



Dwarf megateuthiid belemnites from the Bathonian of Kachchh (India: Gujarat) and their significance for palaeobiogeography

Alexei P. Ippolitov ^{a*} and Bhawanisingh G. Desai ^b

^aGeological Institute of Russian Academy of Sciences; Pyzhevsky Lane 7, 119017 Moscow, Russia; ^bPandit Deendayal Petroleum University; Gandhinagar District, Raisan, 382007 Gujarat, India

(Received 15 November 2016; accepted 20 February 2018)

We describe in detail new finds of dwarf megateuthiid belemnites from the Middle–Late Bathonian of Kachchh (Western India), previously only rarely mentioned in the literature. The material is assigned to a new genus and species, *Challinoria challinori* gen. et sp. nov. Extensive morphological comparison together with analysis of the biogeographical distribution of comparable taxa suggests affinity of the newly described taxon with Early Bajocian megateuthiids from South America, showing the existence of a previously unknown megateuthiid habitat area in the Southern Hemisphere during the Bajocian and Bathonian. The biogeographical patterns and trans-equatorial migration routes of Middle Jurassic megateuthiids are discussed. The occurrence of the newly described taxon in the Bathonian of India, along with the lack of Mediterranean and Indo-Pacific records of similar age, may be connected with the short-term opening of a marine trans-Gondwanan seaway.

<http://zoobank.org/References/urn:lsid:zoobank.org:pub:F5F7B7E6-ABA2-4EAF-A56C-9025075428A0>

Keywords: belemnites; Megateuthiidae; *Challinoria* gen. nov.; Bathonian; Kachchh; palaeobiogeography

Introduction

Belemnite assemblages of the Middle Jurassic of Gondwana, and particularly India, are known to be represented mainly by members of the families Belemnopseidae Naef, 1922 (predominantly the genera *Hibolithes* de Montfort, 1808 and *Belemnopsis* Bayle, 1878) and Dicoelitidae Sachs & Nalnjaeva, 1967; both of these families belong to the suborder Belemnopseina Jeletzky, 1965, which is characterized by alveolar grooves running backwards. On the other hand, in the Northern Hemisphere, members of the suborder Belemnitina von Zittel, 1895, which is characterized by apical grooves, were common from the Early Jurassic to the Early Cretaceous.

Among the former Gondwana fragments, finds of belemnites belonging to the suborder Belemnitina are relatively common in the Bajocian along the western margin of Gondwana (South America and the Antarctic Peninsula; see Stevens 1965; Challinor *et al.* 1992; Doyle *et al.* 1996, 1997; Doyle & Pirrie 1999; Challinor & Hikuroa 2007). In contrast, the northern, north-eastern, eastern and southern margins of Gondwana are marked by only a few records of Middle Jurassic Belemnitina.

Historically, the first record was ‘*Belemnites giganteus* Schloth.’ from the Bajocian of Algeria (Coquand 1862,

1880); a few years later, Lemoine (1906, p. 145) mentioned ‘*Belemnites* cf. *giganteus* Schloth.’ from Madagascar. Outside Africa, there is a small cylindroconical species from the Lower Bathonian of New Caledonia (‘Genus et species nov.’ in Challinor & Grant-Mackie 1989); probably a similar find was mentioned by Stevens (1963, fig. 37; 1973, fig. 1A). In New Zealand, Middle Jurassic belemnite records are presumably Latest Toarcian – Early Aalenian *Hastateuthis otagoensis* Challinor & Hudson, 2017 (= *Cylindroteuthis* sp. in Stevens, 1965 and Challinor *et al.*, 1992) and Late Bathonian ‘*Cylindroteuthis* (*Cylindroteuthis*) sp.’ of Challinor & Hudson (2017). In turn, specimens previously mentioned from the ?Bajocian of New Zealand as ‘*Brachybelus zietenii*’ (Werner, 1912) by Stevens (1965) and as ‘*Brachybelus* sp.’ by Challinor *et al.* (1992) are now supposed to be of latest Early Jurassic age along with other diversified Belemnitina (Challinor & Hudson, 2017).

An unusual single conical rostrum, also falling outside the typical belemnopseine assemblage, was described from Western India by Spath (1927, 1933), who illustrated a longitudinal split of an embedded conical rostrum and tentatively assigned it to ‘*Megateuthis* sp. indet. (?)’. For a long time, this find remained the only record of possible non-belemnopseine belemnites from the Middle Jurassic of India.

*Corresponding author. Email: ippolitov.ap@gmail.com

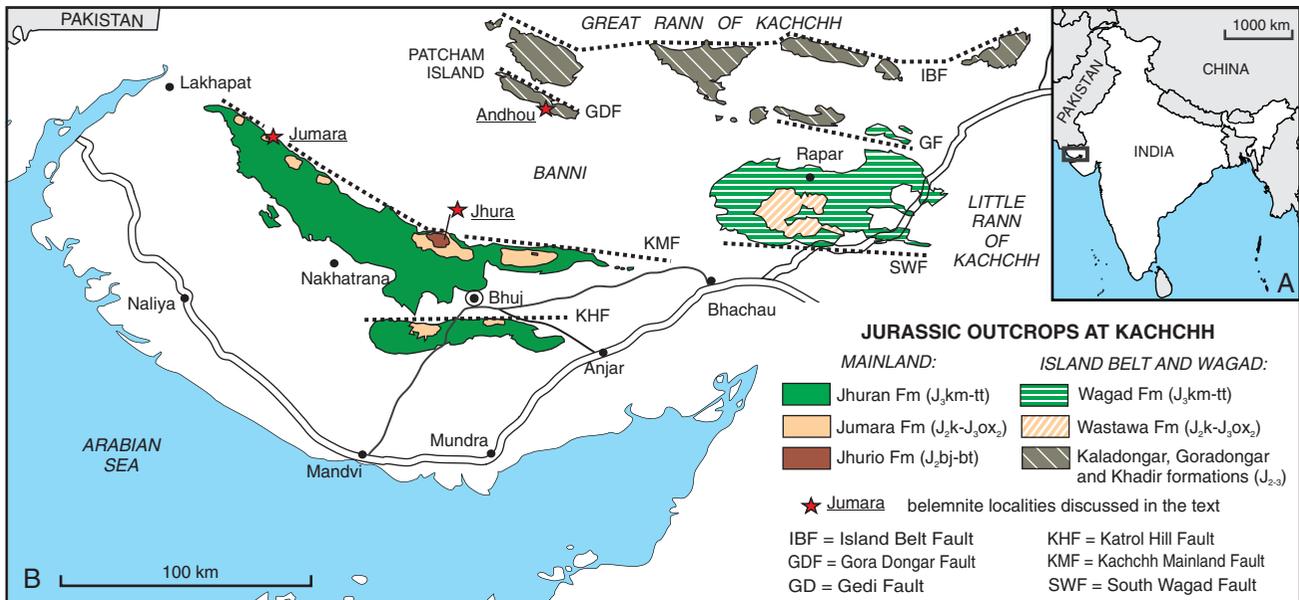


Figure 1. Geographical and geological positions of the belemnite localities discussed in the text. Geological map after Biswas (1980).

During the winter seasons of 2014 and 2015, the authors discovered a new locality in Kachchh containing abundant material that is similar to Spath's enigmatic specimen. Both new and historical specimens are described in detail in the present paper.

Geological setting and material

Short conical rostra representing 120 specimens in total were collected from the core of the Jumara dome section (Figs 1, 2), which is probably the most famous and best studied Middle Jurassic sequence in Kachchh. It exposes a nearly complete sequence from the Bathonian to the Oxfordian (Jain 2014; Dutta & Bardhan 2016). The oldest part of the Jumara dome is represented by shelly limestone of the lower Middle Bathonian Arkelli Zone (Jain 2014; the equivalent of the European Progracilis Zone), which is succeeded by 'coral meadows' and shelly micritic limestone deposited as distal tempestites (Fürsich 1998). The entire carbonate succession exposed in the core of the Jumara dome is Middle to Late Bathonian (Arkelli to Triangularis Zones) in age.

Most of the specimens were collected from the talus at 23°41.660' N, 69°4.125' E, where they were mixed with corals weathered from 'coral bed A' (*sensu* Fürsich *et al.* 1994, 2013). Several specimens were found with fragments of rock matrix comprising yellowish calcareous marl containing numerous bioclasts of corals, bivalves and gastropods as well as smaller indeterminate fossil fragments. The 'spotty' distribution of specimens over the scree and the similarity of matrix rock in all available cases led us to the conclusion that the majority of the fossils came from a single layer.

The outcrop of this layer, containing rostra *in situ*, was found in the same area at 23°41.609' N, 69°4.04' E (Fig. 2C–G). The rock is identical to that described above and is represented by a 50-cm-thick, dense calcareous marl with well-exposed upper and lower bedding surfaces, the top being markedly ferruginous. This surface exposes numerous smaller corals, many of which are lying on their sides or upside-down, disjunct, rolled and chaotically oriented *Solen* shells, crinoid stem fragments, articulated brachiopod shells, and carbonate pebbles. Belemnite rostra are relatively rare and can be fragmentary, their surfaces often densely covered with micro-borings and sometimes with isolated epibionts. All of this indicates a tempestite origin for the belemnite-bearing bed, which corresponds to coral bed A of Fürsich *et al.* (1994, 2013) and bed A4 of Jain (2014), and is dated to the early Middle Bathonian (Arkelli Chron).

A single fragment of a conical rostrum of the same type was picked in the talus of the lowermost part of the Sponge Limestone of Fürsich *et al.* (2013) (23°41.747' N, 69°4.22' E), corresponding to a level 0.7–1 m above its base. This level is dated to the Late Bathonian Triangularis Zone (Jain 2014). Morphologically, the specimen is indistinguishable from those collected from coral beds below, and it remains unclear whether it really originated from the sponge beds or was relocated there anthropogenically. Attempting to clarify this, we produced several thin sections: one with rock material filling the alveolus of the problematic find, a second including the surrounding layers, and two more that included the rock matrix of belemnite-bearing bed A4. Microscopically, the rock material from the Sponge Limestone differs clearly from that of the A4 level in the presence of numerous sponge spicules. Unfortunately, thin sectioning across the alveolus

of the problematic specimen revealed recrystallized crystalline calcite, which could be interpreted as a derivate from both bed A4 and the basal sponge meadows.

Jain (2014, fig. 4a) also mentioned belemnite finds from beds A2, A5b, the middle part of A6 and several levels of A8; these beds are essentially close to A4 and potentially could yield similar finds. During our study of the succession, we failed to find any belemnite rostra in A2 or A5b, while other levels yielded a few poor fragments of *Hibolithes* sp. (family Belemnopseidae) but no megateuthidids. A summary of the distribution of our belemnite finds across the Bathonian of the Jumara section is shown in Figure 2B.

Additionally, materials kept in the Natural History Museum, London (NHMUK) were studied by the first author. The only poorly preserved historical specimen NHMUK C.19961, collected by J. F. Blake in 1907 and figured by Spath (1927), originates from the Patcham Island region, specifically from the ‘Patcham dolomite’ (= Raimalro limestone; see Biswas 1980; Pandey & Dave 1993) at Andhou (Fig. 1B). This level is considered to be equivalent to the Sponge Limestone at Jumara (Fürsich *et al.* 2001, 2013) and is therefore dated to the Late Bathonian Triangularis Zone.

In addition to Spath’s specimen, the NHMUK collection contains another find by Blake (NHMUK C.19926) that has not been referred to and originates from the ‘Nucula Flags, Jooria’ (= Jhura Dome); the exact locality of this find remains uncertain. Blake introduced the term ‘Nucula Flags’ for *Nucula*- and other similar bivalve-rich flagstones; however, he never published any palaeontological or geological work on India. His large palaeontological collection, which has been housed at the NHMUK since the beginning of the twentieth century, was extensively used by later palaeontologists, and the term ‘Nucula Flags’ used in Blake’s sample labels found its way into the literature without any stratigraphical connotations. Several uncertainties exist concerning the precise age of Blake’s horizon at different localities, and the age may vary (Agrawal & Kachhara 1979; Agrawal & Pandey 1985; S. Jain, pers. comm.). Particularly at Jhura Dome, the name ‘Nucula flags’ was applied to shelly beds at different stratigraphical levels. Spath (1924), who reinterpreted the ammonites of Blake’s collection and his localities, discusses the ‘Nucula Flags’ exposed at the East of the Badi Section (within the Jhura Dome) and refers to *Obtusocostites obtusocosta* as occurring within the Nucula Flags. This ammonite genus is a definite Middle Callovian indicator (Dutta & Bardhan 2016). In another view, F. T. Fürsich (Fürsich *et al.* 2013; pers. comm.), in his description of the Jhura Dome succession, recently placed ‘Nucula Flags’ within the middle part of the Lower Callovian succession, listing several species of *Macrocephalites* (*M. formosus*, *M. madagaskariensis* and *M. dimerus*) found nearby. The listed species of

Macrocephalites normally occur at slightly different levels (Prasad 1998; Jain & Desai 2014).

Our examination of several different localities across the Jhura Dome (Jhura Camp, Badi) has shown that neither Lower Callovian ‘Nucula Flags’ nor Middle Callovian ‘Golden Oolite’ strata match the matrix of NHMUK C.19926: the former contains numerous bioclastics, whereas the latter is characterized by numerous ooids. A tiny juvenile conical rostrum, very comparable in matrix with the NHMUK specimen, was found at the Badi section (23°25.627’ N, 69°33.967’ E) within Unit G of the Jhurio Formation *sensu* Biswas (1980, 1993). This unit is interpreted as roughly analogous to the upper part of Jumara Coral Limestone and Sponge Limestone (Biswas 1993; Fürsich *et al.* 2013). The possible stratigraphical range for this find is Upper Bathonian (Procerites to Triangularis Zones).

In addition to the Indian megateuthidids, extensive comparative material was studied, including diverse Bajocian and Bathonian megateuthidids both from the Northern Hemisphere (European Russia: our own collections and the originals of I. S. Barskov (Mitta *et al.* 2004) and V. A. Gustomesov (1960), both housed at the Vernadsky State Geological Museum (VSGM), Moscow; Northern Eurasia: collections of Sachs & Nalnjaeva (1975) kept in the Central Siberian Geological Museum, Novosibirsk), and collections from the Southern Hemisphere, which were examined by API at the Museum La Plata (MLP), La Plata, Argentina.

Methods

The abundance of belemnite material obtained from virtually a single layer of a single locality allows the application of a biometric approach in our study. A list of the measurements performed and their abbreviations, modified after Dzyuba (2012), is given in Figure 3. Several of the measurements outlined on the figure require clarification. Due to imperfect preservation of the material (the apex and the initial part of the alveolus are commonly missing), the ‘classic’ systems used for conical rostra (e.g. Schlegelmilch 1998; Dzyuba 2012) are not fully applicable, as for many specimens it is impossible to obtain the essential standard dimensions – length of postalveolar part of the rostrum (PA), dorsoventral and ventral diameters (DV and LL, respectively) at alveolar tip. To permit analysis of the variability, we used as a principal descriptive characters the diameters of the ‘conventional’ section located in the mid-alveolus (diameter of alveolus II_a ≈ 1/2 outer lateral diameter LL’) with its diameters (DV’, LL’). The precise position of the mid-alveolus section always remains somewhat ambiguous without polishing the rostrum; however, because the variance of bias is accidental, on average the true position of the mid-alveolus section

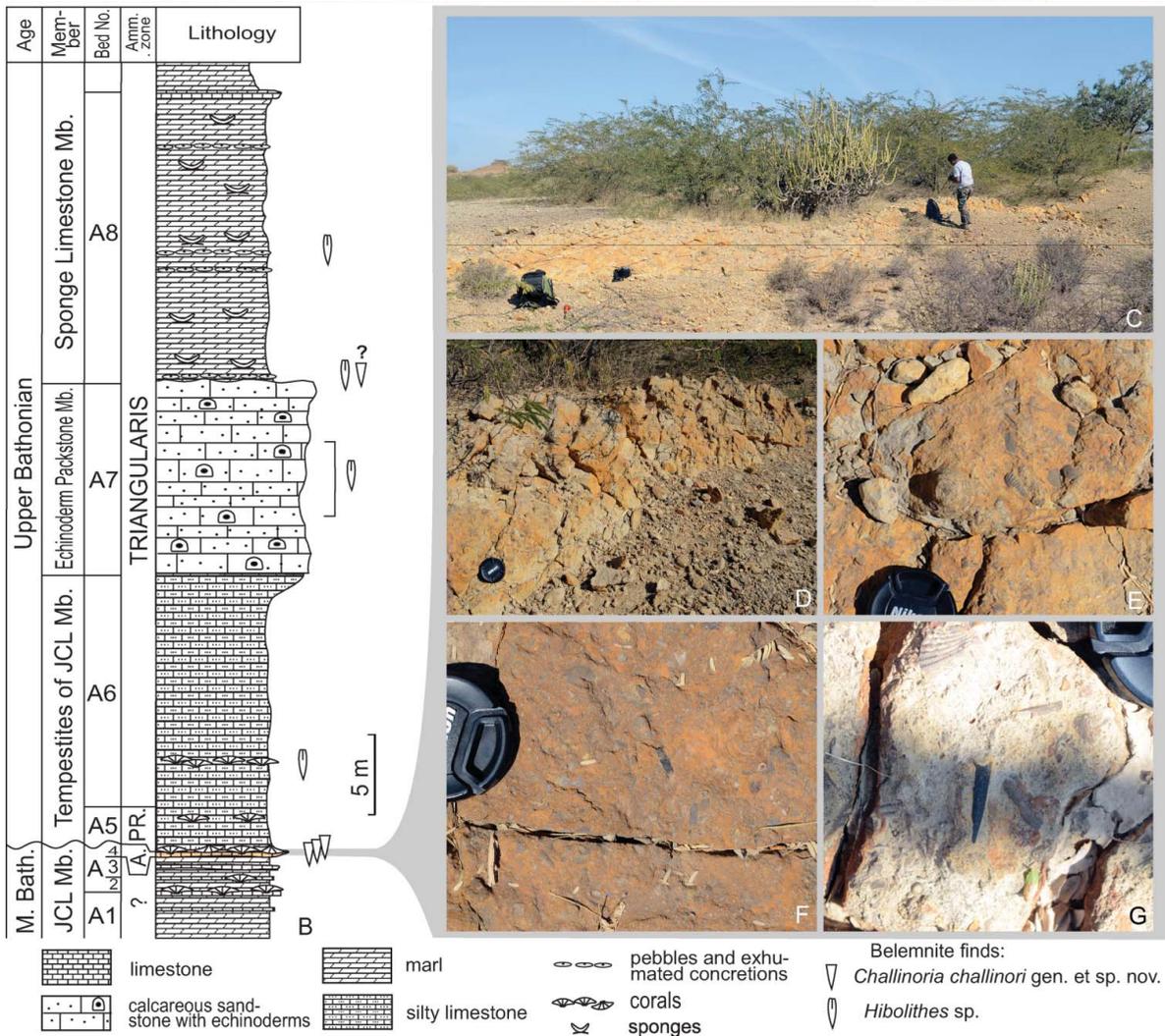
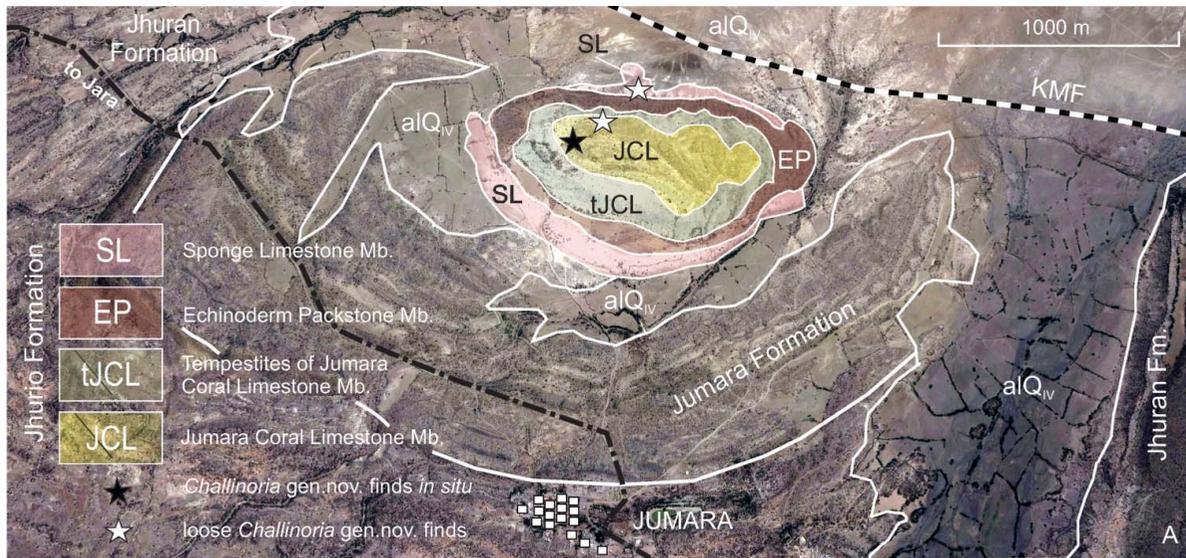


Figure 2. Details of the Jumara locality. **A**, structure of the Jumara dome core. **B**, Bathonian succession at Jumara (adapted from Jain 2014; A = Arkelli Zone, PR. = Procerites Zone) with distribution of belemnite finds. **C–G**, *Challinoria*-bearing level; **C**, general view of the belemnite-bearing bed A4 outcrop; **D**, top of the A4 bed, enlarged; **E**, reworked corals and *Solen* shells; **F, G**, *Challinoria challinori* gen. et sp. nov. rostra in situ. The diameter of the lens cap is 60 mm.

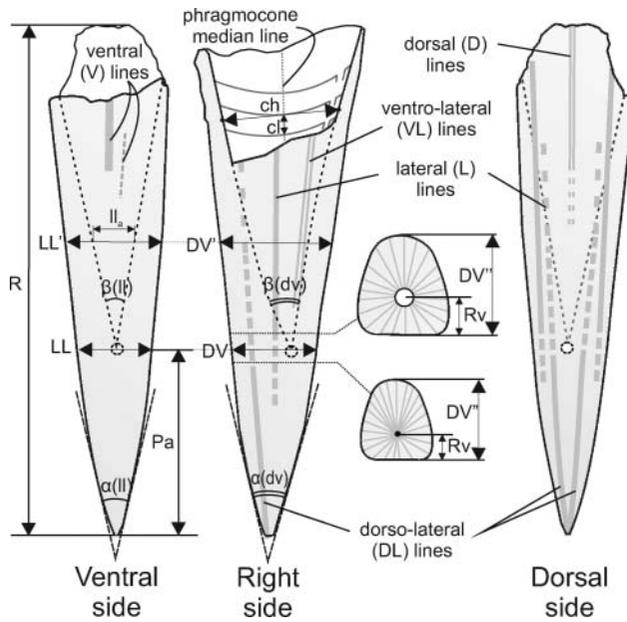


Figure 3. Measurement system applied to the studied material and the positions of grooves and lines over the rostrum surface. The transverse sections show two different ways of measuring the R_v parameter depending on the preservation of the specimen. Abbreviations are explained in the text.

should be reflected more or less confidently. Additionally, the compression ratio, calculated as LL/DV remains almost constant along most of the length (see description below); this means that the precise position of the mid-alveolus section, which obviously affects the LL' and DV' values, does not affect their ratio.

One additional parameter, DV'' – the dorsoventral diameter at preserved posterior cross section near the protoconch – in the ideal case coincides with DV but in practice is slightly shifted anteriorly or posteriorly of the protoconch, depending on the preservation of the specimen.

For characterizing size and shape, we also used the following ratios: D' , the average diameter at the mid-alveolus, calculated as the second root of both its diameters (dorsoventral and lateral; $D' = \sqrt{DV'' \cdot LL'}$), this ratio was counted as a principal size character for further analysis; LL/DV , the compression ratio at the alveolar tip; and LL'/DV' , the compression ratio at the mid-alveolus.

The alveolar angles $\beta(II)$ and $\beta(dv)$ were measured from photographs representing combined three-side projections (alveolar + lateral/ventral + apical sides) and showing the width of two transverse sections of the phragmocone and the distance between them. This method is far from precise but can provide a general idea of the variability of the phragmocone angles across the whole set.

For studying phragmocone ontogeny, we obtained dimensions using high-resolution photographs of polished longitudinal sections along the symmetry plane. We used

the following dimensions: cl , camera length, measured along the median line of the phragmocone; and ch , camera height, measured at the middle of the camera.

Most macro-photographs were prepared using ammonium chloride coating.

The original specimens are housed at the Vernadsky State Geological Museum, Moscow (VSGM) and the Pandit Deendayal Petroleum University (PDPU).

Systematic palaeontology

Subclass **Coleoidea** Bather, 1888

Order **Belemnitida** von Zittel, 1895

Suborder **Belemnitina** von Zittel, 1895

Family **Megateuthididae** Sachs & Nalnjajeva, 1967

Remarks. In its most recent revision (see Dzyuba *et al.* 2015), the Toarcian–Middle Jurassic family Megateuthididae includes a number of genera that show variable rostrum shapes (from lanceolate in *Simpsonibelus* Doyle, 1992 to perfectly conical in some *Megateuthis* Bayle, 1878 and *Paramegateuthis* Gustomesov, 1960) and cross sections (from round or even slightly depressed in *Brevibelus* Doyle, 1992 to strongly compressed in some *Megateuthis*), with very differently pronounced dorsolateral grooves and a ventral groove that may be present or absent. Although all the listed genera seem to be related, the demarcation of the whole family from the more ancient Early Jurassic Passaloteuthididae Naef, 1922, which are characterized by a similar set of rostral shapes but normally less pronounced dorsolateral grooves, is not obvious. Redefining the boundaries between these taxa is a subject for future research, and the monophyletic nature of the family Megateuthididae does not appear convincing at the moment. Especially suspicious among megateuthids are species of *Brevibelus* and belemnites described as *Dactyloteuthis* from Eastern Europe (Nikitin 1975; Ippolitov *et al.* 2015), which lack apical grooves.

Genus **Challinoria** gen. nov.

Type species. *Challinoria challinori* gen. et sp. nov.

Derivation of name. After Arthur Brian Challinor, a belemnite researcher from New Zealand who devoted his life to the study of the belemnite faunas of Gondwana.

Diagnosis. Conical Megateuthididae of dwarf size, not exceeding 40–50 mm in length, without epirostrum; with angular or subangular, rounded to oval, markedly compressed and often egg-shaped cross section, anteriorly flattened both at dorsal and ventral sides in adults; with incised paired dorsolateral apical grooves and a well-defined system of lateral lines over the rostrum. Alveolar angle normally between 17 and 25°.

Differential diagnosis. The genus differs from *Megateuthis* Bayle, 1878 in the tiny size of the adults, the absence of an epirostral growth mode (no epirostrum or ‘diffuse apical line’) and a well-defined system of multiple lateral lines, as well as by the absence of ventrolateral apical grooves. It differs from *Mesoteuthis* Lissajous, 1915, which has been synonymized with *Megateuthis* Bayle, 1878 by a number of recent authors (e.g. Doyle 1992; Dzyuba *et al.* 2015), in its long and remarkably conical shape, as well as its smaller size. It differs from *Paramegateuthis* Gustomesov, 1960 in its smaller size and, more characteristically, by the wider ventral side in the alveolar region, while in *Paramegateuthis* the dorsal side is wider at the anterior end (Fig. 4L–P). A remarkable difference from all three listed genera is the subangular appearance of the cross section at the anterior end and especially the presence of dorsal flattening in the alveolar region. Other genera of the family Megateuthididae included during the most recent revision (Dzyuba *et al.* 2015) demonstrate very different rostrum shapes (not compressed or not conical) and different grooving patterns (e.g. *Homaloteuthis*

Stolley, 1919, *Eocylindroteuthis* Riegraf, 1980), making confusion of any of these genera with *Challinoria* gen. nov. impossible. Latest Toarcian “Megateuthidinae n. sp. A” of Challinor & Hudson (2017), which demonstrate rostrum shape and lateral lines essentially similar to *Challinoria* gen. nov., do not have apical grooves and thus are likely to belong to Passaloteuthididae rather than to Megateuthididae.

Assigned species. Type species and an unnamed species from the Lower Bajocian of Argentina.

Occurrence. Lower Bajocian, Argentina; Middle–Upper Bathonian, Kachchh, India.

Remarks. The MLP collections contain a large number of diverse, conical, small-sized megateuthidids originating from the Neuquen Basin, Argentina. These materials were discussed extensively by Stevens (1965, pp. 158–159) and more recently by P. Doyle and co-authors (Doyle *et al.* 1996, 1997; Doyle & Pirrie 1999) but were never figured. Among numerous poorly preserved rostra

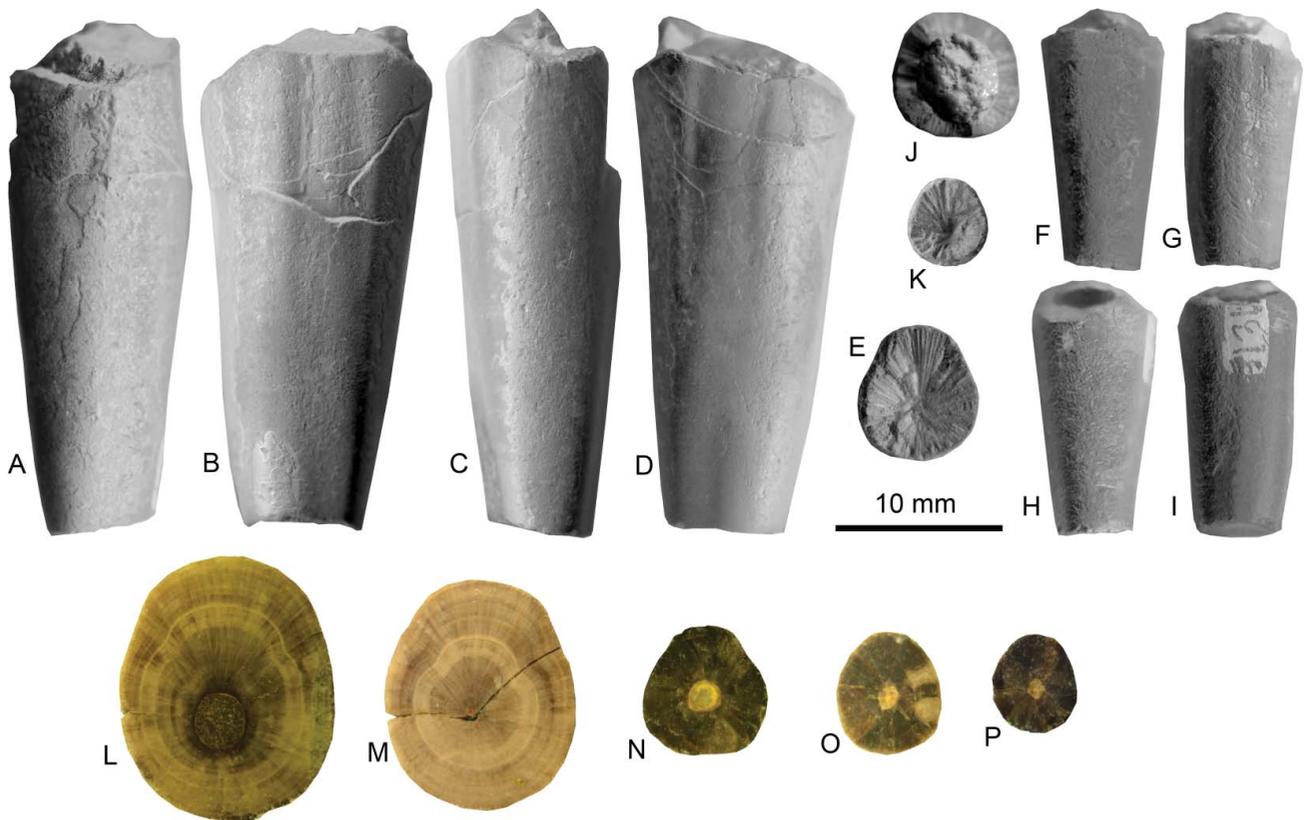


Figure 4. *Challinoria* from the Lower Bajocian of Argentina and comparison between *Challinoria* gen. nov. and early members of *Paramegateuthis*. **A–E**, *Challinoria* sp. 1, MLP 935/593, J. Frenguelli collection, Cerro Lapa, Neuquen, ?Lower Bajocian; **A**, ventral view; **B**, left view; **C**, dorsal view; **D**, right view; **E**, cross section at the posterior end of the fragment. **F–K**, *Challinoria* sp. 1, MLP 939/5131, J. Frenguelli collection, locality Cerro Lapa, Neuquen, ?Lower Bajocian. specimen with subquadrate cross section; **F**, ventral view; **G**, left view; **H**, dorsal view; **I**, right view; **J**, alveolar view; **K**, cross section at the posterior end. **L, M**, *Paramegateuthis gustomesovi* Stoyanova-Vergilova, 1983, VSGM CHU/20, East Caucasus, Dagestan, Lower Bajocian, Discites Zone, Walkeri Subzone (specimen figured in Ippolitov *et al.* 2015, pl. 5, fig. 7); **L**, cross section ahead of alveolar tip; **M**, cross section slightly back from alveolar tip; note the narrowing of the ventral side adorally. **N–P**, *Challinoria challinori* sp. nov. from Kachchh, Western India; cross sections ahead of the alveolar tip; all specimens are from the type locality and the type horizon; **N**, VSGM JUM/183; **O**, VSGM JUM/173; **P**, VSGM JUM/192; note that the cross section is egg-shaped with ventral side wider than dorsal one.

collected by J. Frenguelli in 1932 from the 'Bajocian' at the locality Cerro Lapa, multiple specimens were found that are similar to the Indian material (Fig. 4). According to Leanza *et al.* (1997), this hill exposes only the Los Molles Formation, which in this area is Toarcian–Lower Bajocian, but the fossiliferous part containing belemnites falls into the lower half of the Lower Bajocian (Singularis-Giebeli Zones; see Hillebrandt & Westermann 1985; Leanza *et al.* 1997, pp. 27–28).

These rostra were previously mentioned as '*Dactyloteuthis* sp.' by Stevens (1965, p. 158), and as '*Megateuthis*' or 'a small species of [*Megateuthis*]' by Doyle *et al.* (1996, 1997), and can be conventionally assigned to *Belemnites espinazitensis* Tornquist, 1898. However, under this name, Tornquist figured three rostra with evidently different grooving patterns and possibly even belonging to different genera. Consequently, the status of the name *Belemnites espinazitensis* is uncertain until revision and the designation of a lectotype. Like our specimens from India, some of these Argentinian rostra are characterized by dwarf size and well-defined lateral grooves at the alveolar region, but they are 1.5–2 times larger than Indian *Challinoria*. The cross section of the Argentinian rostra is slightly subangular in adults, and can be flattened at the dorsal side (Fig. 4J) and have the ventral side at the anterior end wider than the dorsal one, exactly as in Indian *Challinoria challinori* gen. et sp. nov. described below. The latter character is not known for the contemporary members of *Paramegateuthis* Gustomesov, 1960, from the Aalenian–Lower Bajocian of the European Tethys (Stoyanova-Vergilova 1983; Ippolitov *et al.* 2015), and justifies the position of Argentinian material within *Challinoria* gen. nov. No alveolar dorsal or ventral lines, which are characteristic of *Challinoria challinori* gen. et sp. nov., were observed.

***Challinoria challinori* sp. nov.**

(Figs 4N–P, 5, 7A–C)

v 1927 *Megateuthis* sp. ind.?; Spath, p. 19, pl. 2, fig. 2.

v 1933 *Megateuthis* sp. ind.?; Spath, p. 665.

v 2017 Megateuthididae gen. et sp. nov.; Ippolitov *et al.*, fig. 5C, D.

Holotype. VSGM JUM/167, almost complete rostrum of a young specimen with missing apical part. Lower part of the Middle Bathonian, Arkelli Zone (bed A4 of Jain 2014), 1.5 km north of Jumara village, Jumara dome, Kachchh, Gujarat, India.

Material. A total of 119 specimens. NHMUK C.19661 (figured by Spath 1927, pl. 2, fig. 2), represented by irregular longitudinal split of unclear orientation embedded in rock, with heavily recrystallized alveolar cavity, Raimalro Limestone, Andhou, Patcham Island. NHMUK C.19926,

full rostrum embedded in rock with right side exposed, Jhura Dome, exact locality and horizon unknown. VSGM JUM/1-33, 158, 165-201; PDPU B/1-7, 9-45, from the type locality and type horizon; of these, only four are relatively complete, while the others represented by fragments usually with missing apical parts; the complete specimens, except for the holotype, are all embedded in rock. VSGM JUM/164, from the type locality but found loose at the base of Sponge Limestone Member (bed A8). VGSM BAD-01, juvenile specimen from Jhura Dome (Badi section), Unit G of the Jhurio Formation.

Diagnosis. Small (rostrum full length, $R < 40\text{--}50$ mm) subconical to subcylindrical rostrum with markedly delimited apical part in adults. The cross section is compressed oval to egg shaped with ventral side clearly wider than dorsal, subangular to angular rounded in adults. In addition to paired apical dorsolateral grooves, the rostrum surface often bears two pairs of incised lateral lines, most pronounced anteriorly, and sometimes a wide and shallow dorsal one in the alveolar region.

Derivation of name. As for the genus.

Description.

Shape. Small-sized, short rostra, usually conical and rarely subconical in outline; the profile varies from conical to subconical and even subcylindrical in the anterior half. The ventral and dorsal margins are straight in the alveolar region and normally become convex when approaching the apex. The lateral margins are straight to slightly convex in the alveolar part when seen in outline and slightly convex near the apex when seen in profile. At the very anterior end of the alveolus, all the margins may be slightly concave, forming an extension.

The cross section is usually compressed (LL/DV and LL'/DV' = 0.81–0.99), egg shaped to rounded high triangular with wider ventral and narrower dorsal sides. However, certain specimens demonstrate relatively weak compression, and in some specimens the cross section is elliptical at least in the alveolar region (VSGM JUM/177). Compression remains seemingly uniform along the whole rostrum. The ventral side becomes clearly flattened anteriorly in most specimens. The narrower dorsal side also becomes clearly flattened anteriorly, but this occurs only in approximately half of the available specimens. The combination of lateral lines (see below) with dorsolateral grooves often produces longitudinal flattening in the upper half of the lateral sides.

The apex is slightly displaced ventrally. The apical part is well defined, being marked by a bend of the dorsal margin in profile view, followed slightly posteriorly by a less clear bend of the ventral side. The holotype also demonstrates a clear transition from a posterior conical to an anterior sub-cylindrical part on both lateral margins. The length of the apical part, observed in a few specimens,

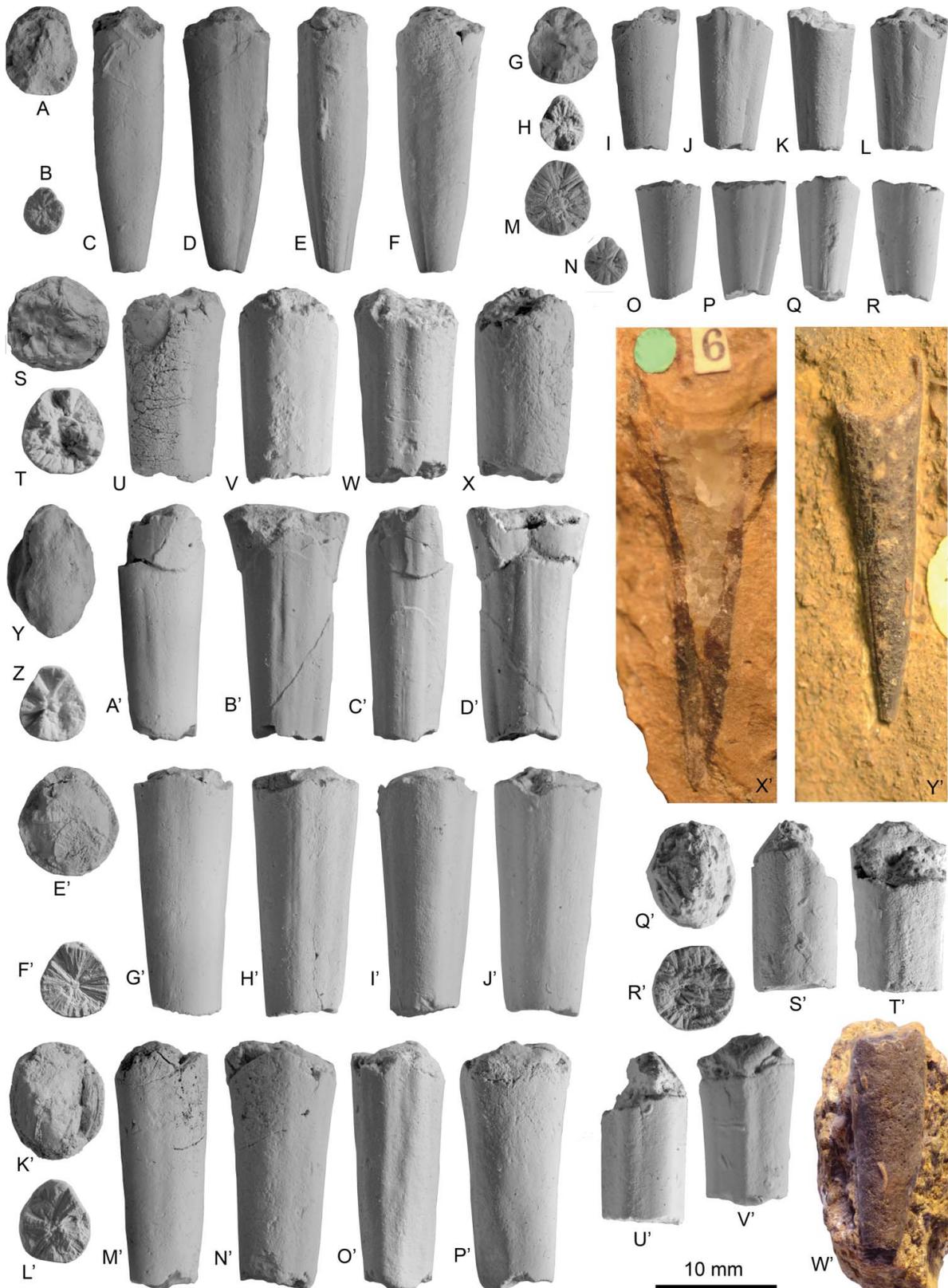


Figure 5. *Challinoria challinori* sp. nov. from Kachchh, Western India. All specimens are from the type locality and the type horizon unless otherwise stated. A–F, VSGM JUM/167, holotype, representing a modification with poorly developed lateral lines; A, alveolar view; B, apical view; C, ventral view; D, left view; E, dorsal view; F, right view. G–L, VSGM JUM/179, pathological (?) juvenile specimen with irregular ventral line and very rough lateral lines; G, alveolar view; H, cross section at the posterior end; I, ventral view; J,

roughly matches the length of the postalveolar part, which, in turn, does not exceed two-fifths of the total length of the rostrum. The apical angle in outline is $\alpha(\text{II}) = 12\text{--}17^\circ$ and in profile it is $\alpha(\text{dv}) = 17\text{--}22^\circ$.

Grooves and lateral lines. The rostrum bears paired adapical dorsolateral (DL) grooves, characteristic of all Megateuthididae. The grooves are deeply incised in the apical (= postalveolar) part of the rostrum and continue as flattened stripes (or rarely as shallow, wide depressions) to the anterior end of the rostrum. Additionally, the rostra demonstrate a complex of shallower longitudinal lateral lines, which are represented by (see also Fig. 3):

1. Mid-lateral lines (L) located just above the mid-height of the rostrum. They begin at the anterior end and tend to disappear in the apical part.
2. Lower lateral lines (ventrolateral, VL), located just below the mid-height of the rostrum and often having the appearance of typical ‘doppellinien’ (Fig. 5B’, D’, H’). They begin at the anterior end and disappear in the apical part. In most specimens, ‘doppellinien’ morphology is not obvious due to preservation, and the lateral lines have the appearance of a single line. The lower lateral lines are located at a distance of two-fifths DV from the ventral side when observed in cross section.
3. An unpaired dorsal (D) line running throughout the full preserved length of some specimens from the anterior end. This line was observed in only 11 of a total of 119 specimens; the depth and width were found to vary from strong flattening (Fig. 5U’) to a single wide and shallow depression (Fig. 5W, O’). In one specimen (Fig. 5C’), there is a distinct longitudinal ridge inside this wide depression, providing the appearance of ‘doppellinien’ in the dorsal line.
4. An unpaired very wide and shallow ventral (V) line of varying appearance (Fig. 5I, A’, S’); this is present only in the very anterior part of the alveolar region in a few specimens and is often somewhat asymmetrically placed (Fig. 5I, A’).

The surface also reveals fine longitudinal striations near the apex. The striae are of maximum length at the dorsal and ventral sides of the rostrum, where they can extend up to the alveolar part (VSGM JUM/03, JUM/167).

In the alveolar part of the rostrum, dorsolateral flattenings together with lateral lines often form flattened surfaces that are separated longitudinally from the lower lateral lines (= double lines) by a weak ridge (Fig. 5D, H’, T’, V’).

All the listed types of lines cannot be observed in a single specimen but are usually present in some combination. Their distribution across the whole set of specimens is shown in Table 1 and Supplementary Table 1. All types of lines tend to be better pronounced in less compressed specimens (Fig. 6), but this rule is not absolute.

Alveolus. The alveolus penetrates up to three-fifths of the total rostrum length. It has a slightly oval cross section, being laterally compressed. The phragmocone angle measured from photos in outline is $\beta(\text{II}) = 15\text{--}29^\circ$ (mode $19\text{--}22^\circ$); in profile, it is $\beta(\text{dv}) = 16\text{--}31^\circ$ (mode $21\text{--}23.5^\circ$). In three longitudinal sections, which provide more accurate results, the profile phragmocone angles are $\beta(\text{dv}) = 16.5^\circ, 19^\circ$ and 20.3° . The alveolus is remarkably asymmetrical in dorsoventral section, with the protoconch displaced ventrally ($\text{Rv/DV}'' = 0.24\text{--}0.50$ with a clear mode at $0.41\text{--}0.46$); in rare cases, it is displaced dorsally ($\text{Rv/DV}''$ up to 0.56). The margins of the alveolus are perfectly straight, not curved. The camera length in mature specimens is approximately $0.12\text{--}0.17$ of the corresponding phragmocone diameter; the septal lines are straight. The protoconch is rounded, $0.35\text{--}0.36$ mm in diameter (measured in two specimens, VSGM JUM/06 and VSGM JUM/170).

Proostracum. This was not observed.

Measurements. See Table 2 and Supplementary Table 1.

Ontogeny. Juvenile specimens tend to have rostra that are more conical in shape than those of adults and that possess distinctly concave margins near the anterior end, forming an extension. A longitudinal section obtained

left view; **K**, dorsal view; **L**, right view. **M–R**, VSGM JUM/03, subapical part showing fine dorsal and ventral striation; **M**, cross section at the anterior end; **N**, cross section at the posterior end; **O**, ventral view; **P**, left view; **Q**, dorsal view; **R**, right view. **S–X**, VSGM JUM/05, specimen with strong dorsal line and low compression; **S**, alveolar view; **T**, cross section at the posterior end; **U**, ventral view; **V**, left view; **W**, dorsal view; **X**, right view. **Y–D’**, VSGM JUM/02, specimen with incised ventrolateral doppellinien, indefinite dorsal doppellinien and asymmetrical ventral lines; **Y**, alveolar view; **Z**, cross section at the posterior end; **A’**, ventral view; **B’**, left view; **C’**, dorsal view; **D’**, right view. **E’–J’**, VSGM JUM/170, later polished; **E’**, alveolar view; **F’**, cross section at the posterior end; **G’**, ventral view; **H’**, left view; **I’**, dorsal view; **J’**, right view. **K’–P’**, VSGM JUM/171, pathologically distorted specimen with strong dorsal line, poorly seen ventral line and without definite lateral lines; **K’**, alveolar view; **L’**, cross section at the posterior end; **M’**, ventral view; **N’**, left view; **O’**, dorsal view; **P’**, right view. **Q’–V’**, VSGM JUM/10, specimen with subangular cross section and flattenings instead of lines on each view; **Q’**, alveolar view; **R’**, cross section at the posterior end; **S’**, ventral view; **T’**, left view; **U’**, dorsal view; **V’**, right view. **W’**, VSGM JUM/158, presumed dorsal side of pathologically curved specimen with micro-drillings and epibionts on the rostrum. **X’**, NHMUK C.19961, specimen figured by Spath (1927); longitudinal section presumably from the left side, showing re-crystallized alveola; Andhou, Patcham Island; Raimalro Limestone (Late Bathonian, Triangularis Zone). **Y’**, NHMUK C.19926, right side of the specimen embedded in rock; Jhura Dome, exact locality and horizon unknown (?Unit G of Jhurio Formation).

Table 1. Frequencies of different types of grooves and lines observed in *Challinoria* gen. nov. Specimens of poor preservation and those embedded in rock have been excluded.

Morph	Position of lines	Number of cases (and % of total)						Dorsal s. D	Ventral s. V
		Left side (^L)			Right side (^R)				
		DL ^L	L ^L	VL ^L	DL ^R	L ^R	VL ^R		
<i>Challinoria challinori</i> , total (n = 105)		50 (48%)	45 (43%)	53 (50%)	45 (43%)	43 (41%)	52 (50%)	11 (10%)	12 (11%)
morph A (n = 45)		21 (47%)	21 (47%)	24 (53%)	22 (49%)	18 (40%)	26 (58%)	5 (11%)	3 (7%)
morph B (n = 60)		29 (48%)	24 (40%)	29 (48%)	23 (38%)	25 (42%)	26 (43%)	6 (10%)	9 (15%)
<i>Challinoria</i> sp. (n = 4)		0	1 (25%)	1 (25%)	0	1 (25%)	1 (25%)	0	0

across one full rostrum (Fig. 7A) did not reveal any other clear ontogenetic changes in rostrum shape; however, the dorsal margins in young rostra can appear somewhat straightened (e.g. Fig. 5J, L). In the phragmocone, there is an obvious trend of reduction of the relative length of the phragmocone camerae (cl/ch), which gradually reduces from 0.26–0.20 in the earliest growth stages (camerae no. 1 to 10) to 0.19–0.16 (camerae no. 19 to ~34) and, finally, to 0.14–0.16 (camerae after the ~35th; see Fig. 7).

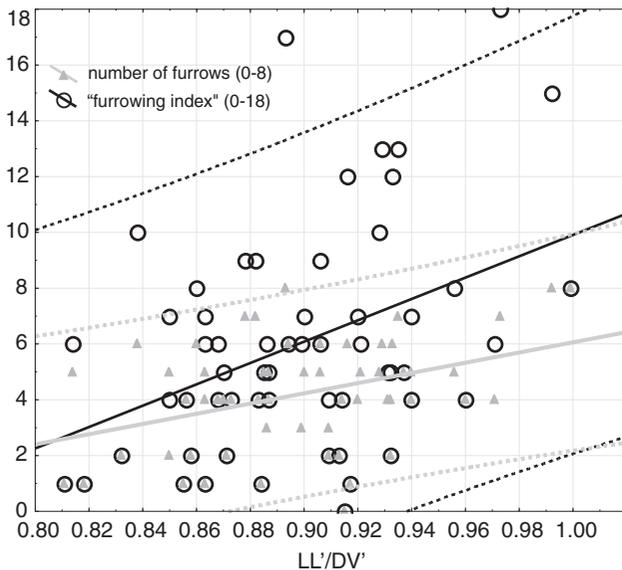


Figure 6. Interrelationships between total number of grooves and lines, ‘grooving index’ and compression rate in *Challinoria challinori* gen. et sp. nov. Both parameters are calculated from the data set in Supplementary Table 1. ‘Grooving index’ = simple sum of ‘+’ for each specimen, showing the total degree of lateral lines incision and their number. Because the descriptive characters of lateral lines are subjective, only specimens from VSGM (measured by API) are considered. The curves show 95% confidence of the prediction for total number of grooves = $-12.2382 + 18.2976 \cdot x$, and ‘Grooving index’ = $-28.361 + 38.272 \cdot x$.

Remarks. Spath’s (1927, p. 19, pl. 2, fig. 2) tentative assignment of his only specimen to the genus *Megateuthis* was based mainly on its general conical rostrum shape, which is similar to the juvenile stages of European Bajocian members of the genus *Megateuthis* Bayle, 1878. However, the Tethyan Middle Jurassic, particularly around the Bathonian–Callovian boundary, contains several taxa that have very similar conical shapes, leaving room for alternative interpretations of Spath’s specimen. Such specimens have been found both in Europe (e.g. *Conodicoelites glojenensis* Stoyanova-Vergilova, 1979; *Conobelemnopsis verciacensis* (Lissajous in de Grossouvre, 1919), see Schlegelmilch 1998, pl. 17, fig. 5) and in the Indo-Pacific area (*Conodicoelites keeuwensis* (Boehm, 1912)). Due to its unclear nature, the discussion of Spath’s find was omitted in all revisions and papers discussing Middle Jurassic belemnite biogeography (e.g. Stevens 1965; Challinor 1991a, b; Challinor et al. 1992), but was mentioned in biogeographical schemes by certain authors (Stevens 1963; Combémoré 1988). Our new finds unequivocally support Spath’s proposed affinity with the family Megateuthididae (formerly included in Passaloteuthididae, to which he refers it) as the new specimens demonstrate incised paired dorsolateral apical grooves that are characteristic of Megateuthididae.

Blake’s specimen NHMUK C.19926 from the Late Bathonian of the Jhura Dome (Fig. 5Y’) differs from most Middle Bathonian Jumara specimens in its pronounced conical shape with poorly defined apical part (the total angle of the conical rostrum is $\sim 10^\circ$, $\alpha(\text{dv}) = 16^\circ$), straight dorsal margin and long, deeply incised dorsolateral groove running along almost the full length of the rostrum. Conical shapes of this type occur in younger rostra (Fig. 5I–L) that are comparable in size to NHMUK C.19926, while incised and long grooves are found simultaneously within the set (Supplementary Table 1). Consequently, despite some stratigraphical isolation and morphological differences from Blake’s specimen, there are currently insufficient data to consider it a separate species different from the Middle Bathonian specimens. Two more finds, undoubtedly coming from the Late Bathonian

Table 2. Measurements and ratios of the selected specimens of *Challinoria challinori* gen. et sp. nov. Low precision measurements and coefficients are presented in italics. *, specimen was later polished for phragmocone study; HT, holotype.

No. in coll.	R, mm	PA, mm	DV, mm	LL, mm	LL/ DV	size (D, mm)	PA/D	DV', mm	LL', mm	LL'/ DV'	Size (D', mm)
VSGM JUM/1	17.06							6.04	5.65	0.94	5.84
VSGM JUM/2	19.55		6.18	5.37	0.87	5.76		7.12	6.36	0.89	6.73
VSGM JUM/3	10.22		6.03	5.31	0.88	5.66					
VSGM JUM/5	16.1							7.21	6.89	0.96	7.05
VSGM JUM/6*	24.8		5.04					5.79			
VSGM JUM/8*	21.06		7.47	6.4	0.86	6.91		7.92	7.13	0.90	7.51
VSGM JUM/158	18										
VSGM JUM/165		18.6	6.54	5.75	0.88	6.13	3.03				
VSGM JUM/167 (HT)	21.85	10.1	5.45	4.99	0.92	5.21	1.94	6.36	5.72	0.90	6.03
VSGM JUM/170	20.59		6.47	5.86	0.91	6.16		7.84	7.28	0.93	7.55
VSGM JUM/171	20.44		6.53	5.51	0.84	6.00		7.28	6.84	0.94	7.06
VSGM JUM/179	11.84		4.42	3.8	0.86	4.10		5.34	4.61	0.86	4.96
PDPUB/1	22.19	12.9	3.4	3.5	1.03	3.45	3.74	4.50	4.42	0.98	4.46

No. in coll.	α (ll) $^\circ$	α (dv) $^\circ$	DV', mm	Rv, mm	Rv, %	β (ll) $^\circ$	β (dv) $^\circ$	Morph	Figure in present paper
VSGM JUM/1	17	22				19	20	B	
VSGM JUM/2			6.2	2.7	43	19	23	A	Fig. 5Y–D'
VSGM JUM/3	12	20							Fig. 5M–R
VSGM JUM/5						18	19	B	Fig. 5S–X
VSGM JUM/6*		17	5.0	2.5	49		19		Fig. 7A,B
VSGM JUM/8*			7.4	3.5	47	24	30	B	Fig. 7C
VSGM JUM/158	16	17							Fig. 5W'
VSGM JUM/165			6.1	2.7	44		19		
VSGM JUM/167 (HT)								B	Fig. 5A–F
VSGM JUM/170			6.6	2.9	44	21	22	B	Fig. 5E'–J'
VSGM JUM/171			6.4	2.6	41	21	25	B	Fig. 5K'–P'
VSGM JUM/179			4.4	1.9	43	20	20	A	Fig. 5G–L
PDPUB/1		19						B	

Triangularis Zone (NHMUK C.19961, an embedded longitudinal section, and VSGM BAD-01, a juvenile rostrum) do not shed any more light on this comparison.

The pattern of distribution of surface lines in *Challinoria* gen. nov. is remarkable: neither dorsal nor ventral alveolar lines are known in any other genus of Megateuthididae. Lines in comparable positions are known from the specialized Late Toarcian family Salpingoteuthididae Doyle, 1992, with its single genus *Salpingoteuthis* Lissajous, 1915, which is characterized by a long epistrostrum developed over a short conical rostrum. In particular, *S. trisulcata* (de Blainville, 1827), *S. macra* (Quenstedt, 1848) and *S. dorsetensis* (Oppel, 1857) have dorsal lines that are differently combined with lateral lines/grooves (see Schlegelmilch 1998). In our opinion, the marked similarity with *Challinoria* gen. nov. does not necessary indicate a close affinity with *Salpingoteuthis* but is a common pattern of two related belemnite families with conical juvenile rostra, reflecting some common architecture of

the soft bodies. In addition, in *Challinoria* gen. nov., the dorsal and ventral lines are most remarkable in the alveolar region and tend to disappear backwards, whereas in *Salpingoteuthis* these lines are best seen on the epistrostrum, where they begin at the apex and slowly decline anteriorly.

Occurrence. Lower part of Middle Bathonian (Arkelli Zone) to Upper Bathonian (Triangularis Zone), except for type locality, Patcham Island and Jhura Dome.

Challinoria sp. 2

Material. Four fragments: VSGM JUM/34,155, 202, PDPUB/8.

Remarks. Several fragments from the Middle Bathonian of Jumara, determined here in open nomenclature, differ from *Challinoria challinori* gen. et sp. nov. by the stronger compression rate at the mid-alveolus ($LL'/DV' =$

cam. No.	VSGM JUM/06			VSGM JUM/08			VSGM JU/170			cam. No.
	$\beta(dv) = 19^\circ$			$\beta(dv) = 16.5^\circ$			$\beta(dv) = 20.3^\circ$			
	ch	cl	cl/ch	ch	cl	cl/ch	ch	cl	cl/ch	
prot.	0.35	0.35	1.00				0.36	0.36	1.00	prot.
1							0.43	0.12	0.29	1
2							0.46	0.12	0.25	2
3										3
4	0.52	0.12	0.23							4
5	0.57	0.13	0.23							5
6	0.62	0.13	0.20				0.65	0.16	0.25	6
7	0.64	0.15	0.23							7
8	0.71	0.16	0.23							8
9	0.79	0.17	0.22				? 0.19 ?			9
10	0.85	0.19	0.23				? 0.18 ?			10
11	0.93	0.24	0.26				? 0.22 ?			11
12	1.04	0.27	0.26				? 0.21 ?			12
13				1.23	0.23	0.19	? 0.25 ?			13
14				1.30	0.24	0.19	1.26	0.28	0.22	14
15				1.38	0.24	0.18	1.35	0.29	0.22	15
16				1.47	0.26	0.18	1.49	0.26	0.18	16
17				1.56	0.31	0.20	1.61	0.36	0.22	17
18				1.69	0.36	0.21	1.75	0.35	0.20	18
19				1.77	0.33	0.19	1.88	0.32	0.17	19
20				1.89	0.35	0.19	2.01	0.36	0.18	20
21				1.97	0.35	0.18	2.16	0.40	0.19	21
22				2.06	0.35	0.17				22
23				2.15	0.35	0.16				23
24				2.26	0.40	0.18				24
25				2.41	0.49	0.20				25
26	2.53	0.43	0.17	2.54	0.41	0.16				26
27	2.70	0.44	0.16	2.70	0.46	0.17				27
28	2.86	0.44	0.15	2.82	0.44	0.16				28
29	3.06	0.45	0.15	2.99	0.37	0.12				29
30	3.25	0.50	0.16	3.14	0.57	0.18				30
31				3.31	0.51	0.16				31
32				3.49	0.58	0.17				32
33				3.68	0.62	0.17				33
34				3.82	0.58	0.15	VSGM JUM/09			34
35				4.02	0.49	0.12	$\beta(dv) = 24^\circ$			35
36				4.23	0.77	0.18	ch cl cl/ch			36
37				4.49	0.55	0.12	4.41	0.69	0.16	37
38				4.79	0.53	0.11	4.73	0.64	0.14	38
39							5.00	0.72	0.14	39
40							5.30	0.79	0.15	40
41							5.64	0.79	0.14	41
42							5.99	0.91	0.15	42
43							6.49	1.06	0.16	43

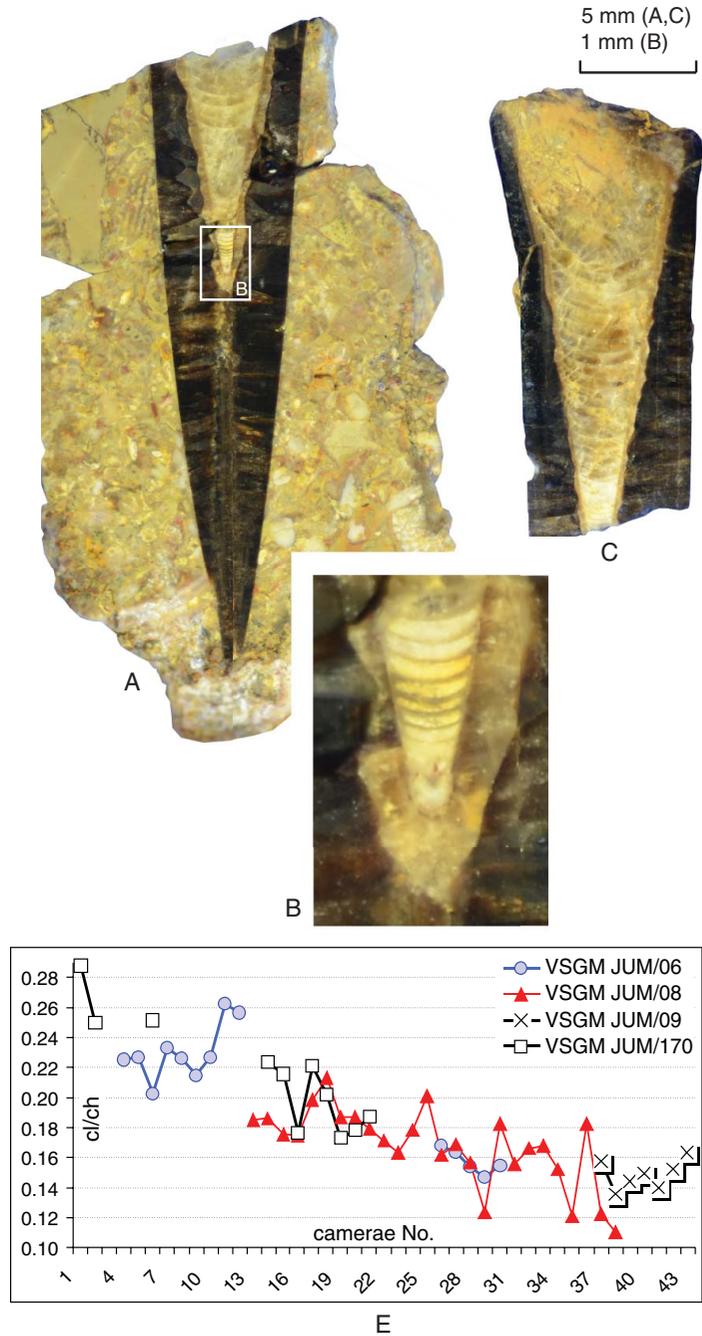


Figure 7. Phragmocones of *Challinoria challinori* gen. et sp. nov. from the Middle Bathonian of Jumara and their ontogeny. **A, B,** longitudinal section of VSGM JUM/06 from the left side; **B** shows the protoconch and the initially aragonitic ‘primordial rostrum’ surrounding it. **C,** longitudinal section through VSGM JUM/08. **D,** measurement data of camera length (cl) and camera height (ch) in specimens with studied phragmocones. The index number of camerae, if the sequence does not start at the protoconch, was determined from its size, compared with the size of the sequence, started immediately from the protoconch or calculated previously. **E,** ontogenetic changes of relative cameral length (cl/ch) in *Challinoria challinori* gen. et sp. nov.

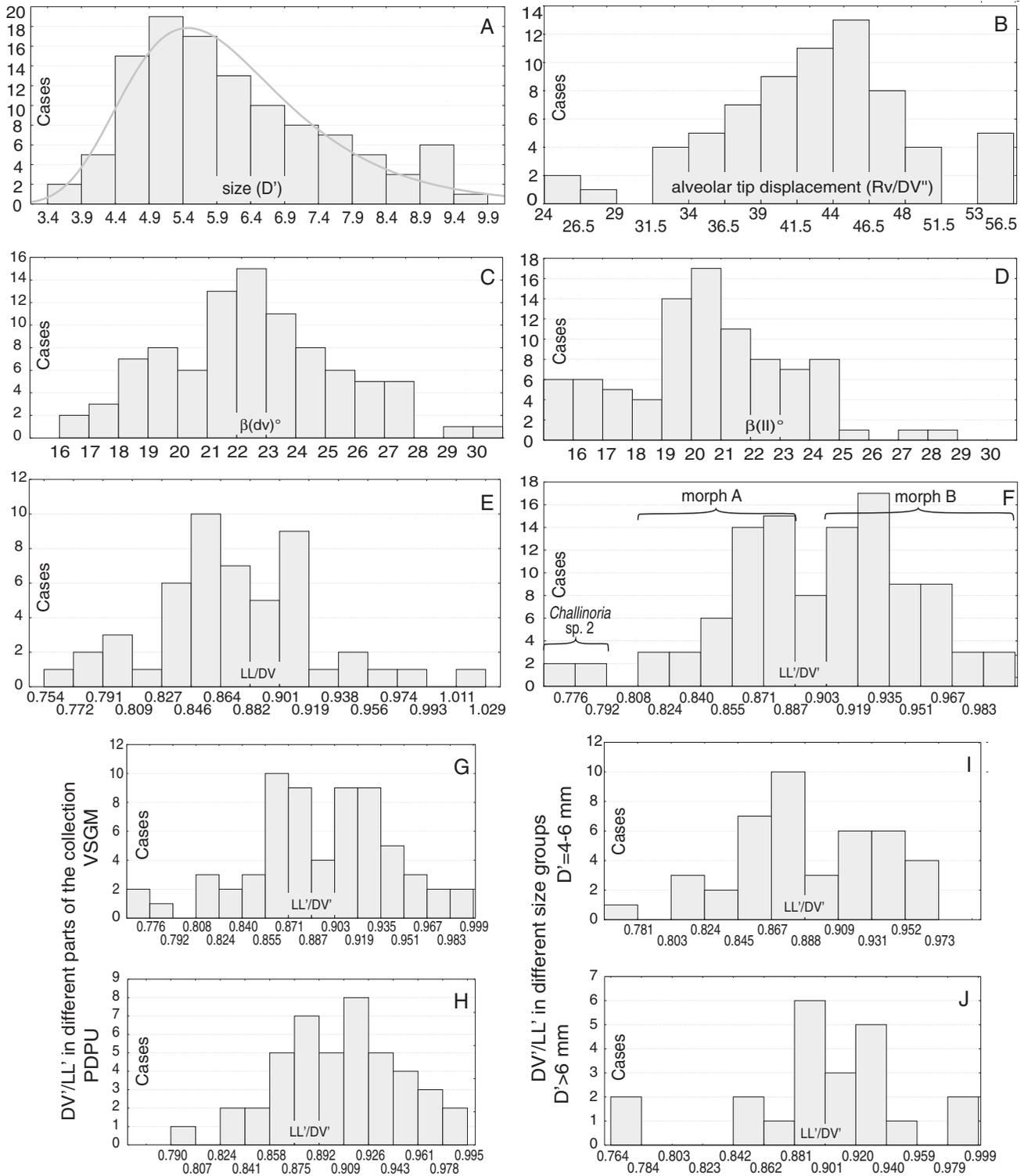


Figure 8. Variability of principal characters in *Challinoria* gen. nov. **A**, size (D') distribution. **B**, alveolar tip displacement (Rv/DV'') distribution. **C**, phragmocone angle measured in profile $\beta(dv)^\circ$. **D**, phragmocone angle measured in outline $\beta(II)^\circ$. **E**, compression ratio at the protoconch section (LL/DV). **F–J**, compression ratios at the mid-alveolus (LL'/DV'); **F**, full set; **G**, subset of specimens housed at VSGM and measured by API; **H**, subset of specimens housed at PDPU and measured by BGD; **I**, subset of smaller ($D' = 4–6$ mm) rostra; **J**, subset of larger ($D' > 6$ mm) rostra.

0.76–0.79) and are isolated from the main set on the histograms (Fig. 8). They have compressed oval (never egg-shaped) cross sections, and three of the four specimens are characterized by smooth surfaces without lateral lines, whereas the remaining specimen has only weakly developed lateral lines. A single juvenile (VSGM JUM/202) has an extremely narrow, almost sharpened dorsal side. The fragments are of different sizes; therefore, their peculiarities are not explained by differences in the stage of ontogeny of the specimens. The listed differences may indicate that the described specimens belong to different species within the same genus. However, the available material is too poorly preserved to firmly support this conclusion.

Occurrence. Jumara dome, 1.5 km North of Jumara village; Middle Bathonian; bed A4 *sensu* Jain (2014).

Discussion

Intraspecific variation in *Challinoria challinori* gen. et sp. nov.

Because all of our specimens, with the exception of VSGM JUM/164, which may possibly come from the base of bed A8, seem to derive from the single level A4, they can be treated as a single palaeopopulation, demonstrating intraspecific variability at the selected time slice.

The size distribution over the set is lognormal (Fig. 8A), showing the mode of D' at 4.9–5.4 mm and a drastic disappearance of juveniles in the set (only two specimens have an average diameter of less than 3.9 mm). The wide and steep right branch of the same histogram shows that the size of the largest specimens is almost twice that of the mode of the whole set. This means that the whole set demonstrates great size diversity and therefore that the locality is more likely to be close to the natural habitat area than to represent burial at a remote spawning point. The tempestite nature of the bed suggests that the observed absence of juveniles is a result of the post-mortem sorting-away of their smaller and lighter rostra. This conclusion is consistent with the presence of partially crushed rostra within the same bed.

The most remarkable character of the whole set is the distribution of compression rates. Both at the protoconch cross section (LL/DV; Fig. 8E) and in the mid-alveolus section (LL'/DV'; Fig. 8F), the set demonstrates bimodal distribution into two classes. The first class is characterized by $LL'/DV' = 0.81–0.89$ with mode 0.855–0.887 (morph A; $n = 45$), and the second has $LL'/DV' = 0.90–1.00$ with mode 0.903–0.935 (morph B; $n = 60$). This separation was confirmed on various subsets of Russian and Indian counterparts of the collection that were measured separately by API and BGD, respectively (Fig. 8G, H), as well as by the presence of two different size classes

($D' = 4–6$ mm and $D' > 6$ mm; Fig. 8I, J). In the $D' > 6$ mm size group, both the peaks and the gap separating them are slightly shifted to the right, indicating a very slight decrease of the compression rate during ontogeny. The holotype belongs to morphotype B.

Morphs A and B demonstrate very similar variability in the expression of the lateral lines and grooves (Table 1). In comparing these morphs, a slight difference was found only in the higher frequency of lower lateral lines in morph A (53–58% versus 43–48% in morph B) and vice versa for any ventral lines (7% in morph A versus 15% in morph B).

Considering the comparable numbers of specimens in the two groups, tentatively such a subdivision can be explained as possible sexual dimorphism. Dimorphism has been discussed extensively in the belemnite literature (see review in Bolton 1982); however, in all cases dimorphism was reflected more in the elongation ratio and in balance differences (Bolton 1982; Doyle 1985; Ippolitov 2006) or size differences (d'Orbigny 1840–1842; Delattre 1956; Košťák & Pavliš 1997; Košťák 2004) than in differences in compression ratios.

Gondwanian megateuthidid records in the literature

Except for material from the Lower Bajocian of Argentina, no figured Middle Jurassic megateuthidid records from Gondwana demonstrate clear similarity with *Challinoria* gen. nov. The 'genus et species nov.' of Challinor & Grant-Mackie (1989) from the Lower Bathonian of New Caledonia and the latest Early Bajocian 'aff. *Brevibelus* sp.' of Challinor & Hikuroa (2007) from the Antarctic Peninsula are both characterized by subcylindrical, not conical, relatively blunt rostra without incised dorsolateral apical grooves, and rounded cross section. These rostra are consistent with the genus *Brevibelus* Doyle, 1992, and the specimens should be placed in this genus, as was proposed by Doyle & Pirrie (1999) for the new Caledonian example. Bajocian material from the Neuquen Basin of Argentina studied in the MLP, along with *Challinoria*, contain numerous rostra of *Brevibelus* sp. (referred as '*Brachybelus* sp.' by Stevens 1965) that are very comparable to those described as 'aff. *Brevibelus* sp.' from the Antarctic Peninsula (Challinor & Hikuroa 2007) and partly represent a closely related or even the same species.

Because of its close palaeogeographical proximity to the Indian finds, particularly interesting is the mention of '*Belemnites* cf. *giganteus* Schloth.' from Madagascar (Lemoine 1906), which was neither described nor figured. Basically, it appears to indicate the presence of Bajocian species of *Megateuthis* Bayle, 1878, or at least of some large-sized species, as can be judged from the general considerations about belemnite morphotypes in the literature. However, the accompanying cephalopod association

(Lemoine, 1906, p. 145) includes the Tithonian ammonite *Hildoglochiceras kobelli* (Oppel, 1863) and belemnopseid belemnites of Late Oxfordian–Kimmeridgian appearance. Both ages are inconsistent with the known stratigraphical distribution of large-sized *Megateuthis* spp., but are comparable with the ages of giant (e.g. *Hibolites ingens* Stolley, 1929) and large (*Parabelemnopsis madagascariensis* (Besairie, 1930)) Belemnopseidae known along the southern Tethyan margin. Remarkably, only a few subsequent authors have mentioned megateuthidids from Madagascar. Bülow-Trummer (1920) cited Lemoine's record and mentioned '*M. quinquesulcata*', but the latter seemingly did not refer to any known specimens. G. R. Stevens placed 'Passaloteuthinae' or 'Belemnitidae' from Madagascar on his Bajocian palaeogeographical maps (Stevens 1963, text-fig. 2; 1973, fig. 2A), also scarcely mentioning them in his revision (Stevens 1965, p. 169), but does not refer to any primary data. Sachs & Nalnjaeva (1975) both cited Lemoine and placed his record on their palaeogeographical map. Combémoré (1988), who performed a comprehensive revision of Madagascar belemnite faunas, stated that he found 'no traces' of records provided by Stevens (1963), and no megateuthidids were described in his own work. All of this indicates that megateuthidid records from Madagascar should be regarded critically and considered doubtful.

In turn, records of '*Belemnites giganteus* Schloth.' from Algeria (Coquand 1862, 1880) probably belong to genuine *Megateuthis*. This interpretation is supported by the latest Early Bajocian age, deriving from co-occurring ammonites listed by Coquand (1862) from the same locality: *Ammonites humphriesianus* Sow. [= *Stephanoceras humphreisianum* (Sowerby, 1825)], *A. brongniarti* Sowerby [= *Sphaeroceras brongniarti* (Sowerby, 1817)] and *A. cycloides* d'Orb. [= *Poecilomorphus cycloides* (d'Orbigny, 1845)]. The genus *Megateuthis* is widely distributed in the Bajocian of Europe, being considered a typical element of 'subboreal' (Mariotti *et al.* 2007; Weis *et al.* 2012) or 'euroboreal' (Weis *et al.* 2017) assemblages and localized mainly in the northern parts of the European Tethys. From the point of view of palaeogeography, Algerian records are close to European Bajocian records, providing some extension of the habitation area to the southern Tethyan margin.

Megateuthidid distribution patterns over Gondwana

Until the beginning of Bajocian time, megateuthidids were widely distributed mainly in the European region and were also common along the west coast of South America (see Fig. 9). Two large clades within the family, clearly separated phylogenetically and each having ancient Toarcian roots, can be delineated at this time, a *Brevibelus* group and a highly diverse *Megateuthis* group.

Members of the former group invaded the Southern Hemisphere during the Toarcian–Aalenian, as indicated by Aalenian–Lower Bajocian finds from Argentina (Doyle *et al.* 1996) and Lower Temaikán (=Latest Toarcian; see Challinor & Hudson 2017) records from New Zealand.

Due to the lack of Toarcian–Aalenian records along the southern Tethyan margin (northern Gondwana) and the poorly defined correlations of regional New Zealand stages with international stages (see Hudson 2003), it is not clear whether the initial penetration of *Brevibelus* into South Pacific provinces employed only one of the circum-Gondwanan routes (through the Hispanic corridor via Argentina, or along the southern Tethyan margin and around Antarctica) or both of them. In any case, younger finds from the Lower/Middle Bathonian boundary strata in Antarctica (Challinor & Hikuroa 2007) and in the Bathonian of New Caledonia (Challinor & Grant-Mackie 1989) presuppose a long-term existence of this lineage in the South Pacific province (Challinor & Hikuroa 2007). Similarly, both *Brevibelus* (see Riegraf 1980) and '*Dactyloteuthis*' (Ippolitov 2017) survived until the end of the Bajocian in Europe. The youngest possible member of this group is the peculiar Lower Cretaceous genus *Patagonibelus* Aguirre-Urreta & Doyle, 1989, but the nature of the latter is as yet poorly understood.

Members of the second group (*Megateuthis* group) during the Middle Jurassic are represented by two subgroups: the *Homaloteuthis-Eocyliindroteuthis* subgroup, which is restricted to the Aalenian–Lower Bajocian of the northern part of the European basins (see Weis & Mariotti 2008), and the *Megateuthis-Paramegateuthis* subgroup, which also includes *Challinoria* gen. nov.

A remarkable event is the appearance of the genus *Paramegateuthis*, first recorded from the Aalenian and Bajocian of Bulgaria (Stoyanova-Vergilova 1983) and later found in the Caucasus (Ippolitov *et al.* 2015). This genus possibly includes at least one Toarcian species, *Mesoteuthis ernsti* Schlegelmilch, 1998, that has elongated dorso-lateral grooves and a conical shape typical of *Paramegateuthis*. As *Paramegateuthis* was originally described and widely recognized as a typical component of Boreal-Arctic assemblages (Gustomesov 1960; Nalnjaeva 1974; Sachs & Nalnjaeva 1975; Doyle & Kelly 1988), the application of the name '*Paramegateuthis*' to warm-water Tethyan forms has been considered ambiguous (Doyle & Kelly 1988, p. 42; Ippolitov *et al.* 2015). As a result, small megateuthidids from the Argentinian Aalenian–Bajocian assemblage, despite being principally compatible with *Paramegateuthis*, were determined by Doyle (Doyle *et al.* 1996, 1997; Doyle & Pirrie 1999) as '*Megateuthis*'. However, the recent discovery of *P. subishmensis* Stoyanova-Vergilova, 1983, originally described from Bulgaria, in coeval deposits of Northern Siberia (de Lagausie & Dzyuba, 2017) indicates the

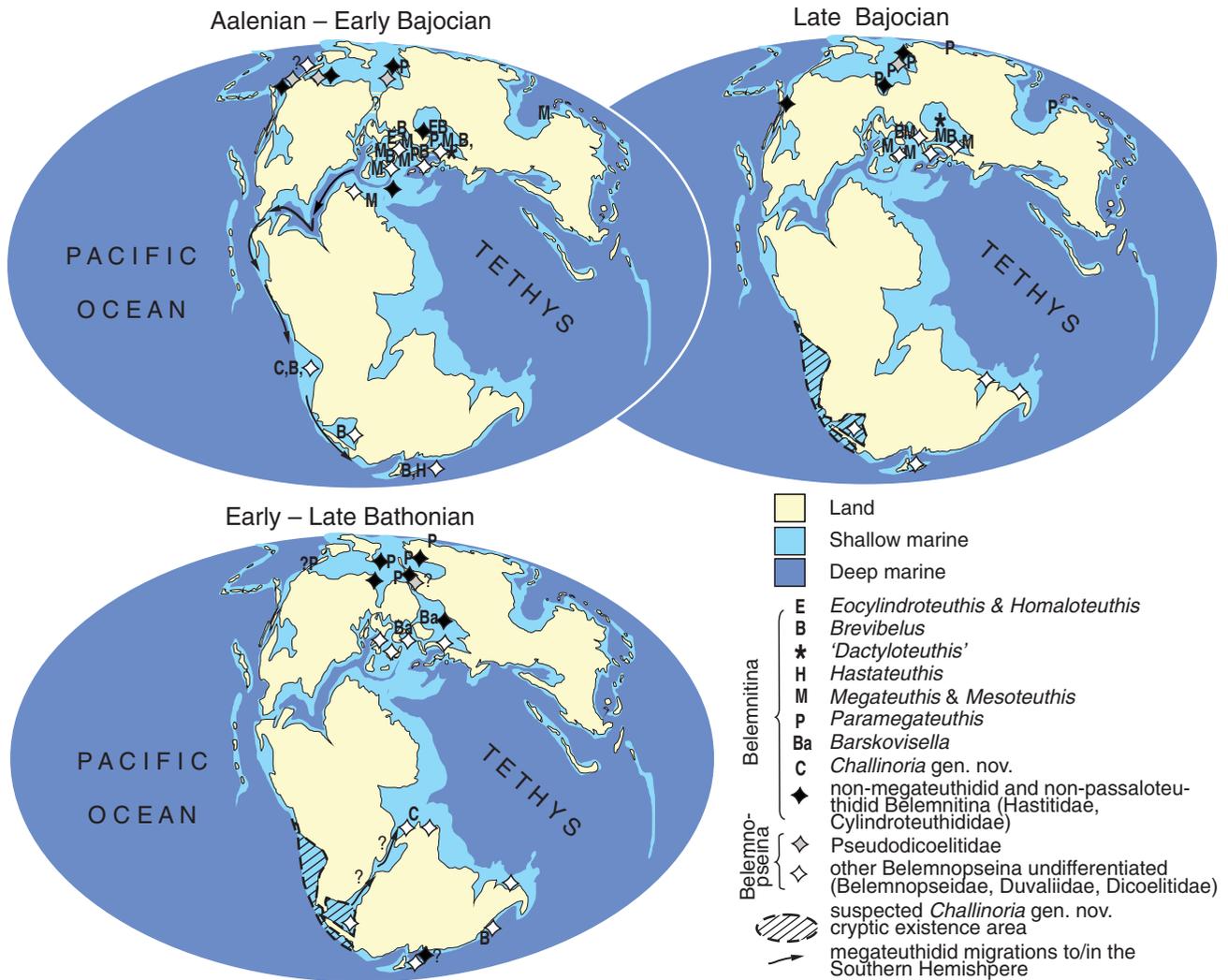


Figure 9. Megateuthididae dispersal patterns during the Aalenian–Bathonian. The palaeogeographical map is after the data of Blakey (2010) for 170 Ma (Middle Jurassic), with changes by the authors. Numerous megateuthidid genera declining in the Northern Hemisphere during the Early–Middle Aalenian (see Dzyuba & Weis 2015; Weis *et al.* 2017) are not shown, for the purpose of simplification. Compiled from numerous sources mentioned in the text and our own data.

authentic nature of Tethyan *Paramegateuthis* records and the secondary nature of its wide distribution in the Bajocian–Bathonian of the Boreal-Arctic province. Tethyan *Paramegateuthis* is very attractive as a potential direct ancestor of our newly described genus, mainly because of its size, its conical shape and its prominent lateral compression. Early representatives of *Paramegateuthis* in Europe are coeval with the appearance of the diverse '*Brevibelus-Dicoelites* fauna' in Argentina (Doyle *et al.* 1996), which include *Challinoria* gen. nov. as well, and probably the genera may be considered sister taxa.

Members of the *Megateuthis* group disappear from the European Tethys at the end of the Bajocian, and only the genus *Paramegateuthis* persists up to the Early–?Middle Bathonian in the Boreal-Arctic province, disappearing

almost synchronously with the Indian occurrences. Additionally, some forms related to it were described as *Nannobelus* (Barskov in Mitta *et al.* 2004; =*Barskovisella* Ippolitov, 2018) from the mixed Tethyan-Arctic assemblage of the Early Bathonian age of Central Russia. The last occurrence of this group in the Northern Hemisphere known so far is an offshoot of the *Paramegateuthis* lineage, described from the Upper Kimmeridgian of Central Russia (Ippolitov *et al.* 2017).

The most peculiar detail about Indian *Challinoria challinori* gen. et sp. nov. is that in neighbouring regions of Gondwana (Indonesia) such rostra are not recorded from either Bajocian or Bathonian strata (see Combémoré 1988; Challinor 1991a, b), whereas in the Middle Bathonian of Kachchh this type of rostrum shows mass occurrence. This poses the question of what dispersal area or

migrational pathway connects the Indian and Argentinian finds, and particularly of where the habitation area of *Challinoria* gen. nov. was located during the Late Bajocian–Early Bathonian.

A southern circum-Gondwanan route (via New Zealand and East Australia) is not supported by megateuthidid records of convenient age and morphology and thus appears unlikely. In several regions, lying along this pathway and more or less fully studied in belemnites (New Zealand, Indonesia; see reviews by Stevens (1965) and Challinor (1991)), no megateuthidids of conical appearance are registered from the Bajocian–Bathonian interval, whereas *Brevibelus* was found.

A northern circum-Gondwanan route (via the Mediterranean region, along the northern Gondwana margin) appears more attractive. In addition to the cosmopolitan genus *Brevibelus*, Late Bajocian belemnite faunas of Europe include large-sized and highly specialized members of the genus *Megateuthis* and poorly understood records of small conical belemnites around the Bajocian–Bathonian boundary (*Belemnites Escheri* sensu Gilliéron, 1873 non Mayer, 1863). The latter are essentially close to *Challinoria* gen. nov. in size, general shape and subquadrate cross section. However, they completely lack apical grooves and possibly are related not to *Brevibelus*, as was recently proposed by Riegraf (1995) and Riegraf *et al.* (1998), but to peculiar megateuthidids from Central Russia that were formerly described as *Nannobelus* spp. by I. S. Barskov (Mitta *et al.* 2004), reinterpreted as deviant *Paramegateuthis* by O. S. Dzyuba (Mitta *et al.* 2014) and now placed into a separate genus *Barskovisella* Ippolitov, 2018. The best-studied Bathonian belemnite assemblages from Poland (Pugaczewska 1961), Bulgaria (Stoyanova-Vergilova 1979, 1993) and Crimea (API, unpublished data) do not contain forms comparable to *Challinoria* gen. nov.

The third option, which best explains both the scattered geographical distribution of *Challinoria* gen. nov. and the absence of similar records both in Mediterranean region and Indonesia, is the long-term cryptic existence of the genus in the South American area combined with a short-duration migration event through the trans-Gondwanan seaway (also known in the literature as the ‘Mozambique channel’, the ‘Gondic corridor’ or the ‘trans-Erythraean seaway’) connecting India and the Antarctic area.

Did the trans-Gondwanan seaway open in the Bathonian?

The available data on the timing of the opening of this marine passage is contradictory. The tectonic framework indicates that the rift splitting of Gondwana into western (Africa and South America) and eastern (Antarctica, Australia, India) parts occurred continuously through the

Middle–Late Jurassic. The initial phase began during the late Early Jurassic, and the most ancient oceanic crust in the northern part of the passage is dated by geomagnetic chron M41n (Leinweber & Jokat 2012), equivalent to the Early Bathonian (Ogg *et al.* 2016). However, in the southern part of the passage, it is only M25n, which is Early Kimmeridgian (Leinweber & Jokat 2012). Of course, plate reconstructions are not the same as palaeogeographical reconstructions, and the absence of oceanic crust does not necessarily exclude the existence of a marine connection suitable for biota migrations. Such a corridor is represented in certain reconstructions of Bajocian–Bathonian time (Scotese 2016) but is absent in others (Scotese & Golonka 1992; Blakey 2010).

Based on marine biota studies, a marine trans-Gondwanan passage is usually considered to open not earlier than the Oxfordian (Enay & Cariou 1997; Damborenea *et al.* 2013) or even later (Riccardi 1991; Krishna 2017). Bathonian ammonite assemblages of South America and Western India contain no common elements at the genus level (compare Riccardi 2008 and Jain 2014). An alternative scenario of the earlier opening of a trans-Gondwanan seaway based on bivalve dispersal studies (Gardner & Campbell 2002; Hikuroa 2004) has been offered, employing early episodes of opening of a marine passage that were connected with major eustatic sea-level rise events in the Late Bajocian and Callovian, while outside such periods the marine passage reverted to swampy lowland.

Earlier investigations of belemnite biogeography touching the history of the trans-Gondwanan seaway (Mutterlose 1986; Doyle & Howlett 1989) were based on Late Jurassic material only and did not discuss Middle Jurassic palaeogeography. Based on relatively scarce belemnite materials obtained from the Antarctic region, Challinor & Hikuroa (2007) documented the presence of the belemnite family Duvaliidae starting from the latest Bathonian and, based on the absence of this family in Argentina and its presence in Madagascar, supported the early opening hypothesis. However, their most ancient duvaliid (*Rhopaloteuthis* sp.) has no clear counterparts in Madagascar, and other members of the family are of Late Jurassic age.

To add to the above, recent restudy of a comparable, longitudinal and short-lived marine passage on the East European platform that connected Northern Tethys with the Arctic ocean during the Early Bathonian, and has been well documented based on the immigration of various taxonomic groups (Mitta *et al.* 2004, 2014), has shown that immigration of small megateuthidid belemnites (*Barskovisella*) precedes the immigration of ammonites, large-sized cylindroteuthidid belemnites and inoceramids (Ippolitov 2018). This means that these small megateuthidids may have been adapted to extremely shallow conditions and low salinity, which enabled them to migrate through marginal environments that served as a barrier to

other cephalopods. A similar explanation can be applied to *Challinoria* gen. nov. Remarkably, the transgression maximum within the Bajocian–Bathonian interval on the tectonically stable East European platform is currently established not in the Late Bajocian, as was offered in the classic work of Sahagyan *et al.* (1996), but in the late Early Bathonian (Mitta *et al.* 2014), which is close to the sudden appearance of *Challinoria challinori* gen. et sp. nov. at the base of the Middle Bathonian in Western India.

Considering the above, the dispersal pattern of *Challinoria* gen. nov. currently supports the early opening of the trans-Gondwanan passage, at least until new finds from the Gondwanan periphery support a different option. Both alternative circum-Gondwanan routes discussed above remain possible, especially if we consider the imperfect state of knowledge of Bajocian–Bathonian belemnite assemblages along the southern Tethyan margin. This would automatically imply a wide circum-Gondwanan distribution for our newly described taxon during Bajocian–Bathonian time.

Conclusions

Abundant material consisting of 120 specimens collected by the authors from the Middle–Upper Bathonian of Kachchh (Gujarat, India) is the first confident record of *Megateuthis*-related belemnites over the entire Indo-Pacific region. Most specimens were assigned to *Challinoria challinori* gen. et sp. nov., and several rostra to *Challinoria* sp. In addition, two historical specimens from Kachchh available at the NHMUK and belonging to the same genus were restudied. Our study indicates the presence of a megateuthidid habitat area in the Southern Hemisphere across the Bajocian–Bathonian time and its continuous presence across the Middle–Late Bathonian in Western India.

The explanation of the observed bipolar distribution pattern of megateuthidids during the Bathonian is probably a general evolutionary trend towards the replacement of this family by more advanced forms (Belemnopseina in the Tethyan region and Gondwana margins, and Cyliandroteuthididae in the high latitudes of the Northern Hemisphere). This process began in the Tethyan region during the Early Bajocian (Weis *et al.* 2017), and in the Bathonian megateuthidids were already superseded in the sub-equatorial zone, which at this time was inhabited by quickly evolving Belemnopseidae and Dicoelitidae. All the lineages that crossed the Bajocian/Bathonian boundary (*Brevibelus*, *Paramegateuthis* and *Challinoria* gen. nov.) were characterized by medium to small size, while gigantic *Megateuthis* died out at this time. The survival of smaller forms can probably be explained by their shorter life cycles, which over the long term allowed a more rapid

response to environmental pressures and to competition by other taxa.

The synchronous replacement of archaic Megateuthididae at the end-Bathonian could be explained by the beginning of global sea-level rise, which led to the formation of large epicontinental seas, triggering quick evolution and diversification of the competitive families.

Acknowledgements

We are grateful to Alberto Riccardi (MLP, La Plata, Argentina) and Zoe Hughes (NHMUK, London, UK) for their help with examining comparative material for this study in the collections of their respective organizations. We thank S. Jain and F. T. Fürsich for their kind advice on Kachchh bio- and lithostratigraphy. Our special thanks are extended to an anonymous reviewer whose kind remarks and suggestions allowed us to improve the manuscript. We also thank the team who took part in our fieldwork in Kachchh (Gaurav Chavan, Nadezhda Ippolitova and Natrajan Madavan). The investigation was supported by RFBR projects No. 15-05-06183, 15-55-45095-ИИД_a and DST project No. INT/RUS/RFBR/P-206 and according to Governmental contract to GIN RAS no 0135-2018-0035.

Supplemental data

Supplemental material for this article can be accessed at: <https://doi.org/10.1080/14772019.2018.1448471>

ORCID

Alexei P. Ippolitov  <http://orcid.org/0000-0003-1612-0376>

Bhawanisingh G. Desai  <http://orcid.org/0000-0003-2851-7493>

References

- Agrawal, S. K. & Kachhara, R. P. 1979. Habo beds near Ler (Kutch): Pt. 3 – Biostratigraphy of the beds on the east of Ler. *Proceedings of the Indian National Science Academy, Series A (Physical Sciences)*, **45**, 129–146.
- Agrawal, S. K. & Pandey, D. K. 1985. Biostratigraphy of the Bathonian–Callovian beds of Gora Dongar in Pachchham ‘Island’, district Kachchh (Gujarat). *Proceedings of the Indian National Science Academy*, **51(A)**, 887–903.
- Aguirre-Urreta, M. B. & Doyle, P. 1989. A problematical belemnite from the Lower Cretaceous of the Austral Basin, Patagonia, Argentina. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1989(6)**, 345–355.
- Bather, F. A. 1888. Shell-growth in cephalopods (Siphonopoda). *Annals and Magazine of Natural History, Series 6*, **1**, 298–310.

- Bayle, E.** 1878. *Explication de la carte géologique de France. Vol. 4. Atlas. Partie I. Fossiles principaux des terrains.* Imprimerie Nationale, Paris, 176 pl.
- Besairie, H.** 1930. Recherches géologiques à Madagascar. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **60**, 345–616.
- Biswas, S. K.** 1980. Mesozoic rock stratigraphy of Kutch, Gujarat. *Quarterly Journal of Geological, Mining and Metallurgical Society of India*, **49**(3–4) [for 1977], 1–51.
- Biswas, S. K.** 1993. *Geology of Kutch. Volume 1.* K. D. Malaviya Institute of Petroleum Exploration, Dendradun, 450 pp.
- Blainville, M. H. D. de** 1827. *Mémoire sur les Bélemnites, considérés zoologiquement et géologiquement.* F. G. Levrault, Paris, 136 pp., 5 pl.
- Blakey, R.** 2010. *Mollewide plate tectonic maps.* Updated at: <http://jan.ucc.nau.edu/rcb7/mollglobe.html>, accessed 4 November 2016.
- Boehm, G.** 1912. Beiträge zur Geologie von Niederländisch-Indien. I Abteilung. Die Südküsten der Sula-Inseln Taliabu und Mangoli. 4 Abschnitt. Unteres Callovien. *Palaeontographica*, Supplement-Band, **4**, 121–179, pl. 32–44.
- Bolton, J. T. F. S.** 1982. *The ontogeny, palaeobiology and systematic palaeontology of some Lower Liassic Belemnitida.* Unpublished PhD thesis, University of Durham, Durham, vii + 270 pp., 29 pls.
- Bülow-Trummer, E. von.** 1920. Cephalopoda dibranchiata. *Fossilium Catalogus. I: Animalia*, **11**, 1–313.
- Challinor, A. B.** 1991a. Belemnite successions and faunal provinces in the southwest Pacific, and the belemnites of Gondwana. *BMR Journal of Australian Geology and Geophysics*, **12**, 301–325.
- Challinor, A. B.** 1991b. Revision of the belemnites of Misool and a review of the belemnites of Indonesia. *Palaeontographica Abteilung A*, **218**, 87–164.
- Challinor, A. B. & Grant-Mackie, J. A.** 1989. Jurassic Coleoida of New Caledonia. *Alcheringa*, **13**, 269–304.
- Challinor, A. B. & Hikuroa, D. C. H.** 2007. New Middle and Upper Jurassic Belemnite assemblages from West Antarctica (Latady Group, Ellsworth Land): taxonomy and paleobiogeography. *Palaeontologia Electronica*, **10**(1), 1–29.
- Challinor, A. B. & Hudson, N.** 2017. Early and Middle Jurassic belemnites of New Zealand. *Australasian Palaeontological Memoirs*, **50**, 1–69.
- Challinor, A. B., Doyle, P., Howlett, P. J. & Nalnyaeva, T. I.** 1992. Belemnites of the circum-Pacific region. Pp. 334–341 in G. E. G. Westermann (ed.) *The Jurassic of the circum-Pacific*. Cambridge University Press, Cambridge.
- Combémourel, R.** 1988. Les bélemnites de Madagascar. *Documents des Laboratoires de Géologie de Lyon*, **104**, 3–239.
- Coquand, M. H.** 1862. Geologie et paléontologie de la région sud de la province de Constantine. *Mémoire de la Société d'Émulation de la Provence*, **2**, 320 pp., 35 pls.
- Coquand, M. H.** 1880. Études supplémentaires sur la Paléontologie algérienne. Faisant suite a la description géologique et paléontologique de la région Sud de la Province de Constantine. *Bulletin Académie d'Hippone*, **15**, 1–450.
- Damborenea S. E., Echevarría, J. & Ros-Franch, S.** 2013. *Southern hemisphere palaeobiogeography of Triassic–Jurassic marine bivalves.* Springer, Netherlands, viii+139 pp.
- Delattre, M.** 1956. Les bélemnites de l'Aalenien de Mamers. *Annales du Centre d'Études de de Documentation Paléontologiques*, **16**, 35–44.
- Doyle, P.** 1985. Sexual dimorphism in belemnite *Youngibelus* from the Lower Jurassic of Yorkshire. *Palaeontology*, **28**, 133–146.
- Doyle, P.** 1992. The British Toarcian (Lower Jurassic) belemnites. Part 2. *Monograph of the Palaeontographical Society, London*, **144**, 50–79.
- Doyle, P. & Howlett, P.** 1989. Antarctic belemnite biogeography and the break-up of Gondwana. *Geological Society of London, Special Publication*, **47**, 167–182.
- Doyle, P. & Kelly, S. R. A.** 1988. The Jurassic and Cretaceous belemnites of Kong Karls Land, Svalbard. *Norsk Polarinstittutt Skrifter*, **189**, 1–78.
- Doyle, P. & Pirrie, D.** 1999. Belemnite distribution patterns. Implications of new data from Argentina. Pp. 419–436 in E. Olóriz & F. J. Rodríguez-Tovar (eds) *Advancing research on living and fossil cephalopods*. Springer US, New York.
- Doyle, P., Kelly, S. R. A., Pirrie, D. & Riccardi, A. C.** 1997. Jurassic belemnite distribution patterns: implications of new data from Antarctica and Argentina. *Alcheringa*, **21**, 219–228.
- Doyle, P., Kelly, S. R. A., Pirrie, D., Riccardi, A. C. & Oliveira, E.** 1996. Jurassic belemnite biostratigraphy of the Southern hemisphere: a comparative study of Antarctica and Argentina. *Revista de la Asociación Geológica Argentina*, **51**, 331–338.
- Dutta, R. & Bardhan, S.** 2016. Systematics, endemism and phylogeny of Indian proplanulitins (Ammonoidea) from the Bathonian–Callovian of Kutch, western India. *Swiss Journal of Paleontology*, **135**, 23–56.
- Dzyuba, O. S.** 2012. Belemnites and biostratigraphy of the Jurassic–Cretaceous boundary deposits of northern East Siberia: new data on the Nordvik Peninsula. *Stratigraphy and Geological Correlation*, **20**, 53–72.
- Dzyuba, O. S. & Weis, R.** 2015. Megateuthididae (Belemnitina) from the Lower–Middle Jurassic of Northern and Eastern Russia: taxonomy and nomenclature. Pp. 62–64 in T. B. Leonova, I. S. Barskov & V. V. Mitta (eds) *Contributions to current cephalopod research: morphology, systematics, evolution, ecology and biostratigraphy*. Borissiak Paleontological Institute, Moscow, 138 pp. [In Russian, with English abstract].
- Dzyuba, O. S., Weis, R., Nalnjaeva T. I. & Riegraf W.** 2015. *Rarobelus* nom. nov. from the Boreal Toarcian–Aalenian and its systematic position (Belemnitida, Belemnitina, Megateuthididae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **275**, 305–315.
- Enay, R. & Cariou, E.** 1997. Ammonite faunas and palaeobiogeography of the Himalayan belt during the Jurassic: initiation of a Late Jurassic austral ammonite fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **134**, 1–38.
- Fürsich, F. T.** 1998. Environmental distribution of trace fossils in the Jurassic of Kachchh (Western India). *Facies*, **39**, 243–272.
- Fürsich, F. T., Alberti, M. & Pandey, D. K.** 2013. Stratigraphy and palaeoenvironments of the Jurassic rocks of Kachchh – Field Guide. *Beringeria, Special Issue*, **7**, 1–174.
- Fürsich, F. T., Pandey, D. K., Callomon, J. H., Jaitly, A. K. & Singh, I. B.** 2001. Marker beds in the Jurassic of the Kachchh basin, Western India: their depositional environment and sequence stratigraphic significance. *Journal of the Palaeontological Society of India*, **46**, 173–198.
- Fürsich F. T., Pandey, D. K., Oschmann, W., Jaitly, A. K. & Singh, I. B.** 1994. Ecology and adaptive strategies of corals in unfavourable environments: examples from the Middle Jurassic of the Kachchh Basin, Western India. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **194**, 269–303.

- Gardner, R. N. & Campbell, H. J.** 2002. Middle to Late Jurassic bivalves of the subfamily Astartinae from New Zealand and New Caledonia. *New Zealand Journal of Geology and Geophysics*, **45**, 1–51.
- Gilliéron, V.** 1873. Aperçu géologique sur les Alpes de Fribourg en général et description spéciale du Monsalvens en particulier. *Matériaux Pour la Carte Géologique de la Suisse*, **12**, viii + 273 pp., 10 pl.
- Grossouvre, A. de.** 1919. Bajocien–Bathonien dans la Nièvre. *Bulletin de la Société Géologique de France, série 4*, **18**, 337–459, pls 13–16.
- Gustomesov, V. A.** 1960. Новые келловейские белемниты Тимана [New Callovian belemnites from Timan]. Pp. 190–210 in B. P. Markovskiy (ed.) *Новые виды древних растений и беспозвоночных СССР. Часть вторая*; [New species of fossil plants and invertebrates of the USSR. Part 2]. Gosgeotekhizdat, Moscow. [In Russian].
- Hikuroa, D. C. H.** 2004. *The fauna and biostratigraphy of the Jurassic Latady Formation, Antarctic Peninsula*. Unpublished PhD thesis, University of Auckland, Auckland, xx + 399 pp.
- Hillebrandt, A. von & Westermann, G. E. G.** 1985. Aalenian (Jurassic) Ammonite faunas and zones of the Southern Andes. *Zitteliana*, **12**, 3–55.
- Hudson, N.** 2003. Stratigraphy and correlation of the Uruoran and Temaikan Stage (Lower–Middle Jurassic, ?Sinemurian–Callovian) sequences, New Zealand. *Journal of the Royal Society of New Zealand*, **33**, 109–147.
- Ippolitov, A. P.** 2006. On the possible expression of sexual dimorphism in *Hibolithes* Montfort, 1808 from the Middle and Upper Jurassic of European Russia. Pp. 57–60 in I. S. Barskov & T. B. Leonova (eds) *Contributions to current cephalopod research: morphology, systematics, evolution, ecology and biostratigraphy. Materials of All-Russian meeting, Moscow, November 8–10, 2006*. Paleontological Institute RAS, Moscow. [In Russian, with English abstract].
- Ippolitov, A. P.** 2017. Late Bajocian belemnites of the Volga region: biodiversity and palaeobiogeographical significance. Pp. 74–77 in V. A. Zakharov, M. A. Rogov & E. V. Shchepetova (eds) *Jurassic System of Russia: problems of stratigraphy and paleogeography. Seventh all-Russian Conference. September 18–22, 2017, Moscow*. Scientific Materials, Moscow, 272 pp.
- Ippolitov, A. P.** 2018. Belemnites and biostratigraphy of the Lower Bathonian of central and southern parts of the East European platform. Part 1. Megateuthididae. *Stratigraphy and Geological Correlation*, **26**, 179–205.
- Ippolitov, A. P., Gulyaev D. B. & Glinskikh L. A.** 2015. Чукна [Chukna]. Pp. 35–49 in V. I. Cherkashin (ed.) *Jurassic deposits of the central part of Mountain Dagestan. Field guide to the VI All-Russian conference 'Jurassic system of Russia: problems of stratigraphy and paleogeography'*. ALEF, Makhachkala. [in Russian].
- Ippolitov, A. P., Berezin A. Yu., Rogov M. A. & Desai B. G.** 2017. The first record of megateuthidid belemnites from the Late Jurassic: *Chuvashiteuthis aenigmatica* gen. et sp. nov. from the Upper Kimmeridgian of Central Russia. *Bulletin of Geosciences*, **92**, 357–372.
- Jain, S.** 2014. The Arkelli Chronozone: a new early Middle Bathonian standard ammonite zone for Kachchh, western India (southern Jurassic Tethys). *Zitteliana*, **A54**, 91–136.
- Jain, S. & Desai, B.** 2014. Biostratigraphic implications of the discovery of Late Bathonian Indonesian ammonite *Macrocephalites* cf. *mantataranus* Boehm [M] from the core of Jara Dome, Kachchh, Western India. *Journal of the Palaeontological Society of India*, **59**(2), 1–11.
- Jeletzky, J. A.** 1965. Taxonomy and phylogeny of fossil Coleoidea (= Dibranchiata). *Geological Survey of Canada, Paper*, **65–2**(42), 72–76.
- Košťák, M.** 2004. Cenomanian through the lowermost Coniacian Belemnitellidae Pavlow (Belemnitida, Coleoidea) of the East European Province. *Geolines*, **18**, 59–109.
- Košťák, M. & Pavliš, W.** 1997. Biometric analysis of *Praeactinocamax plenus* (Blainv.) from the Bohemian Cretaceous Basin. *Acta Universitatis Carolinae – Geology*, **41**, 1–13.
- Krishna, J.** 2017. *The Indian Mesozoic chronicle. Sequence stratigraphic approach*. Springer Singapore, Singapore, lxi + 694 pp.
- Lagausic, B. de & Dzyuba, O.S.** 2017. Biostratigraphy of the Bajocian–Bathonian boundary interval in northern Siberia: new data on belemnites from the Yuryung-Tumus peninsula. *Bulletin de la Société Géologique de France*, **188**(1–2), 1–9.
- Leanza, H. A., Hugo, C. A., Herrero J. C., Donnari, F. & Pucci, J. C.** 1997. Hoja Geológica 3969-II — Picún Leufú, provincias del Neuquén y Río Negro. Programa Nacional de la Carta Geológica a escala 1:250.000. *Boletín del Instituto de Geología y Recursos Naturales*, **218**, 135 pp. + map.
- Leinweber, V. T. & Jokat, W.** 2012. The Jurassic history of the Africa–Antarctica corridor – new constraints from magnetic data on the conjugate continental margins. *Tectonophysics*, **530–531**, 87–101.
- Lemoine, P.** 1906. *Études géologiques dans le Nord du Madagascar. Contribution à l'histoire géologique de l'Océan Indien*. A. Hermann, Paris, 520 pp., 4 pls, 1 map.
- Lissajous, M.** 1915. Quelques remarques sur les bélemnites jurassiques. *Bulletin de la Société d'Histoire naturelle de Mâcon*, **6**, 1–32.
- Mariotti, N., Sanantonio, M. & Weis R.** 2007. Aalenian–Early Bajocian belemnite assemblage from Peri-Mediterranean Tethyan sediments (Calabria, Southern Italy). *Geologica Romana*, **40**, 1–19.
- Mayer, C.** 1863. Liste, par ordre systématique, des bélemnites des terrains jurassiques, et diagnoses des espèces nouvelles. *Journal de Conchyliologie*, **3^e série**, **3** (11), 181–194.
- Mitta, V. V., Kostyleva V. V., Dzyuba, O. S., Glinskikh, L. A., Shurygin, B. N., Seltzer, V. B., Ivanov, A. V. & Urman, O. S.** 2014. Biostratigraphy and sedimentary settings of the Upper Bajocian–Lower Bathonian of the vicinity of Saratov (Central Russia). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **271**, 95–121.
- Mitta, V. V., Barskov, I. S., Gründel, J., Zakharov, V. A., Seltzer, V. B., Ivanov, A. V., Rostovtseva, Yu. A. & Tarasova, L. O.** 2004. The Upper Bajocian and Lower Bathonian in the section near Saratov. *Vernadsky Museum-Novitates*, **12**, 1–39. [In Russian].
- Montfort, P. D. de.** 1808. *Conchyliologie systématique et classification méthodique des coquilles etc.* T. I. F. Schoell, Paris, lxxxvi + 409 pp.
- Mutterlose, J.** 1986. Upper Jurassic belemnites from the Orville Coast, Western Antarctica, and their palaeobiogeographical significance. *Bulletin of the British Antarctic Survey*, **70**, 1–22.
- Naef, A.** 1922. *Die fossilen Tintenfische*. G. Fischer, Jena, 322 pp.
- Nalnjaeva T. I.** 1974. Стратиграфическое и географическое распространение рода *Paramegateuthis* [Stratigraphical and geographical distribution of the genus *Paramegateuthis*]. Pp. 101–105 in V. N. Sachs (ed.) *Biostratigraphy of*

- Boreal Mesozoic*. Nauka, Siberian branch, Novosibirsk, 187 pp. [In Russian].
- Nikitin, I. I.** 1975. Новые виды белемнитов из юрских отложений северо-западной окраины Донбасса [New species of Jurassic belemnites from the northwestern Donets Basin]. *Geologicheskii Zhurnal*, **15**(6), 72–80. [In Russian].
- Ogg, J. G., Ogg, G. & Gradstein, F. M.** 2016. *A concise geological time scale*. Elsevier, Netherlands, 240 pp.
- Oppel, A.** 1857. Die Juraformation Englands, Frankreichs und des südwestlichen Deutschlands, nach ihren einzelnen Gliedern eingetheilt und verglichen. Teil 2. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **13**, 141–396.
- Oppel, A.** 1862–1863. III. Über jurassische Cephalopoden. *Paleontologische Mittheilungen aus dem Museum des königlich Bayerischen Staates*, **1**, 127–262.
- Orbigny, A. D. d'** 1840–1842. *Paleontologie française. Description des mollusques et rayonnés fossiles. Terrains Crétacés, Vol. I. Céphalopodes*. d'Orbigny, Paris, 662 pp., 148 pls.
- Orbigny, A. D. d'** 1842–1851. *Paléontologie française. Description zoologique et géologique de tous les animaux mollusques et rayonnés fossils de France, comprenant leur application à la reconnaissance des couches. Terrains oolithiques ou jurassiques. I. Céphalopodes*. Masson, Bertrand, d'Orbigny, Paris, 624 pp.
- Pandey, J. & Dave, A.** 1993. Studies in Mesozoic Foraminifera and chronostratigraphy of Western Kutch, Gujarat. *Palaeontographica Indica*, **1**, 1–221.
- Prasad, S.** 1998. Ammonite biozonation of the Middle–Upper Jurassic sediments with special reference to Keera and Jara Dome, Kachchh District, Gujarat. *Journal of Geological Society of India*, **52**, 25–40.
- Pugaczewska, H.** 1961. Belemnoids from the Jurassic of Poland. *Acta Palaeontologica Polonica*, **6**(2), 105–236, 26 pls.
- Quenstedt, F. A.** 1845–1849. *Petrefaktenkunde Deutschlands. I. Abt. I. Bd. 1 [Die] Cephalopoden*. F. Fues, Tübingen, 580 pp., 36 pls.
- Riccardi, A. C.** 1991. Jurassic and Cretaceous marine connections between the Southeast Pacific and Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **87**, 155–189.
- Riccardi, A. C.** 2008. The marine Jurassic of Argentina: a biostratigraphic framework. *Episodes*, **31**(3), 326–335.
- Riegraf, W.** 1980. Revision der Belemniten des Schwäbischen Jura. Part 7. *Palaeontographica, Abteilung A*, **169**(4–6), 128–206.
- Riegraf, W.** 1995. Cephalopoda dibranchiate fossiles (Coleoidea). *Fossilium Catalogus I, Animalia*, **133**, 411 pp.
- Riegraf, W., Janssen, N. & Schmitt-Riegraf, C.** 1998. Cephalopoda dibranchiata fossiles (Coleoidea). II. Supplementum ad mandibula fossiles ammonitorum et nautilorum (Rhyncholithi et Rhynchoteuthes, excl. aptychi et anaptychi). *Fossilium Catalogus I, Animalia*, **135**, 519 pp.
- Sachs, V. N. & Nalnjaeva, T. L.** 1967. The separation of the superfamily Passaloteuthacea from the stock of the suborder Belemnioidea (Cephalopoda, Dibranchia, Decapoda). *Doklady Akademii Nauk SSSR*, **173**, 438–441. [In Russian].
- Sachs, V. N. & Nalnjaeva, T. L.** 1975. The early and middle Jurassic belemnites of the north of the USSR. Megateuthinae and Pseudodicoelitiniae. *Transactions of the Institute of Geology and Geophysics, Siberian Branch of Academy of Sciences of the USSR*, **239**, 1–192. [In Russian].
- Sahagian D., Pinous, O., Olfieriev, A. & Zakharov, V.** 1996. Eustatic curve for the Middle Jurassic–Cretaceous based on Russian platform and Siberian stratigraphy: zonal resolution. *AAPG Bulletin*, **80**, 1433–1458.
- Schlegelmilch, R.** 1998. *Die Belemniten des Süddeutschen Jura*. Gustav Fischer, Stuttgart-Jena-Lübeck-Ulm, 151 pp.
- Scotese, C. R.** 2016. *PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program*. Updated at: <https://www.earthbyte.org/paleomap-paleoatlas-for-gplates/>, accessed 01 November 2016.
- Scotese, C. R. & Golonka, J.** 1992. *PALEOMAP Paleogeographic atlas. PALEOMAP Progress Report #20*. Department of Geology, University of Texas, Arlington, 34 pp.
- Sowerby, J.** 1817. *The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the Earth. Volume 2*. Arding & Merrett, London, 251 pp.
- Sowerby, J. D. C.** 1825. *The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the Earth. Volume 5*. B. Meredith, London, 168 pp.
- Spath, L. F.** 1924. On the Blake collection of ammonites from Kachh, India. *Memoirs of the Geological Survey of India (Palaeontologia Indica)*, n. s., **9**(1), 1–29.
- Spath, L. F.** 1927. Revision of the Jurassic Cephalopod fauna of Kachh (Cutch). *Memoirs of the Geological Survey of India (Palaeontologia Indica)*, n. s., **9**(2), 279–350.
- Spath, L. F.** 1933. Revision of the Jurassic Cephalopod fauna of Kachh (Cutch). Part VI. *Memoirs of the Geological Survey of India (Palaeontologia Indica)*, n. s., **9**(2), 659–745.
- Stevens, G. R.** 1963. Faunal realms in Jurassic and Cretaceous belemnites. *Geological Magazine*, **100**, 481–497.
- Stevens, G. R.** 1965. The Jurassic and Cretaceous belemnites of New Zealand and a review of the Jurassic and Cretaceous belemnites of the Indo-Pacific Region. *Paleontological Bulletin of the New Zealand Geological Survey*, **36**, 1–231.
- Stevens, G. R.** 1973. Jurassic belemnites. Pp. 259–274 in A. Hallam (ed.) *Atlas of palaeobiogeography*. Elsevier, Amsterdam.
- Stolley, E.** 1919. Die Systematik der Belemniten. *Jahresbericht des Niedersächsischen Geologischen Vereins*, **11** [for 1918], 1–59.
- Stolley, E.** 1929. XXIX. Über ostindische Jura-Belemniten. *Paläontologie von Timor*, **16**(29), 91–213, pls 248–256.
- Stoyanova-Vergilova, M.** 1979. Bathonian belemnites from Bulgaria. *Geologica Balcanica*, **9**(4), 47–58.
- Stoyanova-Vergilova, M.** 1983. Genus *Paramegateuthis* Gustomesov (Belemnitida) in Bulgaria. *Godishnikh na Sofiyskiya Universitet 'Kliment Orkhidski' Geologo-Geografski Fakultet*, **73**(1) [for 1979], 250–256.
- Stoyanova-Vergilova, M.** 1993. *Les fossiles de Bulgarie. IIIa. Jurassique. Belemnitida*. Academie Bulgare des Sciences, Sofia, 212 pp.
- Tornquist, A.** 1898. Der Dogger am Espinazito-Pass, nebst einer Zusammenstellung der jetzigen Kenntnisse von der argentinischen Juraformation. *Paläontologische Abhandlungen*, **8**(2), 135–204.
- Weis, R. & Mariotti, N.** 2008. A belemnite fauna from the Aalenian–Bajocian boundary beds of the Grand Duchy of Luxembourg (NE Paris Basin). *Bollettino della Società Paleontologica Italiana*, **46**(2–3), 149–174.
- Weis, R., Mariotti, N. & Riegraf, W.** 2012. The belemnite family Holcobelidae (Coleoidea) in the European Jurassic: systematics, biostratigraphy, palaeobiogeography and evolutionary trends. *Palaeodiversity*, **5**, 13–49.

Weis, R., Sadki, D. & Mariotti, N. 2017. Aalenian–Bajocian belemnites from the Middle and High Atlas, Morocco: taxonomy, biostratigraphy and palaeobiogeographical affinities. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **284**(2), 215–240.

Werner, E. 1912. Über die Belemniten des schwäbischen Lias und die mit ihnen verwandten Formen des Braunen Jura (Acoeli). *Palaeontographica*, **59**, 103–146, pls 10–13.

Zittel, K. A. von. 1895. *Grundzüge der Paläontologie (Paläozoologie)*. Oldenbourg, München-Leipzig, 971 pp.