

## Bayesian inference reveals a complex evolutionary history of belemnites

Kevin Stevens, Alexander Pohle, René Hoffmann, and Adrian Immenhauser

### ABSTRACT

Belemnites are an extinct group of Mesozoic coleoid cephalopods, common in Jurassic and Cretaceous marine sedimentary rocks. Despite their significance, their total group phylogeny has rarely been considered in recent decades. In contrast, most researchers restricted the assignment of families to one of the two usually recognized subgroups, the Belemnitina and the Belemnopseina. As for many fossil cephalopods, researchers have been reluctant to employ modern phylogenetic methods to illuminate belemnites' evolutionary history.

To overcome the "dead end" of belemnite systematics, we performed the first tip-dated Bayesian analysis of belemnite phylogeny. In our analysis, the Aulacoceratida are found as the monophyletic sister group to belemnites. The Sinobelemnitidae are resolved as paraphyletic and fall outside the Belemnitina and Belemnopseina, which make up the remaining belemnites. Belemnitina is restricted to Jurassic species with generally no or apical furrows. Holcobelidae are sister group to other Belemnopseina. Cylindroteuthids *sensu lato* (including Oxyteuthidae) are nested within Belemnopseina, contrary to the common hypothesis placing them within the Belemnitina. Duvaliidae and Dicoelitidae are recovered as members of the Belemnopseina, but their precise relationship has to be evaluated based on more taxa and additional characters. We introduce the well-supported unranked clade Pseudoalveolata, which includes Dimitobelidae, Belemnitellidae, and members of the paraphyletic "Belemnopseidae".

The phylogeny presented here, based on reproducible and quantitative methods, contrasts with the usually applied authoritative "stratophenetic" approach to belemnite systematics, based on the overemphasis of single characters. This result is considered the basis for future studies on belemnite phylogeny, allowing for a rigorous testing of evolutionary hypotheses.

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## INTRODUCTION

Belemnites (Belemnitida) are an extinct group of stem-decabrachian coleoids (e.g., Fuchs et al., 2013; Hoffmann and Stevens, 2020). They are characterized by a calcitic rostrum, which is by far the most commonly preserved part of their internal shell. Although exceptional cases of soft-tissue preservation are known from belemnites (e.g., Reitner and Ulrichs, 1983; Klug et al., 2010), their preservation potential is lower than in early octobranchians, likely due to differences in buoyancy mechanisms (Clements et al., 2017). Thus, belemnite systematics is almost entirely based on rostrum morphology. In this paper, the terms belemnites and Belemnitida are used only for these calcite-rostrum-bearing species. This definition excludes groups like the Belemnoteuthida and Diplobelida, sometimes referred to as belemnites. The paraphyletic assemblage of Belemnitida, Aulacoceratida, Belemnoteuthida, and Diplobelida is referred to as "belemnoids" in lieu of a proper understanding of their interrelationships at present (Hoffmann and Stevens, 2020). Diplobelida probably represent close relatives of crown-Decabrachia (Fuchs et al., 2013; Fuchs, 2019). Fuchs et al. (2013) regarded belemnites as sister to a group consisting of crown Decabrachia, the stem-decabrachian *Longibelus*, and the Diplobelida. In a cladistic analysis, Sutton et al. (2016) found the belemnite *Hibolithes* closely related to the coleoid genera *Phragmoteuthis* and *Belemnoteuthis*, nested within the Decabrachia crown group.

The relationship of the rostrum-bearing Aulacoceratida with other "belemnoid" groups, is at present also unclear (Keupp and Fuchs, 2014). Aulacoceratids have aragonitic rostra (also called "telum"; see Jeletzky, 1966) and differ in other morphological aspects from belemnites (e.g., Jeletzky, 1966; Mariotti et al., 2021), but their aragonitic rostrum likely represents the ancestral rostrum structure of coleoids.

The internal phylogenetic relationships of belemnites are even less clear than their relationship to other coleoids. Early subdivisions of belem-

nites relied on general external characteristics, mostly on the number and position of furrows, e.g., the classification of Werner (1913). Abel (1916) subdivided all belemnites into the families "Clavistrostridae" and "Conirostridae" due to their early ontogenetic development. The definitions used nowadays for belemnite families go back to Stolley's (1919) and Naef's (1922) classifications. Jeletzky's (1966) proposal of subdividing the calcite-rostrum bearing belemnites into apically furrowed Belemnitina and alveolar furrowed Belemnopseina has been largely followed by subsequent workers and has been virtually the only applied subdivision of belemnites higher than the family level since. Very few phylogenetic trees have been published that show internal phylogenetic relationships within the Belemnitida – all of them lack a quantitative framework, thus they remain speculative (e.g., Jeletzky, 1966; Schlegelmilch, 1998; Košťák, 2012).

Recognition of the alveolar furrowed Triassic–Early Jurassic Sinobelemitidae as true belemnites (Zhu and Bian, 1984; Iba et al., 2012; Niko and Ehiro, 2022) has significantly altered views on belemnite phylogeny. Apart from the Sinobelemitidae, belemnites are exclusively known from the earliest Jurassic onwards, which is considered their initial radiation (e.g., Dera et al., 2016; Neige et al., 2021). Earlier hypotheses of belemnite phylogeny focused on the well-known European fossil record of the group that suggested their origin during the Hettangian in the diminutive and relatively character-poor genera *Schwegleria* and *Nannobelus*, which both lack alveolar furrows. By the Early Jurassic, belemnites had reached a cosmopolitan distribution and relatively high diversity and abundance (e.g., Iba et al., 2014a, 2014b; Weis et al., 2015a). Although affected by second-order extinction events (e.g., Dera et al., 2016; De Baets et al., 2021; Neige et al., 2021), belemnites continued to be diverse during the Jurassic and early Early Cretaceous (e.g., Schlegelmilch, 1998; Mutterlose, 1988, 1998; Iba et al., 2011), with the two last occurring, disjunctively distributed families, the Boreal Belemnitellidae and the Austral Dimitobeli-

dae, finally becoming extinct at the K/Pg-boundary (e.g., Doyle, 1992; Christensen, 1997; Iba et al., 2011).

The evolutionary history of belemnites as a whole has rarely been studied since Jeletzky (1966). While several authors speculated about the interrelationships of belemnite families (e.g., Christensen, 1997; Iba et al., 2012; Weis et al., 2012), there has been no study of their phylogenetic relationships based on modern phylogenetic methods. This pattern reflects a general tendency of researchers studying fossil cephalopods in the past (Neige et al., 2007; Bardin et al., 2014; Pohle et al., 2022).

This paper presents the first quantitative approach towards belemnite phylogeny based on Bayesian inference. The dichotomous subdivision of all belemnites into Belemnitina and Belemnopseina, as these groups are usually defined, is not supported by these results. Our findings challenge usual assumptions about the evolution of belemnites and identify parts of the belemnite phylogenetic tree that still lack resolution.

## METHODS

We selected 24 belemnite species, representative of the stratigraphic range, geographic distribution, and diversity of the whole group (Table 1) and scored them for 29 characters, mostly describing the rostrum (Figure 1; Table 2; Appendix 1). Three aulacoceratid genera (including one putative genus) were also included. Although other fossil "belemnoid" coleoid groups are likely more closely related to the Belemnitida than aulacoceratids (e.g., Diplobelida, Belemnoteuthida), these do not have proper rostra (sensu Fuchs, 2012) and so do not contribute to the resolution of internal relationships of belemnites, whose phylogeny is here inferred based mostly on rostrum characters. For the vast majority of belemnites, the rostrum is the only known part (e.g., Hoffmann and Stevens, 2020) mimicking the situation for conodonts, where inferences of their phylogenetic relationships must also be based on conodont element data with few characters only (e.g., Donoghue, 2001; Guenser et al., 2021; Bai et al., 2022). Morphological data comes from several published sources and our own observations (Table 1). The terminology of belemnite morphology follows Hoffmann and Stevens (2020) and Stevens et al. (2022). The character matrix was compiled with Mesquite version 3.7 (Maddison and Maddison, 2021). Coding practice follows suggestions by Brazeau (2011) for morphological character coding.

We used Bayesian tip-dating, which has become increasingly popular in recent years for phylogenetic inference from morphological data for diverse extinct groups of invertebrates, including cephalopods (e.g., Wright, 2017; Paterson, 2019; Pohle et al., 2022). The analyses were performed in BEAST 2.6.7 (Bouckaert et al., 2019) using the fossilized birth-death model as a tree prior (Stadler, 2010; Gavryushkina et al., 2014; Heath et al., 2014) and the parametrization of net diversification rate, turnover and sampling proportion (Heath et al., 2014). Morphological character evolution was modeled with the Mk model, including invariant site correction (Lewis, 2001). Characters were partitioned according to their number of states; excepting character 13 ("Doppellinien" type), all characters were binary. The exchangeability rates were set to 1.0 for binary characters and 1.5 for the single three-state character to prevent the artificial upweighting of multistate characters (King et al., 2017), although this is naturally expected to have a minimal impact on the analyses. We furthermore accounted for heterogeneous rates across sites with two discretized gamma shape rate categories. Although usually four or more rate categories are employed in morphological datasets for this purpose (Harrison and Larsson, 2015), we used only two categories due to the small number of characters and states. Tip dates were fixed to the midpoint between the first and last occurrence date of the corresponding species. First and last occurrence dates are based on the literature and are calibrated to the ICS 2020 age model (Appendix 2; Gradstein et al., 2020). We used a strict morphological clock with a lognormally distributed prior (mean = 0.1, standard deviation = 1.25). We placed an exponential prior on the origin (mean = 10 my, offset = 253.1 my), limiting the youngest possible origin date to the age of the oldest taxon of the analysis. This approach avoids unrealistically old estimates while not imposing an overly informative prior. The prior on diversification rate was set to an exponential distribution (mean = 1.0), and the turnover prior to a uniform distribution between 0.0 and 1.0. For the sampling proportion, we used a uniform prior with an upper limit of 0.15, which we justify by a very rough estimate of the number of belemnite species in the Palaeobiology Database (PBDB), which resulted in c. 200 species.

Although this number likely underestimates the true number of belemnite species by some margin due to the incompleteness of both the fossil record and the PBDB, it represents a useful esti-

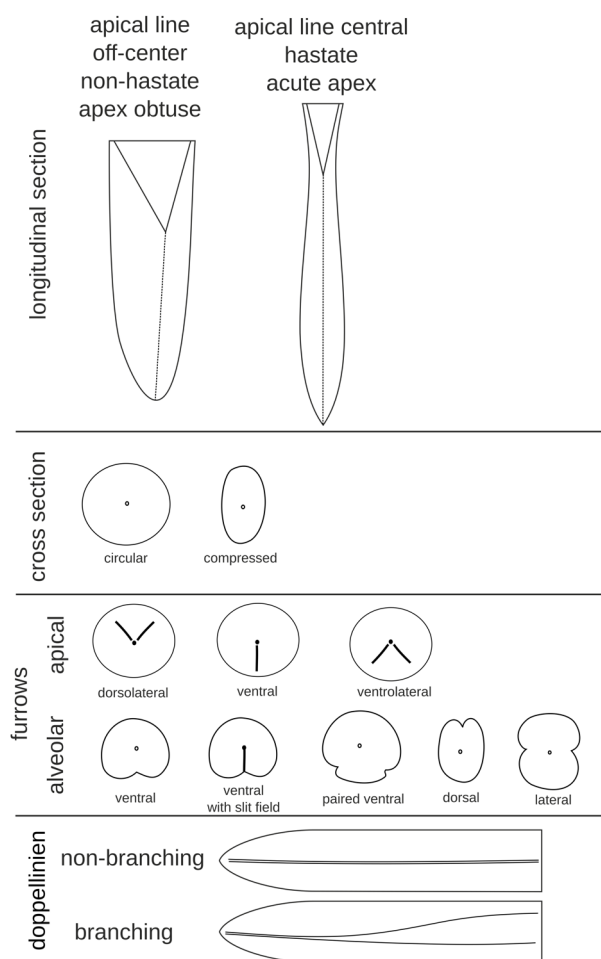
**TABLE 1.** Overview of species used in the analysis. Assignment to suborders is here based on previous taxonomic concepts, which may differ from the results obtained here. For more details, see supplementary material.

Species	(Sub-) order	Age	Main sources
<i>Atractites alpinus</i> von Gümbel, 1861	Aulacoceratida	Early Jurassic	Jeletzky, 1966; Mariotti et al., 2021
<i>Aulacoceras sulcatum</i> von Hauer, 1860	Aulacoceratida	Late Triassic	Jeletzky, 1966; Mariotti et al., 2021
<i>Acrocoelites oxyconus</i> (Hehl in von Zieten, 1831)	Belemnitina	Early Jurassic	Schlegelmilch, 1998
<i>Aulacoteuthis ernsti</i> Mutterlose and Baraboshkin, 2003	Belemnitina	Early Cretaceous	Mutterlose, 1983; Mutterlose and Baraboshkin, 2003
<i>Cylindroteuthis puzosiana</i> (d'Orbigny, 1842)	Belemnitina	Late Jurassic	Schlegelmilch, 1998
<i>Megateuthis gigantea</i> (von Schlotheim, 1820)	Belemnitina	Middle Jurassic	Schlegelmilch, 1998, own data
<i>Oxyteuthis brunsvicensis</i> (Strombeck, 1861)	Belemnitina	Early Cretaceous	Stolley, 1911b; Mutterlose, 1983
<i>Passaloteuthis bisulcata</i> (Blainville, 1827)	Belemnitina	Early Jurassic	Schlegelmilch, 1998
<i>Schwegleria feifeli</i> (Schwegler, 1939)	Belemnitina	Early Jurassic	Schlegelmilch, 1998
<i>Belemnitella mucronata</i> (von Schlotheim, 1813)	Belemnopseina	Late Cretaceous	Christensen, 1997
<i>Belemnitella propinqua</i> (Moberg, 1885)	Belemnopseina	Late Cretaceous	Christensen, 1971
<i>Belemnopsis apiciconus</i> (Blainville, 1827)	Belemnopseina	Middle Jurassic	Schlegelmilch, 1998
<i>Calabribelus pallinii</i> Weis et al., 2012	Belemnopseina	Middle Jurassic	Weis et al., 2012
<i>Dicoelites dicoelus</i> Boehm, 1906	Belemnopseina	Late Jurassic	Stevens, 1964
<i>Dimitobelus diptychus</i> (McCoy, 1867)	Belemnopseina	Early Cretaceous	Whitehouse, 1924; Williamson, 2006
<i>Duvalia grasiana</i> (Duval-Jouve, 1841)	Belemnopseina	Early Cretaceous	Stolley, 1911a; Stoyanova-Vergilova, 1970; Combémorrel, 1973; own data
<i>Gonioteuthis quadrata</i> (Blainville, 1827)	Belemnopseina	Late Cretaceous	Ernst, 1964; Christensen 1997
<i>Hibolites semisulcatus</i> (zu Münster, 1830)	Belemnopseina	Late Jurassic	Schlegelmilch, 1998; own data
<i>Holcobelus munieri</i> (Eudes-Deslongchamps, 1878)	Belemnopseina	Middle Jurassic	Jeletzky, 1966; Weis et al., 2012
<i>Lissajousibelus harleyi</i> (Mayer, 1866)	Belemnopseina	Early Jurassic	Weis et al., 2015b
<i>Mesohibolites minaret</i> (Raspail, 1829)	Belemnopseina	Early Cretaceous	Stoyanova-Vergilova, 1970
<i>Neohibolites ewaldi</i> (Strombeck, 1861)	Belemnopseina	Early Cretaceous	Stolley, 1911a; own data
<i>Neohibolites minimus</i> (Miller, 1826)	Belemnopseina	Early Cretaceous	Stolley, 1911a; Spaeth, 1971; Stevens et al., 2017
<i>Palaeobelemnopsis sinensis</i> Chen, 1982	Aulacoceratida incertae sedis	Late Permian	Mariotti et al., 2021
<i>Praeactinocamax plenus</i> (Blainville, 1827)	Belemnopseina	Late Cretaceous	Christensen, 1997
<i>Sinobelemnites cornutus</i> Zhu and Bian 1984	Belemnopseina	Late Triassic	Zhu and Bian 1984
<i>Tohokubelus takaizumii</i> Niko and Ehiro, 2022	Belemnopseina	Early Triassic	Niko and Ehiro 2022

mate to provide an absolute upper limit for the sampling rate, as it assigns zero probability to any values above 0.15 (corresponding to the ratio between taxa used in the analysis and approximate total number of known species). Lastly, we enforced a monophyletic constraint on the Belemnitida (without the Sinobelemnitidae). We justify this constraint by the strong prior expectation that this group is monophyletic, i.e., a polyphyletic belemnite origin within the Aulacoceratidae or Sinobelemnitidae has never been suggested. At the same time, aulacoceratids and sinobelemnites distinctly predate other belemnites, making an origin of either of these groups from within this con-

strained clade implausible (however, note that this does not preclude potential paraphyletic relationships with respect to other groups such as Diplobelida, Phragmoteuthida, or crown-Decabrachia). The analysis was run for two separate runs of the MCMC algorithm, each with 10 000 000 generations sampling every 10 000 generations and 10% of the samples discarded as burn-in. Convergence was checked using Tracer (Rambaut et al., 2018). The tree files were combined in LogCombiner (Bouckaert et al., 2019), and the Maximum Clade Credibility tree was generated with TreeAnnotator but using the older BEAST version 1.10.4 (Suchard et al., 2018). In contrast to the latter, TreeAnnotator





**FIGURE 1.** Terminology of some of the characters applied coded for the analysis (modified after Mutterlose, 1983; Doyle, 1990; Schlegelmilch, 1998; Hoffmann and Stevens, 2020).

in BEAST 2.6.7 treats sampled ancestors as not belonging to the same clade, which may result in underestimated posterior probabilities (Barido-Sottani et al., 2020). The xml script to run the analysis in BEAST, the resulting combined log and tree files and the annotated summary tree are contained in Appendix 3-6

## RESULTS

The parameter estimates of the tip-dated analyses are listed in Table 3. Although these parameters were not a focus of our current study, and more extensive model testing should be carried out before drawing any definite conclusions, they provide some insights. According to the estimated sampling rate (95% HPD interval between 0.015 and 0.15 with 27 included species), we

would expect a total number of belemnite and aulacoceratid species that existed until the end of the Cretaceous to be somewhere between approximately 180 and 1 800. Although this is a rather large credible interval, it appears to be a reasonable estimate that could be refined by adding more species or occurrence data. The omission of the diplobelids and phragmoteuthids, which probably belong to the same clade, may also have caused slightly biased estimates. Furthermore, refined models with variable rates through time may also improve these estimates. The age of the last common ancestor (origin parameter) of belemnites and the aulacoceratids included here was estimated to lie within the Permian, which roughly agrees with previous hypotheses (e.g., Jeletzky, 1966; Kröger et al., 2011).

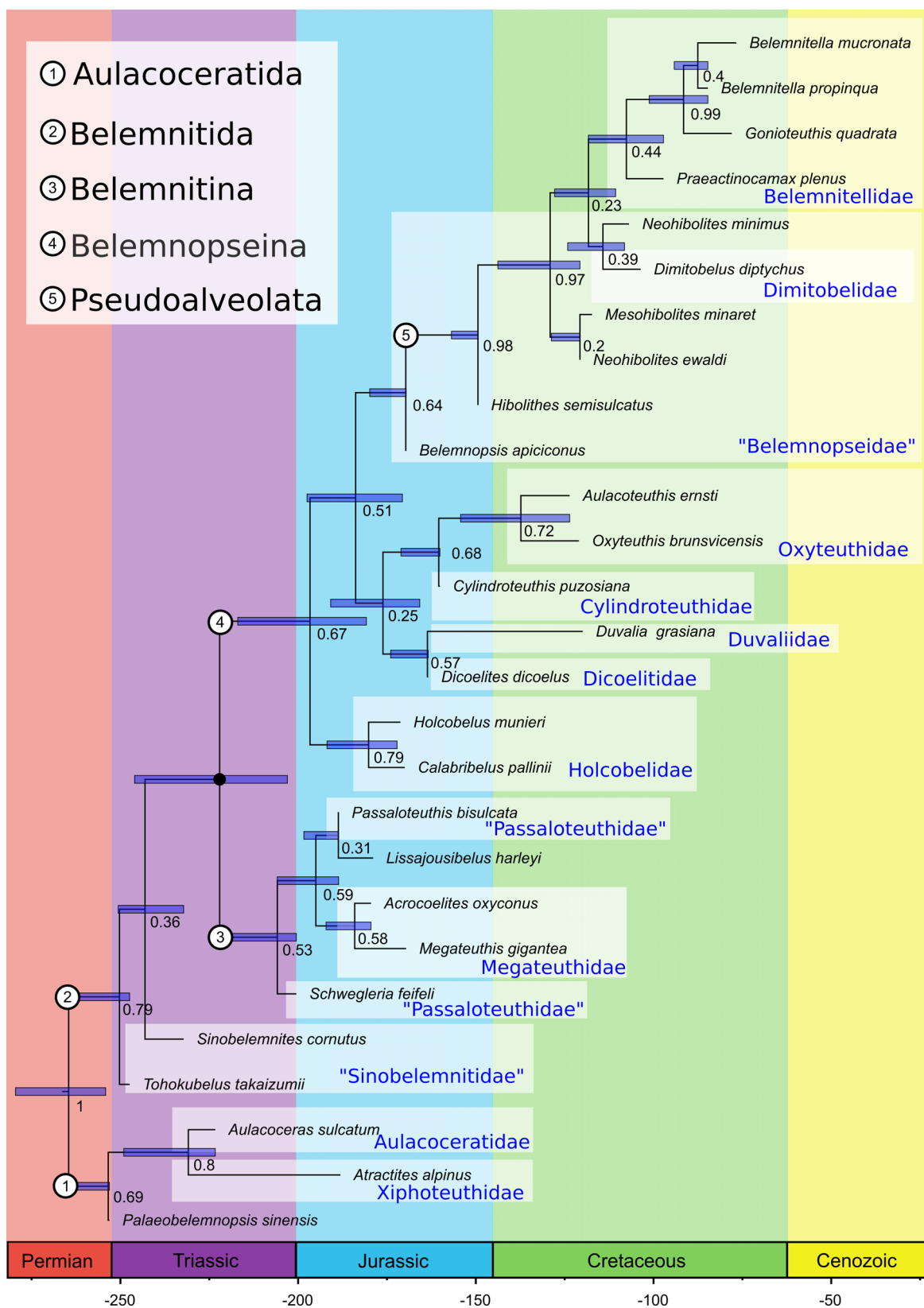
The topology of the maximum clade credibility tree (Figure 2) reveals several well-supported clades, although there are uncertainties in other areas of the tree. The placement of *Palaeobelemnopsis sinensis* within the Aulacoceratida is moderately well supported (posterior probability = PP = 0.69) as sister to the *Atractites alpinus* and *Aulacoceras sulcatum* clade. The Aulacoceratida were recovered as the sister group to the Belemnitida, with an estimated divergence date within the Permian. Furthermore, there is high support for including the sinobelemnitids within the Belemnitida (PP = 0.79), although the Sinobelemnitidae itself is paraphyletic. Within the Belemnitida, there is weak support for a group containing Jurassic taxa traditionally recognized as part of the Belemnitina (PP = 0.53), including *Schwegleria feifeli*, *Passaloteuthis bisulcata*, *Acrocoelites oxyconus*, *Megateuthis gigantea*, as well as *Lissajousibelus harleyi*, which was so far of uncertain placement inside Belemnitida. Within the Belemnitina, we recovered *Schwegleria feifeli* as sister group to the remainder of the Belemnitinae (PP = 0.59), with the Megateuthidae as monophyletic sister group (PP = 0.58) to *Passaloteuthis bisulcata* and *Lissajousibelus harleyi* (PP = 0.31). Sister to this Belemnitina clade is a larger group containing the remaining belemnites, here referred to as the Belemnopseina (PP = 0.67). The uncertainty of the divergence date between those two clades essentially covers the entire Triassic. Within the Belemnopseina clade, several subclades displayed relatively high support: 1) the sister group relationship between *Holcobelus munieri* and *Calabribelus pallinii* (PP = 0.79), which diverged from the rest of the clade (PP = 0.51) between the Late Triassic and Early Jurassic. 2) A large clade containing belemnitids

**TABLE 2.** List of included characters. Representation of hierarchical character state dependencies follows Pohle et al. (2022), i.e., subordinate characters are scored as “inapplicable” (-), if higher level character is scored as state 0. See also Figure 1 for examples.

#	Character description	Character states
1	Two dorsolateral apical furrows	absent (0), present (1)
2	Apical ventral furrow	absent (0), present (1)
3	Two ventrolateral apical furrows	absent (0), present (1)
4	Ventral alveolar furrow(s)	absent (0), present (1)
4.1	Ventral alveolar furrow type	intermediate (0), reaching alveolus (1)
4.1.1	Ventral alveolar furrow number	one (0), two (1)
4.1.2	Ventral furrow reaches from alveolus towards apical region	no (0), yes (1)
4.2	Ventral splitting surface (slit, slitfield, “Schlitzfeld”)	absent (0), present (1)
4.2.1	Ventral splitting surface type	rudimentary (0), full (1)
5	Dorsal alveolar furrow	absent (0), present (1)
5.1	Dorsal splitting surface (slit, slitfield, “Schlitzfeld”)	absent (0), present (1)
6	Doppellinien	absent (0), present (1)
6.1	Doppellinien type	parallel (0), diverge towards alveolus (1), multiple (2)
7	Proper rostrum mineral	aragonite (0), calcite (1)
8	Pseudoalveolus, secondary erosion of alveolus forming a concave or conical structure	absent (0), present (1)
8.1	Pseudoalveolus type	convex (0), concave (1)
9	Alveolus angle	low, < 11° (0), high > 11°
10	Alveolus type	central (0), ventrally displaced (1)
11	Rostrum surface	ribbed with longitudinal ridges (0), smooth (1)
12	Two dorsolateral longitudinal depressions	absent (0), present (1)
13	“Vascular” imprints	absent (0), present (1)
14	Apex type	acute (0), obtuse (1)
15	Epirostrum	absent (0), present (1)
16	Cameral deposits	absent (0), present (1)
17	Juvenile rostrum type	conirostrid (0), clavirostrid (1)
18	Rostrum hastate in dorsal view	no (0), yes (1)
19	Deep lateral furrows	absent (0), present (1)
20	Cross-section at position of protoconch	+/- circular (0), compressed (1)
21	Ventral tongue-like extension	absent (0), present (1)

**TABLE 3.** Results of the parameter estimates. Abbreviations: stdev = standard deviation, HPD int = highest posterior density interval, SA = sampled ancestors.

Parameter	mean	median	stdev	95% HPD int
Clock rate	0.0052	0.0051	0.0013	0.0030 – 0.0075
Diversification	0.012	0.011	0.0069	0.00084 – 0.025
Turnover	0.918	0.926	0.049	0.821 – 0.992
Sampling	0.075	0.073	0.039	0.015 – 0.147
Origin	270.6	269.3	8.63	256.5 – 288.1
SA count	4.71	5	1.98	1 – 8



**FIGURE 2.** Maximum clade credibility tree of the Bayesian tip-dated analysis. Numbers at nodes represent posterior probability, while the blue bars indicate the 95% highest posterior density interval of the divergence time estimates. The small black dot represents the constrained clade. Tips with zero-length branches represent sampled ancestors.

that share a pseudoalveolus (PP = 0.98) and appeared during the Late Jurassic. 3) The same clade but excluding *Hibolites semisulcatus*, which was either sister group or sampled ancestor to the latter (PP = 0.97), diverging from the latter during the Late Jurassic. 4) The clade that included *Gonioteuthis quadrata* and the two species of *Belemnitella* (PP = 0.99) The clade that includes *Belemnopsis apiconus* as sister group to the pseudoalveolus-bearing clade is moderately supported (PP = 0.64). The clade containing *Praeactinocamax plenus*, *Gonioteuthis quadrata*, *Belemnitella propinqua*, and *B. mucronata* (= *Belemnitellidae*) is only weakly supported (PP = 0.44), its origin estimated to the late Early Cretaceous. Other clades received low to moderate support. Among these, we recovered a monophyletic clade containing *Cylindroteuthis puzosiana*, *Aulacoteuthis ernsti*, and *Oxyteuthis brunsvicensis* (PP = 0.68), which formed a weakly supported monophyletic clade (PP = 0.25) together with *Duvalia* and *Dicoelites* (PP = 0.57). In our analysis, this clade diverged from the pseudoalveolus-bearing belemnites including *Belemnopsis* between the Early to Middle Jurassic. Furthermore, we recovered a polyphyletic *Neohibolites* with *N. minimus* forming a monophyletic clade with *Dimitobelus diptychus* (PP = 0.39) and *N. ewaldi* as sister to *Mesohibolites minaret* (PP = 0.2).

## DISCUSSION

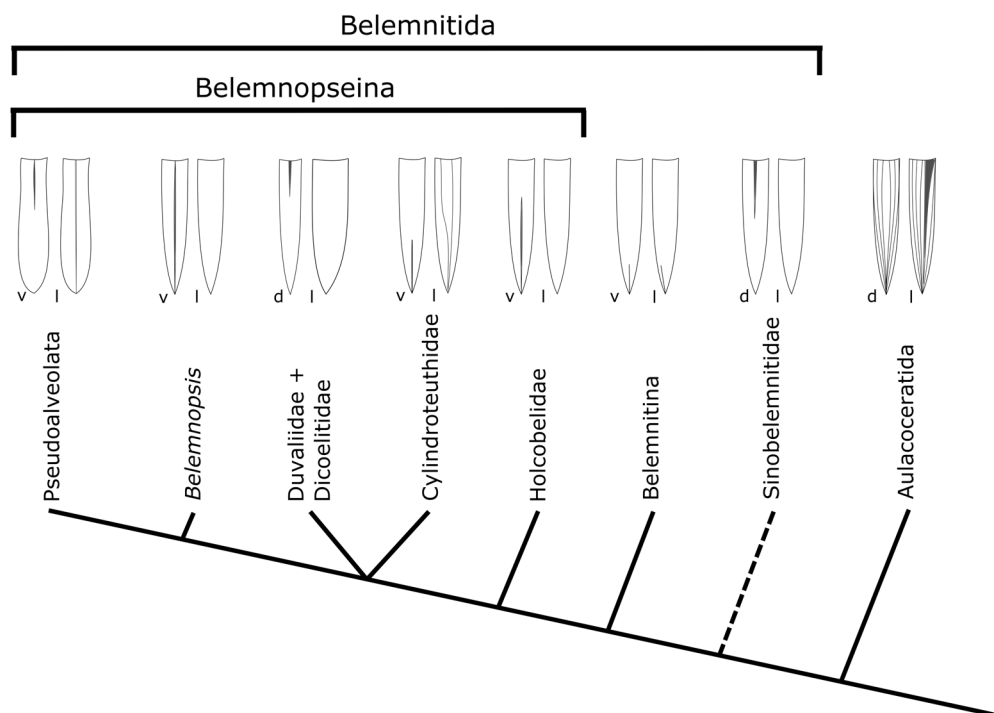
Due to the shared regeneration pattern and growth mode of Xiphoteuthidae (in the phylogeny represented by *Atractites alpinus*) and belemnites, Keupp and Fuchs (2014) suggested aulacoceratid paraphyly. On the other hand, Jeletzky (1966) argued for aulacoceratid monophyly, going so far as to view the group as an independent offshoot of baccitrid cephalopods, leaving no descendants. Doyle et al. (1994) favored the derivation of belemnites from within the Aulacoceratida potentially via the Phragmoteuthida. Aulacoceratida are here recovered as a monophyletic group and sister to belemnites, with the Permian *Palaeobelelemnopsis sinensis* confirmed as a member of the Aulacoceratida. However, since we only included a limited number of aulacoceratids in our analysis, we cannot rule out that the total group Aulacoceratida is paraphyletic, also with respect to other groups of early coleoids such as the Phragmoteuthida.

Since Jeletzky (1966), all belemnites were usually divided into two suborders; Belemnitina and Belemnopseina, with members of the former group considered ancestral to the latter. Under this

traditional scheme, Belemnitina groups taxa with apical furrows and Belemnopseina taxa with alveolar furrows. Problematic under the Belemnitina/Belemnopseina scheme is that the earliest belemnites of the Sinobelemnitidae are considered to be Belemnopseina with a gap of ca. 25 Ma between the youngest Sinobelemnitida and remaining Belemnopseina (Iba et al., 2012). At least one of the two sinobelemnitids in the current analysis, on the other hand, forms the sister group to the remaining belemnites (Figure 2). This result is in better agreement with the fossil record than the earlier hypothesis. It casts doubt on the homologization of dorsal alveolar furrows in belemnites, which was discussed as a potential uniting character of the Sinobelemnitidae with the Duvaliidae or Dicoelitidae (Iba et al., 2012). Still, a well-resolved position of the Sinobelemnitidae and clarification of their mono- or paraphyly will require a detailed study of this still sparsely known group and a better sampled Triassic fossil record of belemnites in general.

The species *Lissajousibelus harleyi* displays a ventral furrow in addition to dorsolateral apical furrows and was considered close to Belemnopseina by Weis et al. (2015b). In the present analysis, *L. harleyi* was found to be closely related to typical Belemnitina. Our Bayesian approach demonstrates how the relationship of belemnite taxa that do not easily fit the Belemnitina/Belemnopseina-scheme of Jeletzky (1966) can be resolved quantitatively by taking into account the maximally inclusive morphological and stratigraphic evidence. Belemnitina as defined herein is recovered as a monophyletic group with a likely origin in the Late Triassic but otherwise restricted to the Jurassic (Figures 2 and 3). A close relationship between these taxa was already suggested by Stolley (1919), who grouped them into his family "Polyteuthidae". This new definition includes at least the likely paraphyletic "Passaloteuthidae" (following the definition of Schlegelmilch, 1998) and the Megateuthidae (Acrocoelitidae); it remains to be investigated in which way other Jurassic families not considered in the present analysis (e.g., Hastitidae, Salpingoteuthidae) are related to this group. Likewise, as taxonomic concepts differ for groups such as the "Passaloteuthidae", including more species of these families may help clarifying their relationships further.

The Holcobelidae, Duvaliidae, and Dicoelitidae have an uncertain phylogenetic placement (e.g., Stolley, 1911a, 1911b; Stevens, 1964; Jeletzky, 1966; Combémoré, 1973; Weis et al., 2012). Our results place the Holcobelidae as the



**FIGURE 3.** Cladogram showing the here suggested systematics of the Belemnitida based on the Bayesian tip-dated analysis. Sketches show the general outer morphological features of a typical representative of the groups in either dorsal (d), ventral (v), or lateral (l) view.

sister group to the rest of the Belemnopseina. This leaves it ambiguous whether their ventral furrow that does not reach the alveolus represents the ancestral state of the Belemnopseina or if this character represents a secondary development from an alveolar furrow reaching the alveolus as seen in typical "Belemnopseidae". In our tree, the placement of Duvaliidae as sister to Dicoelitidae finds moderate support, but the placement of this clade itself has only weak support (Figure 2). The Duvaliidae share with the Dicoelitidae the presence of a dorsal alveolar furrow. However, a belemnopseine ventral alveolar furrow is also developed in the Dicoelitidae. *Duvalia grasiana* has recently been shown to display more organic-rich primary rostrum calcite than other belemnites (Stevens et al., 2022). A similar detailed description of the microstructure of other duvaliids and potentially related forms might reveal the phylogenetic position of this enigmatic group in future studies with more certainty.

The monophyletic clade containing the Oxyteuthidae as sister to *Cylindroteuthis puzosiana* confirms earlier thoughts on their phylogenetic relationships (e.g., Mutterlose, 1983). However, in contrast to these earlier hypotheses, we recovered

the Cylindroteuthidae *sensu lato* clade within the Belemnopseina instead of within the Belemnitina. Still, the problem of the phylogenetic placement and evolution of Cylindroteuthidae and Oxyteuthidae needs further focused analyses, especially for Boreal belemnites of the Jurassic-Cretaceous transition, which will also have to include closely related species of the Pachyteuthidae. Our analysis suggests homology of the ventral furrow present in many Cylindroteuthidae *sensu lato*, not with the apical ventral furrow as is typical for the Mega-teuthidae/Acrocoelidae, but with the belemnopseine ventral furrow. This hypothesis contrasts with the "stratophenetic" reasoning of the independent evolution of a ventral furrow in the genus *Aulacoteuthis* (Mutterlose and Baraboshkin, 2003; Baraboshkin and Mutterlose, 2004).

A name is suggested here for a newly identified and well-supported clade inside the Belemnopseina, the unranked Pseudoalveolata (see Appendix 7; PP=0.98; Figure 2). The Pseudoalveolata is characterized by the synapomorphy of pseudoalveolus formation, a secondary alveolus-deepening, developing by dissolution/erosion of anterior organic-rich rostrum sections (Stevens et al., 2022). The pseudoalveolus is further character-

ized by a well-mineralized “spike” projecting anteriorly toward the protoconch (*Nadelspitze* of Stolley, 1911a). *Hibolithes* has here been recovered as the earliest pseudoalveolate belemnite. Pseudoalveolus types have been considered of great importance in the phylogeny of the Belemnitellidae (e.g., Košťák, 2012), but contrary to suggestions by Dauphin et al. (2007) and Košťák and Wiese (2008), there is no conclusive evidence for the anterior rostrum of pseudoalveolate belemnites being of primarily aragonitic composition, as it likely consisted of calcite with primarily high organic contents (see Stevens et al., 2017; 2022). Irrespective of its composition, it still seems to be a different structure, which is consistently recovered.

The two species of *Neohibolites* analyzed herein (*N. ewaldi* and *N. minimus*) are not recovered as sister species. This indicates the possibly polyphyletic or paraphyletic nature of *Neohibolites*, a genus which has long been seen as ancestral to the two only belemnite families left after the Cenomanian, the Belemnitellidae and Dimitobelidae, (e.g., Mutterlose, 1998). Future studies focusing on the origin of Belemnitellidae and Dimitobelidae might shed more light on the exact origins of these two last surviving belemnite groups and their origins in the paraphyletic “Belemnopseidae”. “Belemnopseidae” has long been recognized as paraphyletic with respect to the Belemnitellidae and Dimitobelidae (e.g., Jeletzky, 1966; Mutterlose, 1988). However, a new phylogenetic definition of the family containing all belemnites closer to *Belemnopsis* than to the Pseudoalveolata seems possible. This would require a more thorough sampling of the diverse “belemnopseid” taxa of the earliest Cretaceous and a thorough revision of not only the genus *Belemnopsis* but also *Hibolithes*, encompassing detailed revision of the diverse *Belemnopsis* species of the Austral Realm (e.g., Stevens, 1965; Challinor, 1990). Based on the unclear and absent types for both genera (e.g., Combémorel and Howlett, 1993; Mitchell, 2015), the assignment of species to either genus was often based on superficial morphological assessment. We here confirm that there is no pseudoalveolus formation in the type species of *Belemnopsis*, *B. apiciconus*. Pseudoalveolus formation had already been suggested as a differentiating character of the genera *Belemnopsis* and *Hibolithes* by Stolley (1911a) but was unfortunately not followed on by later authors.

The tip-dated Bayesian analysis confirms earlier ideas that the epirostrum, a “tertiary” rostrum formation (Fuchs, 2012), which is developed only

in some belemnites, represents a parallelism and does not indicate a close relationship (Bandel and Spaeth, 1988; Arkhipkin et al., 2015; Stevens et al., 2017). Epirostra are present in the analyzed species *Megateuthis gigantea*, *Holcobelus munieri*, *Calabribelus pallinii*, and *Neohibolites minimus*, found on disparate parts of our tree (Figure 2). However, it is unclear how preservation, ontogeny and producing polished sections may affect whether an epirostrum is recovered or not. According to Arkhipkin et al. (2015), it forms rather late in ontogeny and similar structures evolved repeatedly in different coleoid lineages. Thus, it is possible that they have been overlooked in some cases, but it likely presents a highly homoplastic character.

In our proposed systematic framework (Figure 3, Table 4), we regard the potentially paraphyletic Sinobelemnitidae as the earliest belemnites. The remainder of the belemnites still falls into two large monophyletic clades, the Belemnitina and Belemnopseina. To align with the current taxonomy as far as possible, we retain those two clades as suborders but slightly adjust the included families. We consider the Cylindroteuthidae *sensu lato*, Duvaliidae, and Dicoelitidae more derived than the Holcobelidae inside the Belemnopseina but otherwise of uncertain position with regard to the *Belemnopsis* + Pseudoalveolata clade.

The presented topology represents only a first step towards a well-resolved phylogeny of all belemnites. To achieve further resolution, it will likely be necessary to detect and evaluate further microstructural and geochemical data of several belemnite taxa and incorporate more taxa and characters into the analysis. This includes the use of continuous characters, which are currently not straightforward to implement in Bayesian analyses. Morphometric analyses show their potential in this regard, as belemnite morphospace appears to reflect taxonomic units (Dera et al., 2016). Furthermore, well-preserved specimens from Konservat-Lagerstätten may provide additional valuable insights into the variability of soft-part anatomy, statoliths, radulae, hooks, or jaws within belemnites (e.g., Klug et al., 2010; Fuchs and Hoffmann, 2017), potentially adding other characters to include into phylogenetic analysis. Unfortunately, many of these characters will probably remain unknown for the majority of belemnite species. However, they would be potentially informative for a more inclusive phylogenetic analysis involving non-rostrum bearing “belemnoids” to resolve the decabrachian crown and stem groups.

**TABLE 4.** Proposed revised systematic scheme for the Belemnitida based on the Bayesian tip-dated analyses. For families, we follow previous systematic concepts (see also Table 1), although some were recovered as paraphyletic, indicated with (\*). Note that only families that were included in the analyses are listed here. Aulacoceratids are omitted here because they were not a central focus of the study, providing only limited insights for their classification.

Class Cephalopoda Cuvier, 1797
Subclass Coleoidea Bather, 1888
Order Belemnitida Zittel, 1895
Family Sinobelemitidae (*) Bian and Zhu, 1984
Suborder Belemnitina Zittel, 1895
Family Passaloteuthidae (*) Naef, 1922
Family Megateuthidae Sachs and Naljaeva, 1967
Suborder Belemnopseina Jeletzky, 1965
Family Holcobelidae Gustomesov, 1977
Family Dicoelitidae Sachs and Naljaeva, 1967
Family Duvaliidae Pavlov, 1914
Family Cylindroteuthidae Stolley, 1919
Family Oxyteuthidae Stolley, 1919
Pseudoalveolata nov. [unranked]
Family Belemnopseidae (*) Naef, 1922
Family Dimitobelidae Whitehouse, 1924
Family Belemnitellidae Pavlov, 1914

## CONCLUSIONS

The first tip-dated analysis of belemnite (Belemnitida) phylogeny is presented. Our results suggest that the usually applied dichotomous subdivision of all belemnites into Belemnitina and Belemnopseina based only on the presence of apical *versus* alveolar furrows needs some adjustment. We consequently suggest the subdivision of all belemnites, except the early and potentially paraphyletic Sinobelemitidae, into newly phylogenetically defined Belemnitina and Belemnopseina. Holcobelidae are the sister group to all other Belemnopseina, and Duvaliidae and Dicoelitidae are confirmed as Belemnopseina but are still of uncertain placement inside this group. A major change involves the transfer of the Cylindroteuthidae (including Oxyteuthidae) from the Belemnitina to the Belemnopseina. A new well-supported subgroup of the Belemnopseina, the unranked Pseudoalveolata, is suggested here, including a phylogenetic definition and the suggestion of a potential synapomorphy.

Because of their high fossilization potential and often high abundance in the marine fossil record, belemnites are particularly important in tracking faunal changes of the Jurassic and Cretaceous pelagic realms. The present study is only a first step; further analyses based on more taxa and characters, including continuous characters and detailed microstructural analyses of the rostra, are needed to further resolve more details of the belemnites' evolutionary history. Applying quantitative and reproducible phylogenetic methodology in contrast to earlier approaches relying on authoritative overemphasis of single characters will lay a solid foundation for the future study of belemnites.

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## **APPENDICES**

### **APPENDIX 1.**

Nexus file containing the character matrix used for the phylogenetic analysis. (Appendix 1-6 available for download at <https://palaeo-electronica.org/content/2023/3819-belemnite-phylogeny>)

### **APPENDIX 2.**

CSV file containing first occurrences (FO) and last occurrences (LO) for all included taxa and the corresponding references. Note that only the midpoint between those dates was actually used in the analysis. (Appendix 1-6 available for download at <https://palaeo-electronica.org/content/2023/3819-belemnite-phylogeny>)

### **APPENDIX 3.**

XML input file to run the Bayesian phylogenetic analysis in BEAST 2.6.7. (Appendix 1-6 available for download at <https://palaeo-electronica.org/content/2023/3819-belemnite-phylogeny>)

### **APPENDIX 4.**

LOG output file of the Bayesian phylogenetic analysis, containing all sampled states for the model parameters. (Appendix 1-6 available for download at <https://palaeo-electronica.org/content/2023/3819-belemnite-phylogeny>)

### **APPENDIX 5.**

TREES output file of the Bayesian phylogenetic analysis, containing the (post-burn-in) posterior tree sample, i.e., 1802 trees. (Appendix 1-6 available for download at <https://palaeo-electronica.org/content/2023/3819-belemnite-phylogeny>)

### **APPENDIX 6.**

TRE output file of the Bayesian phylogenetic analysis, containing the annotated maximum clade credibility (MCC) tree. This tree corresponds to the tree shown in Figure 2. (Appendix 1-6 available for download at <https://palaeo-electronica.org/content/2023/3819-belemnite-phylogeny>)

**APPENDIX 7.**

## Phylogenetic Definition of Pseudoalveolata.

**Pseudoalveolata** unranked K. Stevens, A. Pohle, R. Hoffmann, and A. Immenhauser, new clade name. Phylogenetic definition: the least inclusive clade containing the Belemnitellidae Pavlow, 1914, Dimitobelidae Whitehouse, 1924, and the species *Hibolites semisulcatus* (zu Münster, 1830), *Neohibolites ewaldi* (Strombeck, 1861), *N. minimus* (Miller, 1826), and *Mesohibolites minaret* (Raspail, 1829). Etymology: derived from the belemnite morphological term pseudoalveolus, itself derived from Greek pseúdo, meaning “to lie” or “to deceive”, and alveolus, from Latin, meaning a small cavity. Reference phylogeny: Figure 2. Diagnosis: In belemnite morphological terminology, the alveolus is the approximately cone-shaped cavity of the rostrum, which contains the phragmocone. If the alveolus is secondarily enlarged by abrasion or dissolution of the anterior part of the rostrum due to an anterior primarily porous and organic-rich composition of the rostrum (e.g., Stolley, 1911a; Ernst, 1964; Stevens et al., 2022), the resulting secondary deepening is termed a pseudoalveolus. Anterior primarily porous and organic-rich rostra, which might result in a pseudoalveolus, accordingly represent the synapomorphy of the Pseudoalveolata.