted in the still common usage of different stage names in the two realms. The Tithonian and Berriasian stages (149–138 Ma) of the Tethyan Realm correspond to the Volgian and Ryazanian stages of the Boreal Realm (e.g. Shurygin & Dzyuba 2015). The two sequences have not a single, biostratigraphically relevant ammonite species in common and the magnetostratigraphically defined boundaries of the two stage systems are stratigraphically offset to each

other. Subsequently, in central Europe a transgression in the earliest Valanginian (138 Ma) established marine gateways between the two realms, allowing exchange of marine faunas and floras via the Carpathian seaway in the east and the Rockall Trough in the west (e.g. Mutterlose *et al.* 2020). Despite these seaways, which enabled marine floras and faunas to migrate, a distinctive provincialism existed until the end of the Barremian (121 Ma).

In the Valanginian various ammonite genera of Tethyan origin (*Olcostephanus*, *Neohoplloceras*, *Karakaschiceras*, *Valanginites*, *Saynoceras*, *Bochianites*, *Varlheidites*, *Oosterella*, *Juddiceras*, *Stoicoceras*) migrated into the north-west European waters of the Boreal Realm (e.g. Kemper *et al.* 1981; Rawson 1995). Most of these Tethyan taxa mark short-lived episodes in the late Valanginian of the Boreal Realm. *Platylenticeras*, the ancestry of which is still controversially debated, occurs in the earliest Valanginian of south-east France (*Thurmanniceras* *pertransiens*

ammonite Zone) and in northern Germany. Boreal ammonites in turn occasionally made their way into the Tethys, documented by findings of *Polyptychites*, *Prodichotomites* and *Dichotomites* in the Valanginian of the Vocontian Basin (VB, south-east France; Thieuloy 1977). *Polyptychites* and *Prodichotomites/Neocraspedites* entered the VB in the late early Valanginian (*Karakaschiceras inostranzewi* ammonite Zone) and in the early late Valanginian (basal *Saynoceras verrucosum* ammonite Zone), *Dichotomites* entered the VB in the late Valanginian. None of these migration faunas colonized the new Tethyan habitat permanently.

Tethyan belemnites (*Duvalia*, *Pseudobelus*, *Hibolithes*) have been described from the Valanginian of North-East Greenland (Alsen & Mutterlose 2009), but only *Hibolithes* has hitherto been mentioned from Svalbard and north-west Europe (e.g. Doyle & Kelly 1988). Boreal belemnites, however, are so far unknown from the Tethys.

The first record of the boreal belemnite genus *Liobelus* (Cylindroteuthidae) from the Tethys, which is here reported from the Lower Cretaceous (Valanginian) of the VB, revises the spatial distribution pattern of this group. We aim to evaluate this finding in its palaeobiogeographical context. We discuss potential gateways, migration routes and palaeoenvironmental factors controlling the migration patterns. These biogeographical distribution patterns also shed light on the ecology and evolution of Early Cretaceous belemnites. Based on the northward migration of three belemnite genera of Mediterranean origin (*Duvalia*, *Pseudobelus*, *Hibolithes*) two different belemnite faunas are established for the Tethys (Tethyan Fauna 1 and Tethyan Fauna 2). These in turn are interpreted here with respect to their ecology.

## BELEMNITE PALAEOBIOGEOGRAPHY

The biogeographical separation of the Tethyan and Boreal Realms is mirrored by the evolution and radiation of taxonomically different belemnite assemblages. The Tithonian–Hauterivian sediments of the Tethys are characterized by representatives of the Duvaliidae (*Berriasibelus*, *Castellani-belus*, *Conobelus*, *Duvalia*, *Produvalia*, *Pseudoduvalia*, *Pseudobelus*) and the Belemnopseidae (*Adiakritobelus*, *Hibolithes*, *Mirabelobelus*, *Vaunagites*). The Tithonian–Barremian successions of the Boreal Realm are, in contrast, dominated by the Cylindroteuthidae. The cylindroteuthids mainly consist of *Acroteuthis* and *Boreioteuthis*. *Arctoteuthis*, *Lagonibelus*, *Liobelus* and *Pachyteuthis*, which are less common, disappeared in the Hauterivian. *Cylindroteuthis* and *Simobelus*, being even rarer, became extinct in the Valanginian. Both faunas are well documented and have been described in detail for the Tethys (e.g. Stoyanova-Vergilova 1970; Ali-Zade 1972; Combémoré

1972, 1973; Combémoré & Gayte 1981; Janssen & Clément 2002; Janssen & Fözy 2004; Mutterlose & Wiedenroth 2008; Tibuleac 2018; Janssen 2021; Vaňková *et al.* 2021), and the Boreal Realm (e.g. Sachs & Naljaeva 1964, 1966, 1972; Mutterlose *et al.* 1983, 2020; Doyle & Kelly 1988; Mutterlose 1988a; Dzyuba 2004, 2012, 2013).

Following the early Valanginian transgression in central Europe three Tethyan belemnite genera (*Duvalia*, *Pseudobelus*, *Hibolithes*) were able to migrate into the Boreal Realm. We consider *Hibolithes* as a genus of Tethyan ancestry for the following reasons. It is the dominant belemnite genus throughout the entire Valanginian in Morocco, where it comprises 77% of the belemnite assemblages (Mutterlose & Wiedenroth 2008). In the early Valanginian of the VB *Hibolithes* represents 8% of the belemnite rostra, and its abundance increases to 20% in the late Valanginian. This is contrasted by the abundance patterns observed in the Boreal Realm. In North-East Greenland and northern Europe records of early Valanginian *Hibolithes* are based on a few isolated or poorly dated specimens. Well-dated findings in both areas go back to the early late Valanginian. In the late Valanginian of North-East Greenland *Hibolithes* is present but it comprises <1% of the entire belemnite assemblage (Alsen & Mutterlose 2009). The genus is even rarer in the late Valanginian of northern Europe, suggesting a migration from the Tethys via the Rockall Trough to North-East Greenland. *Duvalia*, *Pseudobelus* and *Hibolithes* arrived in North-East Greenland, but only *Hibolithes* spread from there to northern Europe and Spitsbergen. No detailed stratigraphic data are available for the Valanginian from Spitsbergen and Kong Karls Land.

The boreal Cylindroteuthidae, which have been documented for the Early Cretaceous as far south as Japan (Sano *et al.* 2015; Haggart & Matsukawa 2019) and California (Anderson 1938), remained otherwise restricted to the Boreal Realm, where they radiated. Coquand (1862) has listed *Acroteuthis subquadratus* from the Neocomian (Berriasian–Hauterivian) of Algeria, without giving a figure. Apart from this debatable finding, Cylindroteuthidae are unknown from the Tethys, although boreal ammonites, for example, are well documented from the Valanginian of the VB (Thieuloy 1977). It is only in the earliest Aptian that this clear separation of the two biogeographical realms, based on belemnites, vanished. The Tethyan Duvaliidae and the boreal Cylindroteuthidae went extinct and were replaced by *Neohibolites*, which experienced a major radiation.

## MATERIAL AND STRATIGRAPHY

A total of 502 belemnite rostra have been collected bed by bed from the Valanginian Col Lazarier section,



c. 5 km north-east of the village of Villeperdix (Drôme Department, south-eastern France) throughout the years 2002–2021. The specimens were collected from a c. 250-m-thick Valanginian marl-limestone sequence, exposed c. 20 km north-east of Nyons at 44.469874 N, 5.319903 E (Fig. 1). The Valanginian strata represent the basin-slope facies of the VB. The VB formed the westernmost extension of the French Subalpin Basin, bordered in the west and north by shallow carbonate platforms. Following a regression in the Upper Jurassic (Atrops 1984), the VB experienced a continuous subsidence throughout the Berriasian and Albian, caused by extensional tectonics. Starting in the late Albian the basin was filled and emergence took place in the Santonian.

In the Col Lazarier section, belemnites and ammonites are present throughout the entire Valanginian. The biostratigraphy of the belemnite material, collected bed by bed from the outcropping ammonite zones, follows the standard zonation of the Kilian Group (Reboulet *et al.* 2014). Lithology and thicknesses of the sequence correspond to those of the Vergol section, positioned 30 km further south (Reboulet 1996). The *Liobelus* belemnite rostrum described here was collected during a field campaign by Dr G. Thomel in 1978 from the upper lower Valanginian of the section. Given that most specimens from outcrops of the VB are loosely exposed on weathered rock surfaces, a potential downslope transport cannot be excluded. In order to obtain a robust stratigraphic age for the specimen studied here, the calcite of the rostrum has been analysed for strontium isotopy. Belemnite-based  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope data enable a precise age assignment independent of biostratigraphy (e.g. McArthur *et al.* 2004; Meissner *et al.* 2015). An  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope value of 0.707364 has been obtained for the specimen under discussion, assigning it to the *Saynoceras verrucosum* ammonite Zone of the lower upper Valanginian.

The studied material, its biostratigraphic origin, preservation, size and the methods used ( $^{87}\text{Sr}/^{86}\text{Sr}$  isotopes) are

documented in Appendix S1. The section had a palaeolatitude of c. 30°N during the Valanginian.

*Institutional abbreviations.* CSGM, Center for Collective Use «Collection GEOCHRON» at Trofimuk Institute of Petroleum Geology and Geophysics of the Siberian Branch of the Russian Academy of Sciences (formerly Central Siberian Geological Museum), Novosibirsk, Russia; RHP, Réserve Naturelle géologique Haute-Provence, Digne, France.

## PALAEOBIOGEOGRAPHY OF VALANGINIAN BELEMNITES

### *Assemblages of the western Tethys*

Various studies describe the taxonomically closely related belemnite assemblages from the Valanginian of the western Tethys. Unfortunately only few quantitative data are available.

The shallow water faunas from Morocco are of high abundance and low diversity. They are dominated by a few genera, including *Berriasibelus*, *Duvalia*, *Pseudobelus*, *Hibolites* and *Vaunagites?*. Most of the 218 specimens of Valanginian age that have been evaluated (Fig. 2) can be attributed to the two belemnite taxa *Hibolites* (77%) and *Vaunagites?* (14%). The duvaliid taxa *Berriasibelus* (4%), *Duvalia* (5%) and *Pseudobelus* (<1%) comprise c. 9% of the Valanginian belemnite assemblage (Mutterlose & Wiedenroth 2008).

Spanish belemnite material of Valanginian age has been listed by Janssen (2003). *Berriasibelus*, *Castellanibelus*, *Duvalia*, *Pseudobelus*, *Hibolites*, *Mirabelobelus* and forms that are morphologically close to *Vaunagites* are described from the Caravaca–Cehégín area (south-eastern Spain).

Various sections in the VB of southern France have provided rich belemnite faunas, which have been described in the past (e.g. Combémoré 1972, 1973; Janssen & Clément 2002; Janssen 2021).

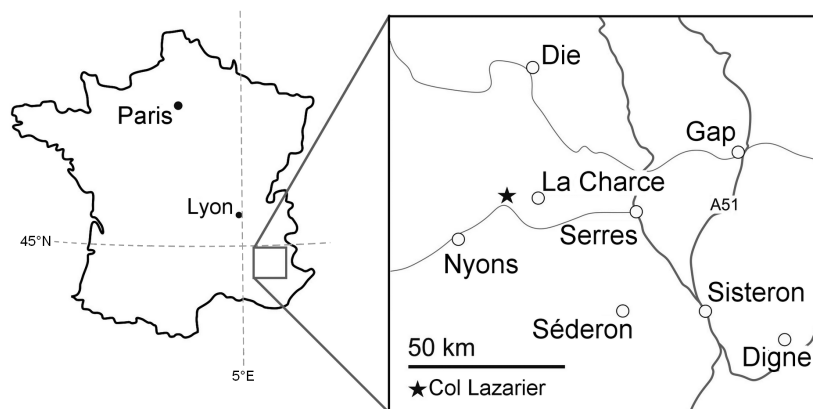
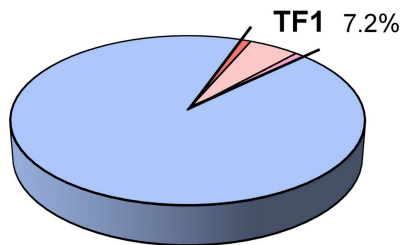
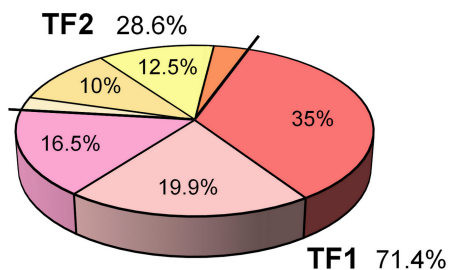


FIG. 1. Location map of the Col Lazarier section (Drôme, south-eastern France).

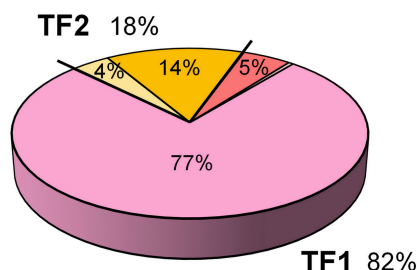
**A Boreal Realm, North-East Greenland**  
Palaeolatitude c. 51°N, 873 specimens



**B Tethys, Vocontian Basin**  
Palaeolatitude c. 30°N, 14 638 specimens



**C Tethys, Morocco**  
Palaeolatitude c. 23°N, 218 specimens



**Boreal genera**

■ Cylindroteuthididae

**Tethyan Fauna 1 (TF1)**

■ *Duvalia*

■ *Pseudobelus*

■ *Hibolithes*

**Tethyan Fauna 2 (TF2)**

■ *Adiakritobelus*

■ *Berriasibelus*

■ *Castellanibelus*

■ *Mirabelobelus*

■ *Vaunagites*

**FIG. 2.** Abundances of belemnite genera in the Valanginian of: A, North-East Greenland; B, the Vocontian Basin; C, Morocco. Based on Mutterlose & Wiedenroth (2008), Alsen & Mutterlose (2009) and this paper. Palaeolatitudes shown in A–C from the palaeolatitude calculator of Van Hinsbergen *et al.* (2015).

The material from the Col Lazarier section (502 specimens), which has been used for this study, was compared with a population of 14 638 rostra recovered from various localities throughout the VB by the second author.

All specimens have been collected bed by bed. The taxonomic composition of the Col Lazarier fauna is amazingly consistent with that observed for the rest of the basin. Of the 502 belemnite rostra that have been retrieved from the Valanginian of the Col Lazarier section (14 638 throughout the VB), 79.6% (77.4% VB) were unambiguously assigned to the Duvaliidae and 20.4% (22.6% VB) to the Belemnopseidae (Fig. 2). The Duvaliidae from all localities of the VB include *Berriasibelus* (10%), *Castellanibelus* (12.5%), *Duvalia* (35%) and *Pseudobelus* (19.9%). The Belemnopseidae consist of *Adiakritobelus* (2.5%), *Hibolithes* (16.5%), *Mirabelobelus* (3.5%) and *Vaunagites* (0.1%). Only one specimen out of 14 638 rostra (= 0.01%) can be attributed to the boreal genus *Liolobus*, described here.

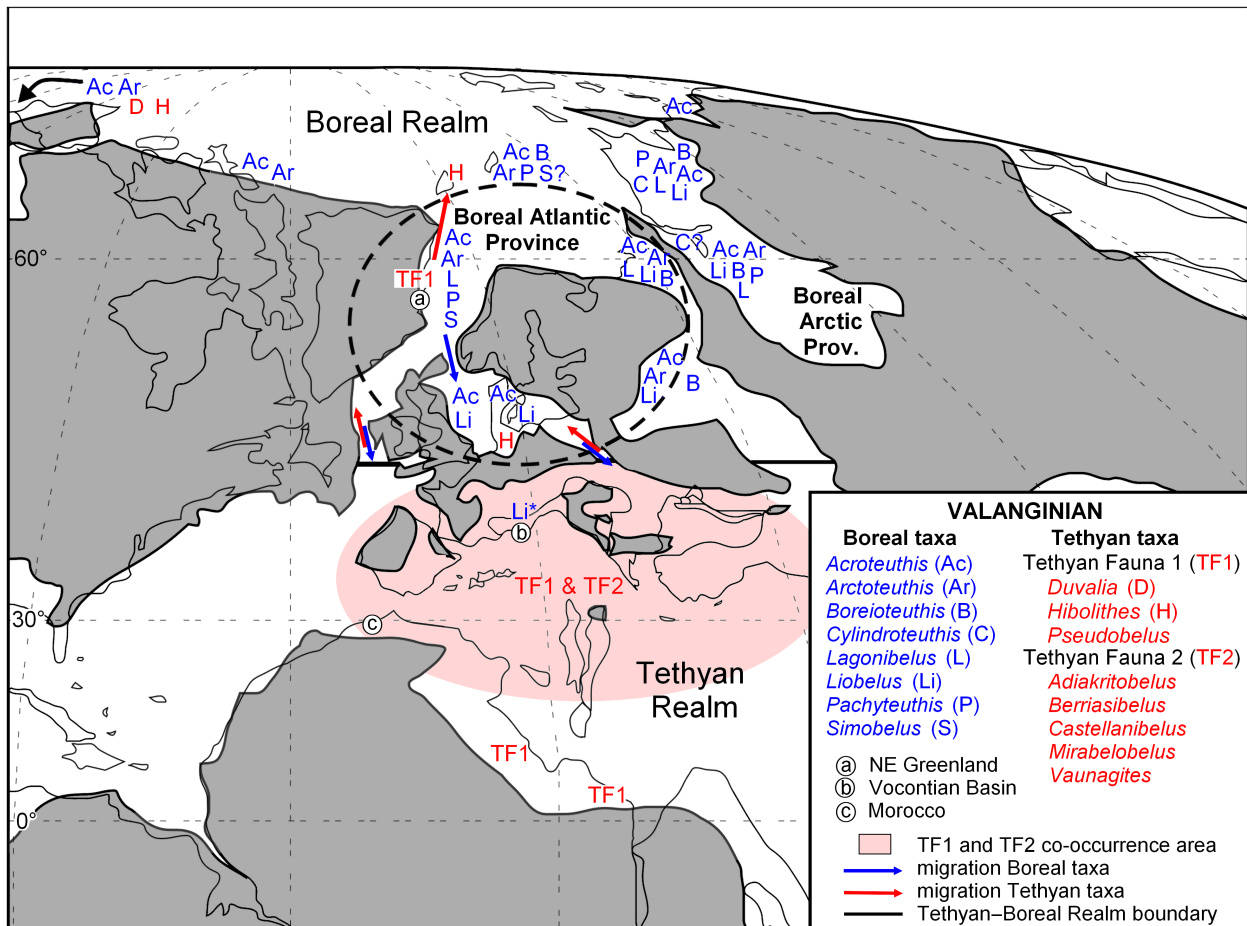
*Berriasibelus*, *Duvalia*, *Pseudobelus* and questionable *Hibolithes* have been reported from the Czech Republic (Vaňková *et al.* 2021). Hungarian assemblages of late Valanginian age consist of *Duvalia*, *Pseudobelus*, *Hibolithes*, *Adiakritobelus* and *Vaunagites* (Janssen & Fözy 2004). Rare findings of *Duvalia*, which are stratigraphically poorly constrained, have been recorded from the earliest Valanginian of Romania (Tibuleac 2018). Bulgarian belemnites have been thoroughly studied by Stoyanova-Vergilova (1964, 1970), who listed *Duvalia* and *Pseudobelus* for the Valanginian. Crimean belemnite assemblages of Valanginian age include *Duvalia*, *Pseudobelus* and *Berriasibelus* (Weiss 1991). Ali-Zade (1972) documents a diverse belemnite assemblage from the Valanginian of Azerbaijan, including *Berriasibelus*, *Pseudobelus*, *Duvalia*, *Hibolithes* and *Curtohibolites*.

*Boreal assemblages*

Valanginian belemnites from the Boreal Realm are taxonomically attributed to the Cylindroteuthididae. Their biogeographical patterns, with the exception of the east Pacific faunas, are documented in Figure 3.

A handful of belemnite rostra of latest Jurassic and Early Cretaceous age are known from Arctic Canada (Northwest Territories, Nunavut) and adjacent regions (e.g. Alaska), and the state of knowledge has recently been summarized by Mutterlose *et al.* (2020). The specimens of Valanginian age are attributed to *Acroteuthis*, *Arctoteuthis* and *Lagonibelus* (Fig. 3). No Tethyan elements of Valanginian age have been recorded from Arctic Canada or northern California. A specimen of *Hibolithes*, figured from northern California (Anderson 1938), is of Hauterivian age. Most recently a finding of *Duvalia* sp. from the Valanginian of northern Washington State (USA) has been documented (W. Clifton, University of Ohio, unpub. data).

The Valanginian belemnite assemblages of North-East Greenland are much more abundant and diverse than



**FIG. 3.** Palaeobiogeography of the Valanginian interval showing the spatial distribution patterns of belemnites for the Tethyan and the Boreal Realms. Arrows indicate migration routes. Compiled from numerous sources (see text).

those of Arctic Canada. They consist of Boreal Arctic forms (*Arctoteuthis*, *Pachyteuthis*, *Lagonibelus*, *Simobelus*), Boreal European forms (*Acroteuthis*) and Tethyan-derived genera (*Duvalia*, *Pseudobelus*, *Hibolithes*). The Tethyan taxa comprise c. 7% of the entire belemnite faunas encountered in the Valanginian of North-East Greenland (*Duvalia* 1%, *Pseudobelus* 5.2%, *Hibolithes* 1%) out of a total of 873 specimens. Approximately 93% of the specimens can be attributed to boreal belemnite genera (*Acroteuthis*, *Arctoteuthis*, *Lagonibelus*, *Simobelus*, *Pachyteuthis*, *Cylindroteuthis*), which by far dominate the assemblages (Fig. 2). A more detailed account of the assemblage composition is given by Alsen & Mutterlose (2009).

Svalbard and Kong Karls Land also yielded diverse and rich belemnite assemblages of Valanginian age, described by Blüthgen (1936) and Doyle & Kelly (1988). Additionally Nalnjajeva *et al.* (2011) figured some Valanginian belemnites from Spitsbergen. The boreal genera *Acroteuthis*, *Arctoteuthis*, *Boreioteuthis*, *Pachyteuthis* and

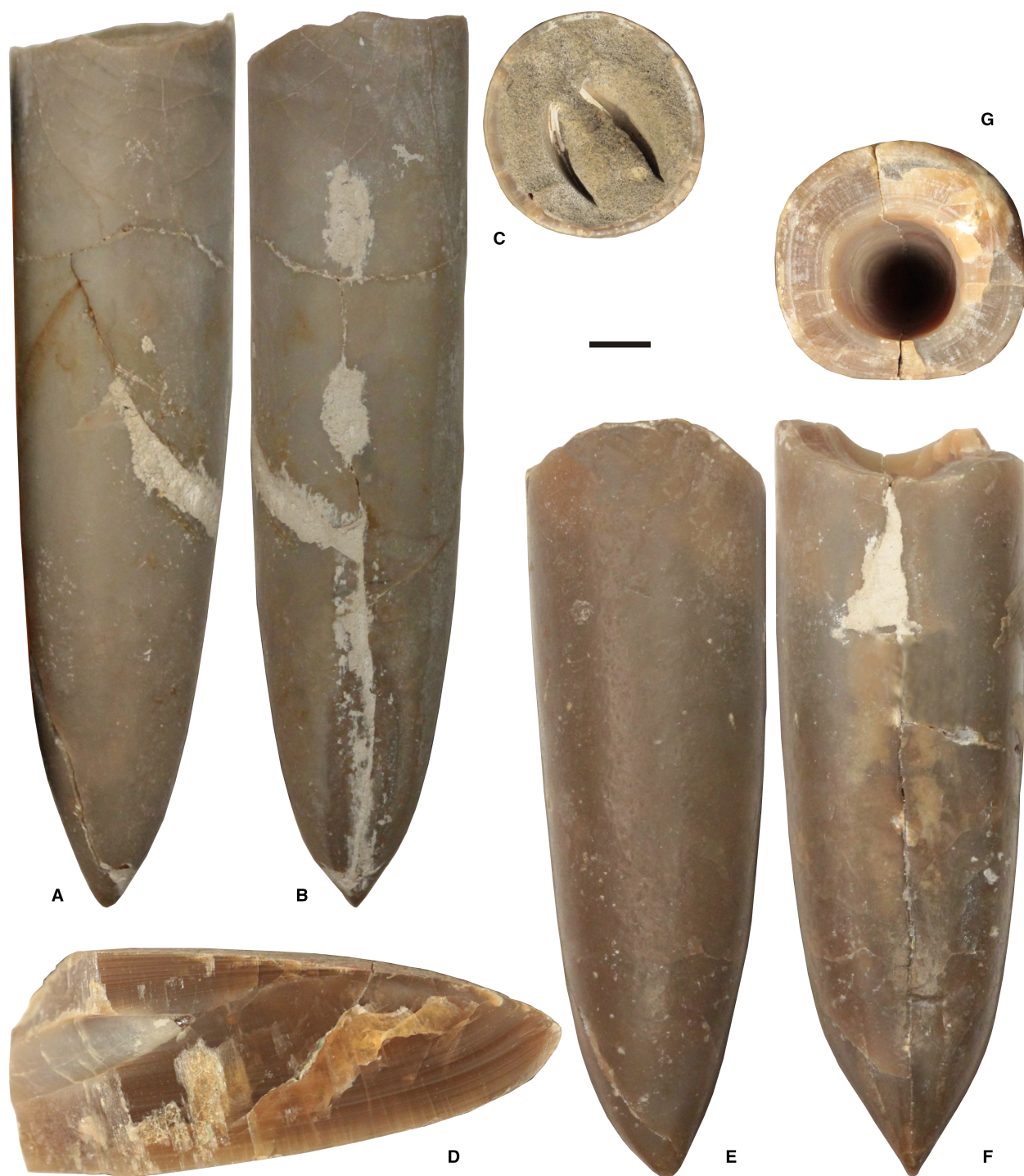
possibly *Simobelus* are common in the Valanginian of Svalbard, while *Duvalia* and *Pseudobelus* are unknown. Species of *Hibolithes* endemic to Spitsbergen and which are morphologically closely related to those of North-East Greenland, are present.

Further east, in the Pechora Basin the Valanginian belemnite faunas consist only of boreal *Cylindroteuthidae* (*Acroteuthis*, *Arctoteuthis*, *Boreioteuthis*, *Lagonibelus*, *Liobelus*). Tethyan-derived elements, including *Hibolithes*, are entirely absent.

Siberia supplied the most diverse boreal belemnite assemblages. The Valanginian faunas can be attributed entirely to the *Cylindroteuthidae*. *Acroteuthis*, *Arctoteuthis* and *Boreioteuthis* are common, *Pachyteuthis*, *Lagonibelus*, *Liobelus* (Fig. 4) and *Cylindroteuthis* are rarer, and Tethyan elements are missing (Sachs & Nalnjajeva 1964, 1966, 1972; Efremenko 2022).

In central Russia the Valanginian belemnites are still poorly investigated (Sachs & Nalnjajeva 1972). Representatives of *Acroteuthis*, *Boreioteuthis* and *Liobelus* are





**FIG. 4.** The boreal belemnite species *Liobelus acrei* (Swinerton, 1936) from the Valanginian of the Boyarka River, northern Siberia. A–C, CSGM 84-53: A, lateral view, venter right; B, ventral view; C, cross-section at the anterior end (also figured in Sachs & Nalnjaeva 1966, pl. 29, fig. 1a, b). D, CSGM 84-55, longitudinal section, venter top (also figured in Sachs & Nalnjaeva 1966, text-fig. 42). E–G, CSGM 84-52: E, lateral view, venter right; F, ventral view; G, cross-section at the anterior end (also figured in Sachs & Nalnjaeva 1966, pl. 30, fig. 1a, b). Scale bar represents 10 mm.

especially numerous, but rare *Arctoteuthis* has also been mentioned. Belemnites of Tethyan affinity are unknown.

The Valanginian belemnite assemblages of north-west Europe (north-east Britain, north-west Germany) are mainly composed of *Acroteuthis* and the more recently

established genus *Liobelus*. Belemnite rostra are very common from the upper part of the lower Valanginian onwards (Pinckney & Rawson 1974; Mutterlose 1988a, 1990). *Duvalia* and *Pseudobelus* are missing, and isolated specimens of *Hibolithes* are known.

The high-latitude belemnite faunas of Arctic Canada, British Columbia and Alaska thus show close affinities to those of North-East Greenland, Svalbard, the Pechora Basin and Siberia. The most diverse belemnite complex was centred in Siberia. Towards the west the diversity patterns gradually decrease from seven genera in Siberia to two in Arctic Canada. In the Valanginian, *Acroteuthis* (middle Volgian to lower Barremian) became the dominant belemnite genus in the entire Boreal Realm, including the Arctic and the northern Pacific. *Liobelus* is absent in the Pacific, but migrated far south into the European seas. The belemnite assemblages of central Russia, North-East Greenland and north-west Europe show differences at the genus level. The central Russian belemnite association is predominantly composed of *Acroteuthis*, *Boreio-teuthis* and *Liobelus*. The material from Greenland is dominated by *Acroteuthis* and *Liobelus* with other Arctic taxa being common. The belemnite faunas of north-west Europe, however, consist only of *Acroteuthis* and *Liobelus*.

## MIGRATION PATTERNS AND ECOLOGY

### *Migration patterns*

The biogeographical patterns of the Tethyan belemnites in the Valanginian enable the recognition of two different faunas. *Duvalia*, *Pseudobelus* and *Hibolithes* have a very wide, near to cosmopolitan distribution, and they occur throughout the western Tethys and in North-East Greenland. These three genera are grouped here as Tethyan Fauna 1 (TF1; Fig. 5A–C).

The genera *Adiakritobelus*, *Castellanibelus*, *Mirabelobelus* and *Vaunagites*, in contrast, are restricted to south-east Spain, France, Switzerland, the Austrian Alps and Hungary. This group of belemnites, labelled as Tethyan Fauna 2 (TF2; Fig. 5D–H), is absent or rare in various other localities of the western Tethys (Morocco, Hungary, Bulgaria), thereby reflecting an endemic distribution (Figs 2, 3).

Given that Tethyan Fauna 1 and Tethyan Fauna 2 co-occur in the VB and other areas, the diverging spatial patterns of both groups have some implications for the ecology of belemnites: (1) factors in addition to the existence of gateways controlled the successful colonization of new territories; (2) the initially purely morphologically defined genera also indicate different biological or ecological susceptibilities; and (3) to understand their environmental signals, belemnites are here interpreted not on the species but on the genus level.

*Duvalia*, *Pseudobelus* and *Hibolithes* outcompeted other Tethyan taxa (Fig. 6), which were less well adapted to long-distance migration. *Pseudobelus*, which is rare in the shallow water deposits of Spain (Janssen 2003) but relatively common in the deeper water sites of the VB, has been interpreted as a hemipelagic dweller (Alsen & Mutterlose 2009). The findings of *Pseudobelus* in the Valanginian of North-East Greenland suggest that the genus expanded its distribution range by actively swimming northward into the proto-North Atlantic. *Duvalia* and *Hibolithes* followed similar pathways. *Hibolithes* was the most widespread belemnite genus, finding its way via North-East Greenland to Svalbard, Kong Karls Land and north-west Europe (Blüthgen 1936; Mutterlose *et al.* 1983; Doyle & Kelly 1988), where it evolved endemically. Apart from reports from the Pacific of California (Anderson 1938), the genus has been recorded from Japan (Sano *et al.* 2015) and the southern hemisphere (e.g. Challinor 1991; Doyle 1992).

In northern Europe (UK, North Sea, northern Germany) very rare *Hibolithes* are known from the Valanginian and early Hauterivian, and the belemnite assemblages are dominated by *Acroteuthis* and *Liobelus*. In the late early Hauterivian *Hibolithes* abruptly outcompeted *Acroteuthis/Liobelus* and evolved endemically throughout the Hauterivian and Barremian. *Hibolithes* is also mentioned from the Hauterivian of central Russia (Baraboshkin *et al.* 2001) and the Pechora Basin (Sachs & Nalnjajeva 1966). The common occurrence of *Hibolithes* in North-East Greenland and its rarity in northern Europe/central Russia indicates a first migration via the Rockall Trough in the Valanginian. A second migration pulse in the late early Hauterivian reached northern Europe and central Russia potentially via the Carpathian and Peri-Caspian seaways.

The biogeographical patterns exposed by the boreal Cylindroteuthidae also document spatial differences on the genus level. The Valanginian of the Boreal Atlantic Province, yields *Acroteuthis* and *Liobelus*. Based on cylindroteuthidid rostrum morphology Zakharov *et al.* (2014) attributed the 13 genera of the Cylindroteuthidae to three palaeoecological groups (PG I, PG II, PG III). *Acroteuthis* and *Liobelus*, which are characterized by short, robust rostra, were assigned to PG I. This group includes the least active swimmers, which preferred shallow near-shore waters. Both *Acroteuthis* and *Liobelus*, perhaps nektobenthic organisms, are dorsoventrally depressed and ventrally flattened. This may have allowed them to successfully populate the shallow marine environments of the Boreal Atlantic Province (central Russia, north-west Europe) since the end of the Jurassic (Dzyuba 2013). In the Boreal Arctic Province (Siberia, Arctic), both genera were significant components of the belemnite assemblages since the end of the

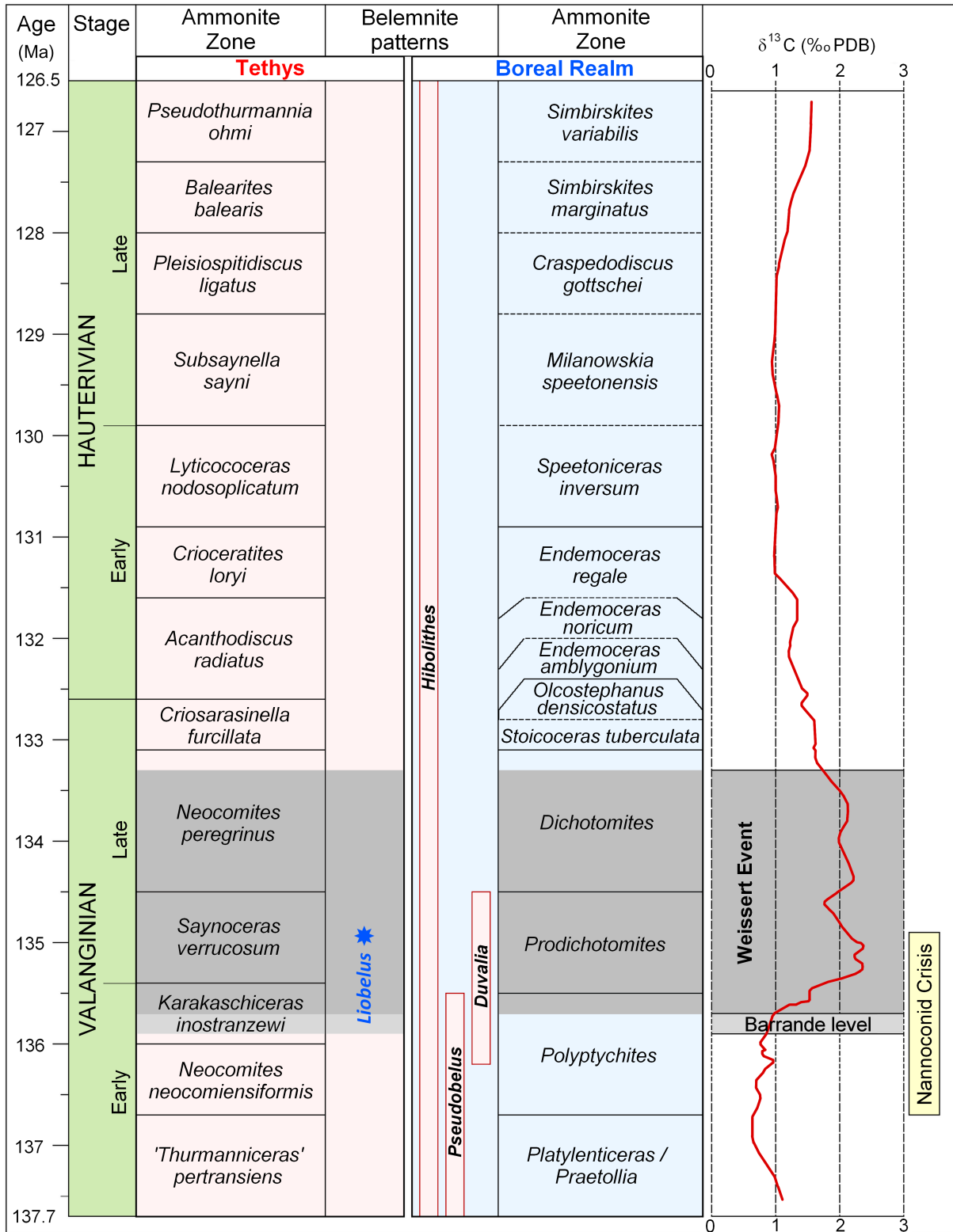




**FIG. 5.** Typical belemnites of Tethyan Faunas 1 and 2 (TF1, TF2) from the Valanginian of the Vocontian Basin (south-east France). A–C, TF1: A, RHP.07101-001.AA506, *Pseudobelus* Blainville, 1827, lower Valanginian, *Neocomites neocomiensiformis* ammonite Zone, Grospierres; B, RHP.26376-001.AA505, *Duvalia* Bayle, 1878, lower Valanginian, *Neocomites neocomiensiformis* ammonite Zone, Col Lazarier section; C, RHP.26130-001.AA507, *Hibolithes* Denys de Montfort, 1808, lower Valanginian, *Neocomites neocomiensiformis* ammonite Zone, Eyroles. D–H, TF2: D, RHP.04199-001.AA508, *Adiakritobelus* Janssen & Fözy, 2004, *Criosarasinelia furcillata* ammonite Zone, Saint Vincent-sur-Jabron; E, RHP.26193-001.AA509, *Mirabelobelus* Janssen & Clément, 2002, lower Valanginian, *Neocomites neocomiensiformis* ammonite Zone, Vergol section; F, RHP.26278-001.AA512, *Vaunagites* Combémoré & Gayte, 1981, upper Valanginian, *Criosarasinelia furcillata* ammonite Zone, La Roche/Buis; G, RHP.26376-002.AA511, *Castellanibelus* Combémoré, 1972, upper Valanginian, *Saynoceras verrucosum* ammonite Zone, Col Lazarier section; H, RHP.05135-001.AA510, *Berriasibelus* Delattre, 1952, lower Valanginian, *Neocomites neocomiensiformis* ammonite Zone, Sainte Colombe. Scale bar represents 10 mm.

Ryazanian. This time interval coincides with the beginning of a Neocomian regression of Siberian seas when they experienced shoaling.

Further to the north, in the Boreal Arctic Province the diversity of the bathymetric settings was significantly higher than in the epicontinental north-west European



**FIG. 6.** Tethyan and boreal ammonite zonation schemes of the Valanginian and Hauterivian interval. The asterisk marks the occurrence of the boreal genus *Liobelus* in the Vocontian Basin. Ranges of Tethyan taxa observed in North-East Greenland are indicated in red. Absolute ages and ammonite zonation from Gradstein *et al.* (2020); belemnite data from Alsen & Mutterlose (2009) and the present study.

basin and the central Russian sea (Nikitenko *et al.* 2013; Kontorovich *et al.* 2014). This resulted in a higher taxonomic diversity of the belemnite associations. The genera *Arctoteuthis* and *Boreioteuthis* with a well-developed ventral groove and a circular to dorsoventrally depressed cross-section are common. According to Zakharov *et al.* (2014) these moderately active swimmers (PG II) inhibited perhaps the bottom layers of the seawater. The most active swimmers, common in the neritic zone (PG III), are characterized by slender, moderately elongated to elongated rostra, a weak ventral groove and a laterally compressed cross-section. The PG III genera (*Cylindroteuthis*, *Lagonibelus*, *Pachyteuthis*) began to decline from the Valanginian. According to the results of a detailed study of the basal Cretaceous sections in the Anabar region of northern Siberia, they were never the dominant group of belemnites in the Valanginian. They are most typical in the Berriasian (uppermost upper Volgian to Ryazanian; Zakharov *et al.* 2014; Efremenko 2021), where they are also common in the West Siberian Basin (Dzyuba *et al.* 2018).

*Cylindroteuthis*, *Arctoteuthis*, *Pachyteuthis* and *Lagonibelus*, present in Siberia, are rare or missing in the Boreal Atlantic Province. *Boreioteuthis*, common in the Pechora Basin and the central Russian Sea, migrated to north-west Europe only in the Hauterivian (*B. rawsoni*). *Arctoteuthis* is clearly dominating the Boreal Atlantic Province. The distinctive biogeographical provincialism exposed by boreal genera is not unlike that observed for the Tethyan faunas.

### Ecology

Both biological and autecological factors potentially controlled the biogeographical patterns discussed here. Biological limitations include reproductive strategies as well as the swimming capabilities of individual genera. Ontogeny steers the spatial dispersal via the course and duration of the post-spawning egg and paralarval stages. Most recent squids attach large numbers of fertilized eggs to the substrate, which then develop on their own. This is in contrast to a post-spawning, pelagic egg care behaviour, which has been observed for some deep-sea squids (Seibel *et al.* 2005). *Gonatus onyx*, one of the most abundant coleoid species in the Pacific and Atlantic Oceans, transports bundles of 2000–3000 eggs in water depths of 1500–2500 m. Large, yolk-rich eggs and cold temperatures mean that it may require up to 9 months until the hatchlings are released (Seibel *et al.* 2000). The lifespan and ontogeny of the planktonic paralarvae is yet another regulating factor. Recent squid paralarvae of *Doryteuthis opalescens* actively control their distribution and dispersal after a short passive drifting period of about a month

(Vidal *et al.* 2018). Most recent coleoids, in particular the squids, are fast swimmers. Recent *Brachioteuthis picta*, for example, has been observed throughout the water column to a depth of 1000 m, with little evidence of ontogenetic descent (Rodhouse & Piatkowski 1995). *Galiteuthis glacialis*, in contrast, occurring from 200 to 1000 m, shows evidence of ontogenetic descent with larger sized specimens being caught at 800–1000 m. In addition, diel vertical migration has been described by Rodhouse & Piatkowski (1995).

It has been suggested that most belemnites were fast-swimming predators that lived in shallow marine settings relatively close to the coast (e.g. Naef 1922; Christensen 2002; Mutterlose *et al.* 2012, 2020; Doguzhaeva *et al.* 2013). Although rare occurrences of belemnites have been recorded from open ocean settings, belemnite assemblages of high abundance have so far been described only from epicontinental environments. These are rich in benthic, nektobenthic and nektonic organisms as a plentiful food supply.

Alternatively, a nektobenthic lifestyle and possible diurnal vertical migration in the water column has been suggested (Wierzbowski & Joachimski 2007). This view is based on positive  $\delta^{18}\text{O}$  values of some Jurassic belemnites, indicating low seawater temperatures close to those obtained for co-occurring benthic organisms. Higher positive  $\delta^{18}\text{O}$  values, which have also been observed in Cretaceous belemnites, have been explained by a nektonic lifestyle below a shallow thermocline with a depth habitat of perhaps 50–100 m (Mutterlose *et al.* 2010). Various  $\delta^{18}\text{O}$  data gained from several ontogenetic growth lines of individual belemnite rostra support the view of a consistent, stable nektonic life without major ontogeny-related depth changes.

Autecological factors, which control the survival of a genus, include physical and chemical parameters such as food, temperature or salinity. Not very much is known about the diet of belemnites. The assumption of Schweigert (2018) that belemnites were preying on small fish, ammonites and nautiloids is based on the co-occurrence of well-preserved *Hibolithes* rostra and their potential prey in the same horizons from the Late Jurassic. This view is supported by the occurrence of belemnites in Toarcian and Cretaceous black shales, which were deposited under anoxic bottom water conditions. These findings in sediments, which are barren of benthos but rich in nektonic organisms, indicate that belemnites lived as active predators of co-occurring fish and/or ammonites.

The existence of a Tethyan and a Boreal Realm has been related to different climate regimes, where surface water temperatures controlled the spatial distribution of belemnites and other organisms (Stevens 1973a, 1973b). Varying temperature tolerances of individual genera (eurythermal, stenothermal) may thereby explain the

biogeographical differentiation described here (e.g. Mutterlose 1988a; Christensen 2002). It cannot, however, be excluded that competition (i.e. the presence of different belemnite genera, well adapted to a specific setting and to a specific diet) may have limited the expansion of potential migrants. *Hibolithes*, in contrast, was able to spread over large areas, it colonized the Boreal Realm successfully and evolved endemic species.

In summary both biological and ecological factors probably regulated the dispersal of the actively swimming belemnites. As nektonic organisms they preyed on soft-bodied organisms, most probably fish. The varying biogeographical patterns of individual genera suggest genus-specific biological differences (ontogeny, swimming capabilities). *Hibolithes* was the most euryoecious belemnite taxon in the Valanginian and Hauterivian, and it settled in both the Tethyan and the Boreal Realms.

## CONCLUSIONS

The biogeographical patterns of Valanginian belemnites, described here, allow us to draw the following conclusions:

1. Boreal belemnite taxa show distinctive, genus-specific migration patterns. *Acroteuthis* is the most cosmopolitan genus in the high latitudes, being present in all different provinces of the Boreal Realm. Both *Acroteuthis* and *Liobelus* dominated the periphery of the Boreal Realm (north-west Europe, central Russia), suggesting that they were ecologically robust taxa.
2. *Liobelus* migrated to the Tethys, either via the Rockall Trough or, more likely, via the Carpathian seaway.
3. Our observations enable the differentiation of two assemblages: Tethyan Fauna 1 (*Duvalia*, *Pseudobelus*, *Hibolithes*) and Tethyan Fauna 2 (*Adiakritobelus*, *Berriasibelus*, *Castellanibelus*, *Mirabelobelus*, *Vaunagites*). The former group was able to invade the Boreal Realm, the latter remained rather restricted to parts of the western Tethys (south-east Spain, southern France, Switzerland, the Austrian Alps, Moravia-Silesia, Hungary and Crimea).
4. North-East Greenland served as a hub for Tethyan belemnite genera immigrating into the Boreal Realm. *Duvalia*, *Pseudobelus* and *Hibolithes* (Tethyan Fauna 1) successfully made their way into the Boreal Realm. The capacity to spread to Svalbard, and further to north-west Europe and east to the Pechora Basin and Siberia, decreased. Only *Hibolithes* obtained a near cosmopolitan distribution, with species-specific endemic adaptations in the Boreal Realm.
5. The biogeographical patterns discussed here suggest that the successful colonization of new ocean areas by

belemnites was in part controlled by their swimming abilities and/or their ontogeny. Certain taxa were able to outcompete others, which were less well adapted. This applies to both Boreal and Tethyan taxa. In the Valanginian, *Acroteuthis* and *Liobelus* were most typical for the Boreal Arctic and Boreal Atlantic provinces, while *Hibolithes* is the most cosmopolitan Tethyan genus. *Hibolithes* also formed the stock group for the *Neohibolites*–*Praectinocamax* assemblages of the middle and Late Cretaceous belemnite faunas.

## SYSTEMATIC PALAEOLOGY

One rostrum of boreal origin, *Liobelus acrei*, has been encountered in the 502 specimens of the Col Lazarier section. The remainder of the material can be attributed to the Tethyan belemnite families Duvaliidae (*Berriasibelus*, *Castellanibelus*, *Duvalia*, *Pseudobelus*) and Belemnopseidae (*Adiakritobelus*, *Hibolithes*, *Mirabelobelus*, *Vaunagites*).

Order BELEMNITIDA Zittel, 1895

Suborder BELEMNITINA Zittel, 1895

Family CYLINDROTEUTHIDIDAE Stolley, 1919

The boreal family Cylindroteuthididae is defined by cylindrical to cylindrical, medium- to large-sized rostra, with a ventral apical groove and a cyrtolinate apical line. The family first appeared in the Bajocian and became extinct in the Aptian. Currently it includes 13 genera, which have been described in detail by Dzyuba (2004, 2011). The family consists of five subfamilies, including the Pachyteuthidinae (*Pachyteuthis*, *Acroteuthis*, *Boreio-teuthis*, *Microbelus*) and the Simobelinae (*Simobelus*, *Liobelus*). The species under discussion, originally described by Swinnerton (1936) as *Acroteuthis acrei*, has more recently been assigned to *Liobelus* by Dzyuba (2004) based on the stout rostrum solidum and the very deep alveolus.

Genus LIOBELUS Dzyuba, 2004

*Type species.* *Belemnites russiensis* d'Orbigny, 1845 (by original designation).

*Species included.* *Liobelus lindseyensis*, *L. partneyi*, *L. praecorpulentus*, *L. prolateralis* (middle to upper Volgian), *L. aulacolateralis*, *L. russiensis* (middle Volgian to Ryazanian), *L. lateralis* s.l. (upper Volgian to Valanginian), *L. uralensis* (Ryazanian), *L. chetae* (lower Valanginian), *L. acrei*, *L. posterior* (Valanginian to lower Hauterivian), *L. paracmonoides* (upper Valanginian to lower Hauterivian), *L. stolleyi*, *L. trautscholdi* (upper Hauterivian).

*Diagnosis.* Medium to large-sized, robust rostrum, cylindrical to cylindrical with a flat venter; rostrum solidum mostly



stout; apex round acute to wide acute; cross-section depressed, subquadrate to elliptical; ventral apical groove may be well-defined, short or long; apical line strongly cyrtolineate; alveolus occupies one-half to two-thirds of the rostrum, tip of alveolus ventrally displaced; alveolar angle 19–26°; juvenile rostrum solidum generally moderately slender.

*Stratigraphic and geographical distribution.* Middle Volgian to Hauterivian of northern Europe, eastern Europe, western Kazakhstan, and Siberia.

*Liobelus acrei* (Swinerton, 1936)

Figure 7

- 1906 *Belemnites* aff. *pseudopanderi* Sinzow; Danford, pl. 3, fig. 16; pl. 6, fig. 16.  
 1936 *Acroteuthis acrei* Swinerton, p. 14, pl. 4, figs 7, 8; pl. 5, figs 9–13.  
 1966 *Acroteuthis (Acroteuthis) acrei* Swinerton; Sachs & Nalnjaeva, p. 119, pl. 29, figs 1–3; pl. 30, fig. 1; text-fig. 42.  
 1988b *Acroteuthis (Acroteuthis) acrei* Swinerton; Mutterlose, p. 76, pl. II.2/1, fig. 1.  
 1992 *Acroteuthis acrei* Swinerton; Kemper, pl. 3, fig. 3.  
 1992 *Acroteuthis (Acroteuthis) acrei* Swinerton; Mutterlose, pl. 12, fig. 2.  
 2004 *Simobelus (Liobelus) acrei* (Swinerton); Dzyuba, p. 70, 72.

*Material.* One specimen from the *Neocomites neocomiensiformis* ammonite Zone (lower Valanginian) of the Col Lazarier section (RHP.26376-001.AA504). Rostrum almost completely lacking the alveolar part. The specimen is stored in the Thomel-Picollier collection.

*Description.* Large and very stout, cylindrical rostrum, ventral flattening, apex wide acute, almost centrally located; cross-section moderately depressed; weak and short apical groove; alveolus very deep.

*Remarks.* The species resembles *L. chetae* but differs in its more acute apex ending in a keeled tip. From *L. posterior* it is distinguished by a stouter rostrum, which is larger in size, and its faint and shorter apical groove. *Liobelus acrei* is similar to *L. paracmonoides* in groove and apex, but is larger and more robust.

*Stratigraphic and geographical distribution.* Lower Valanginian (*Neocomites neocomiensiformis* ammonite Zone) at Col Lazarier (this study). Upper Ryazanian?, Valanginian–Hauterivian in North-East Greenland, lower–upper Valanginian in western and north-central Siberia (Sachs & Nalnjaeva 1966; Efremenko 2021), upper Valanginian in the Pechora Basin (Sachs & Nalnjaeva 1966), Germany (Pinckney & Rawson 1974; Mutterlose 1990), Bed D2D (i.e. condensed upper Valanginian at Speeton, UK; Swinerton 1936). The absence of *L. acrei* in the lower Valanginian of the Pechora Basin, the Russian Platform, Germany and Speeton is here explained by its poorly studied status in these regions, as it has been recorded in the lower Valanginian from North-East Greenland and Siberia.

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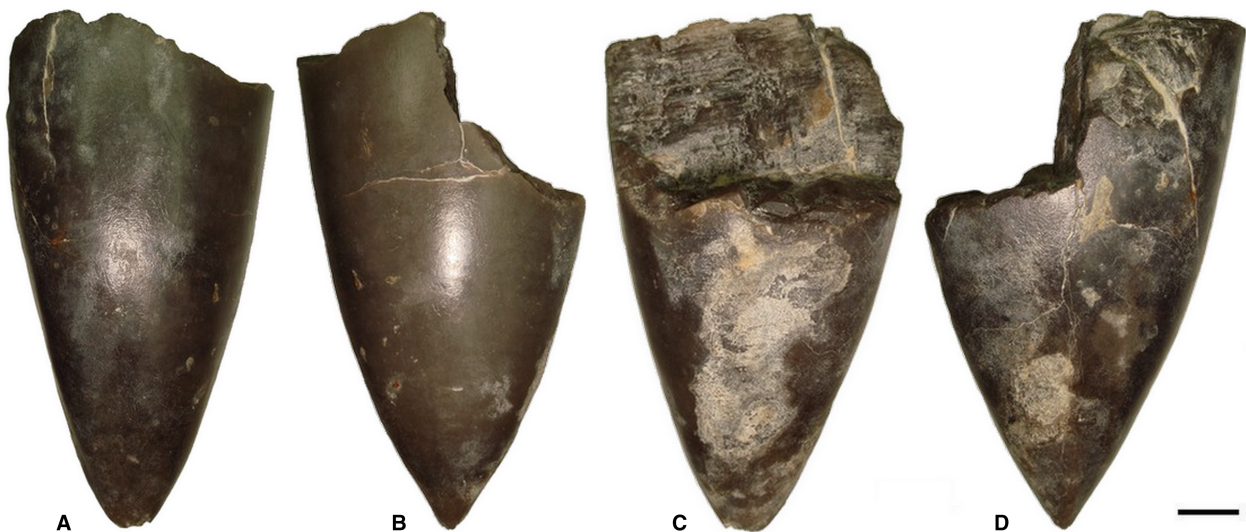


FIG. 7. The boreal belemnite species *Liobelus acrei* (Swinerton, 1936) from Col Lazarier, Vocontian Basin, France (RHP.26376-001.AA504). A, lateral view, venter left. B, dorsal view. C, lateral view, venter right. D, ventral view. Scale bar represents 10 mm.



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*Author contributions.* JM conceptualized the current paper, compiled the text and designed some of the figures. MCP collected the belemnite material from the Vocontian Basin, provided the taxonomy and drafted some of the figures. OD supplied information on the taxonomy and distribution of the boreal belemnites.

*Editor.* John Jagt

## SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.1455>):

**Appendix S1.** Further information on strontium isotope ratios and a list of all belemnite specimens included in this study.

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