1 Belemnite phylogeny and decline during the mid-Cretaceous

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5 ABSTRACT

6 Belemnites are common fossil coleoid cephalopods of the Mesozoic. They began to diversify in
7 the Triassic-Early Jurassic and maintained this diversity until the early Early Cretaceous.
8 During the mid-Cretaceous, they declined in diversity and distribution, being restricted to only
9 the Boreal and Austral Realm since the Turonian. Here, I present the first cladistic analysis of
10 belemnite phylogeny, spanning taxa representative of the whole diversity and stratigraphic
11 range of the group. This analysis shows that the usually applied subdivision of all belemnites
12 into “Belemnitina” and “Belemnopseina” is not supported. A newly identified clade, the
13 Pseudoalveolata, is suggested here. Pseudoalveolate belemnites represent the last remaining
14 belemnites after the Aptian. Oceanic anoxia and warming are likely the main cause of the mid-
15 Cretaceous belemnite decline, resulting in the Aptian-Albian dominance of the warm-adapted
16 pseudoalveolate genus *Neohibolites*. The rise of teleost fish diversity during the mid-
17 Cretaceous is discussed and its relevance for belemnite evolution. Some teleosts (e.g.,
18 *Enchodus*) might have taken over the mesopredator niches left by belemnites during the mid-
19 Cretaceous, being better adapted to warming seas. Belemnites were not able to recover their
20 earlier widespread distribution and diversity and the last remaining, disjunctly distributed
21 families, the northern Belemnitellidae and southern Dimitobelidae, became extinct at the
22 K/Pg-boundary.

23

24 **Introduction**

25 Belemnites (Belemnitida) are an extinct group of stem-decabrachian coleoids (e.g., Fuchs et
 26 al., 2013; Hoffmann & Stevens, 2020). They are characterized by a calcitic rostrum, which is by
 27 far the most commonly preserved part of their internal shell. In this paper, I use the terms
 28 belemnites and Belemnitida only for these calcite-rostrum bearing species. This definition
 29 excludes groups like the Belemnoteuthida and Diplobelida, which are sometimes also referred
 30 to as belemnites. The paraphyletic assemblage of Belemnitida, Aulacoceratida,
 31 Belemnoteuthida, and Diplobelida is referred to as “belemnoids” in lieu of a proper
 32 understanding of their interrelationships at present (following Hoffmann & Stevens, 2020).
 33 Diplobelida probably represent close relatives of crown-Decabrachia (Fuchs, 2019; Fuchs et
 34 al., 2013).

35 The oldest belemnites are known from the Late Triassic (Carnian) of the northeastern Tethys
 36 (Zhu & Bian, 1984; Iba et al., 2012). By at least the Early Jurassic they had reached a
 37 cosmopolitan distribution and relatively high diversity, with the two usually recognized
 38 belemnite subgroups, the “Belemnitina” and “Belemnopseina” (Jeletzky, 1966), already
 39 present (e.g., Iba et al., 2014a; 2014b; Weis et al., 2015a). Belemnites continued to be diverse
 40 during the Jurassic and early Early Cretaceous (Iba et al., 2012; 2014a; 2014b).

41 After a major faunal and floral turnover at the Barremian-Aptian boundary (Mutterlose,
 42 1998), the cosmopolitan belemnite genus *Neohibolites* dominated the Aptian-Albian of the
 43 Tethys, North Pacific, Austral, and Boreal Realms. *Neohibolites* went extinct during the Albian
 44 in the North Pacific Realm resulting in the local extinction of belemnites in this region (Iba et
 45 al., 2011). In the Tethys, the genus *Parahibolites* went extinct during the early Cenomanian,
 46 while *Neohibolites* went extinct during the middle Cenomanian, which led to the regional
 47 extinction of belemnites in the Tethys (Combémoré et al., 1981). The mid-Cretaceous is

regarded as the time of the highest global temperatures as well as the highest global sea-level of the younger Phanerozoic, especially during the Cenomanian-Turonian (e.g., Miller et al., 2005; O’Brien et al., 2017).

Neohibolites is considered to be closely related to the last two surviving belemnite families: The Belemnitellidae, which were largely restricted to the Boreal Realm (Cenomanian – Maastrichtian) and the Dimitobelidae of the Austral Realm (Aptian—Maastrichtian). Only one genus of belemnitellid belemnites (*Praeactinocamax*) is present in the upper Cenomanian of the Boreal Realm, only afterwards does the group diversify (Combémoré et al., 1981; Christensen, 1997). From the Aptian until the Cenomanian, the Dimitobelidae were widespread in the southern seas. They are recorded from Aptian – Cenomanian sediments of Antarctica, India, New Guinea, Australia, southern Argentina, and New Zealand, while being restricted to Antarctica, southern Argentina, Australia, and New Zealand during the Turonian – Maastrichtian. Dimitobelids are very rare in the upper Maastrichtian and probably already became extinct before the Cretaceous/Paleogene-boundary event (Crame et al., 1996).

Several authors have discussed the ecological relationship and co-evolution of cephalopods (specifically coleoids) with teleost fishes (Packard, 1972; O’Dor & Webber, 1986; Tanner et al., 2017). The earliest teleost fishes are known from the Middle-Late Triassic boundary (Arratia, 2014). Teleost fishes diversified during the mid-Cretaceous owing in part to the origin of the hyperdiverse spiny-rayed teleosts or Acanthomorpha in the Cenomanian (e.g., Patterson, 1993; Davesne et al., 2014; Cantalice et al., 2021). Acanthomorphs are characterized by sharp spines in their fins as well as highly protrusible mouths. Teleost and especially acanthomorph diversity increased sharply after the Cretaceous/Paleogene extinction, with the morphological disparity of this group also increasing (Patterson, 1993; Friedman, 2010). Acanthomorphs represent more than half of all living teleost fishes and 25% of all extant vertebrate species

(e.g., Friedman et al., 2010; Near et al., 2012; Nelson et al., 2016; Dornburg & Near, 2021).

The mid-Cretaceous was a pivotal time of belemnite evolution. This paper presents the first cladistic study of belemnite phylogeny, which identifies the Aptian as turning point in their evolution. I introduce a new monophyletic group of belemnites, the Pseudoalveolata, and point out problems with the dichotomous subdivision of all belemnites into Belemnitina and Belemnopseina. I discuss the influence of environmental factors on the belemnite decline of the mid-Cretaceous and the potential co-evolution with teleost fishes during this time.

Methods

20 belemnite genera (*Acrocoelites*, *Acroteuthis*, *Aulacoteuthis*, *Belemnitella*, *Belemnopsis*, *Calabribelus*, *Dicoelites*, *Dimitobelus*, *Duvalia*, *Hibolites*, *Holcobelus*, *Lissajousibelus*, *Megateuthis*, *Mesohibolites*, *Neohibolites*, *Oxyteuthis*, *Passaloteuthis*, *Praeactinocamax*, *Sinobelemites*, *Schwegleria*), representative of the stratigraphic range, biogeography, and diversity of the whole group, were coded for 18 rostrum characters (Supplementary files 1, 2). Two aulacoceratid genera (*Aulacoceras*, *Atractites*) were also included with *Aulacoceras* serving as the outgroup for the analysis, following the hypothesis of aulacoceratid paraphyly by Keupp and Fuchs (2014). 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 on rostrum characters only. Morphological data comes from several published sources (e.g., Stolley, 1911; Stoyanova-Vergilova, 1970; Combémoré, 1973; Zhu & Bian, 1984; Mutterlose, 1983; Mutterlose et al., 1987; Doyle, 1987; Christensen, 1997; Schlegelmilch, 1998; Weis et al., 2012; 2015b; Mariotti et al., 2021) and own observations.

The phylogenetic analysis was performed with TNT version 1.5 (Goloboff & Catalano, 2016).

96 Coding practice follows suggestions of Brazeau (2011) for morphological character coding.
 97 Terminology of belemnite morphology follows Hoffmann & Stevens (2020). Exact
 98 enumeration was applied to search for most parsimonious trees (MPTs). Bootstrap support
 99 was calculated as standard (sample with replacement) with 100 replicates and jackknife
 100 support with 50% removal probability with 100 replicates, both using “traditional” tree
 101 search method. The consensus tree was calculated as a strict (Nelson) consensus.

102 **Results**

103 Five MPTs were found (Fig. 1) (consistency index = 0.75, retention index = 0.8696). In all five
 104 trees Belemnitida is found as monophyletic with the aulacoceratid genus *Atractites* as sister.
 105 The resulting strict consensus tree finds a polytomy for the intrarelationships of Belemnitida.
 106 The only clades present in the strict consensus tree are clade 1 (*Aulacoteuthis*, *Acroteuthis*),
 107 clade 2 (*Lissajousibelus*, *Megateuthis*, *Acrocoelites*, *Passaloteuthis*), and clade 3 (*Dimitobelus*,
 108 *Neohibolites*, *Mesohibolites*, *Hibolithes*, (*Belemnitella*, *Praeactinocamax*)) (Fig. 2). The clade
 109 Belemnitida is well supported in the present analysis, while many taxa inside the Belemnitida
 110 remain unresolved. The here inferred subclades of the Belemnitida have relatively low
 111 support by bootstrap and jackknife values, but support for clade 3 is relatively high (63/51;
 112 Fig. 2).

113 **Discussion**

114 **Belemnite phylogeny**

115 Since Jeletzky (1966), belemnites were usually subdivided into two suborders; Belemnitina
 116 and Belemnopseina, with some members of the former seen as ancestral to the latter.
 117 Belemnitina groups taxa with apical furrows and Belemnopseina taxa with alveolar furrows. It
 118 has long been known that many belemnites do not fit into this dichotomous subdivision. For
 119 example, the genus *Lissajousibelus* displays a ventral furrow with slit in addition to

dorsolateral apical furrows but was considered close to “Belemnopseina” by Weis et al. (2015b). In the present analysis it was found to be closely related to typical “Belemnitina”, *Passaloteuthis*, *Acrocoelites*, and *Megateuthis*. The Duvaliidae, Dicoelitidae, and Holcobelidae have also been of uncertain phylogenetic placement (e.g., Stevens, 1964; Weis et al., 2012). The present analysis unfortunately cannot resolve these taxa with certainty either, but in four of the five MPTs *Duvalia* and *Dicoelites* form a clade (Fig. 4), which might give impetus for further analyses of a close relationship. The two holcobelids *Holcobelus* and *Calabribelus*, while not found to form a monophylum in any of the MPTs, are close to “belemnopseine” belemnites (Fig. 1), confirming Weis et al. (2012).

The oxyteuthid *Aulacoteuthis* and cylindroteuthid *Acroteuthis* are sister taxa in the present analysis (Fig. 2). While no monophyletic Oxyteuthidae have been found, the present analysis might point towards a close relationship of the oxyteuthids to *Acroteuthis* as suggested by Mutterlose (1983). Still, the problem of the phylogenetic placement and evolution of the Oxyteuthidae needs further focused analyses, especially with respect to the oxyteuthids of the Russian platform (Mutterlose & Baraboshkin, 2003; Baraboshkin & Mutterlose, 2004).

Overall, there is no support from the present analysis for a dichotomous subdivision of all belemnites into Belemnitina and Belemnopseina, as these groups are usually defined (Figs. 1, 2). Based on the present analysis, all belemnites cannot be grouped under the traditional simple dichotomous scheme, although a phylogenetic redefinition of Belemnitina and Belemnopseina seems possible. The present consensus topology represents only a first step towards a better 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, in order to get a better understanding of the phylogeny of this group.

A name is suggested here for the newly identified clade 3 as the unranked Pseudoalveolata

(Fig. 2). Pseudoalveolata is defined by the synapomorphy of pseudoalveolus formation, i.e., the alveolus of members of this group is usually found to be in part eroded. A pseudoalveolus might be present as a concave secondary deepening of the alveolus (e.g., some *Dimitobelus*) or as formation of a conical structure by complete loss of the rostrum cavum and anterior rostrum solidum (e.g., *Hibolithes*, *Praeactinocamax*). Pseudoalveolus types have been of great importance in the phylogeny of the Belemnitellidae (e.g., Košťak, 2012). Contrary to suggestions by Dauphin et al. (2007) and Košťak & Wiese (2008), there is no conclusive evidence for the alveolus of pseudoalveolate belemnites being of primarily aragonitic composition, it instead consisted of calcite with primarily high organic contents (Stevens, 2017; Stevens et al., 2017). Inside the Pseudoalveolata the belemnitellids *Praeactinocamax* and *Belemnitella* were found as sister taxa, but a more extensive analysis of the Late Cretaceous family Belemnitellidae would be needed to confirm its monophyly (Fig. 2).

Belemnite decline during the mid-Cretaceous

Belemnite diversity was significantly reduced during the Aptian (Fig. 3). In the Albian, only members of the Pseudoalveolata persist (Fig. 4), namely the genera *Neohibolites* and *Parahibolites* in the Tethys and Boreal Realm as well as the Dimitobelidae in the Austral Realm (e.g., Christensen, 1997; Doyle, 1992). The early Aptian is characterized by OAE1a, an oceanic anoxic event triggered by volcanism of the Ontong-Java Plateau (e.g., Jenkyns, 2010; Erba et al., 2015). Volcanism resulted in a pronounced warming and rise of oxygen minimum zones in the oceans, resulting in widespread deposition of organic rich sediments and the disappearance of metazoan-dominated carbonate platforms in the Tethys (Bottini & Mutterlose, 2012; Huck et al., 2014; Hueter et al., 2019; Bauer et al., 2021).

OAE1a was likely the driving factor in the extinction of the oxyteuthids, which are usually viewed as the last members of the “Belemnitina”. Members of the last-occurring genus

168 *Oxyteuthis* are recorded from German and Russian sections until black shale formation in
 169 association with OAE1a (Hoffmann & Mutterlose, 2011; Lehmann et al., 2012; Rogov et al.,
 170 2019). The pseudoalveolate *Neohibolites* originated in the earliest Aptian and is regarded as a
 171 warm-adapted genus (Mutterlose, 1998). Its survival might be linked to being better able to
 172 cope warming and anoxia in association with OAE1a. The local extinction of *Neohibolites*
 173 during the late Albian in the North Pacific Realm is thought to be linked to a cooling phase in
 174 this region (Iba et al., 2011) and similarly, warm-water *Neohibolites* might have become
 175 extinct due to cooling during the middle Cenomanian Plenus Cold Event (Combémorrel et al.,
 176 1981; Ernst et al., 1983). The Belemnitellidae originated in the early Cenomanian with
 177 *Praeactinocamax* and were apparently well-adapted to cooler conditions, which is suggested
 178 by the mass-occurrence of *Praeactinocamax plenus* during the short-lived mid-Cenomanian
 179 Plenus Cold Event, when they even spread into the northern Tethys (Gale & Christensen,
 180 1996). During the Aptian there are two phases during which belemnites of the mostly Tethyan
 181 family Duvaliidae spread northward, shortly after OAE1a and during the late Aptian
 182 (Mutterlose, 1998). Duvaliids become extinct later in the Aptian (Fig. 4) and therefore
 183 represent the last surviving non-pseudoalveolate belemnites. Dimitobelids also seem to have
 184 been adapted to cool conditions. From the Turonian onwards they are restricted to the shelf
 185 seas of the southernmost remnants of Gondwana (Doyle, 1992; Crame et al., 1996), potentially
 186 becoming extinct further north due to warming during the mid-Cretaceous. While
 187 pseudoalveolate belemnites form a monophyletic group, they do not seem to have shared the
 188 same ecological preferences regarding temperature.

189 Although belemnites are often viewed as nekto-benthic, this assumption is problematic
 190 (Hoffmann & Stevens, 2020). A demersal habitat of several belemnites is unlikely given their
 191 common occurrence in sediments deposited below anoxic bottom waters but cannot be
 192 excluded for all belemnite taxa (Rexfort & Mutterlose, 2006; Mutterlose et al., 2010; Stevens et

193 al., 2014). It therefore seems unlikely that anoxia affected belemnites directly in their upper
 194 water habitat but warming and the general effects on ecosystems of the spread of anoxic
 195 waters might have resulted in their decline during the mid-Cretaceous.

196 Molecular clocks indicate a diversification of teleosts during the mid-Cretaceous, which is
 197 congruent with fossil data based on the skeletal (Fig. 3, Cavin et al., 2007; Near et al., 2012;
 198 Guinot & Cavin, 2016) and otolith record (Schwarzshans, 2018). This radiation has been shown
 199 not to be an artifact of a “lagerstätten effect” (Cavin & Forey, 2007). It seems unlikely that the
 200 newly emerged acanthomorphs and other teleosts replaced belemnites via competitive
 201 displacement. Competitive displacement in the fossil record can be shown, if: 1) both groups
 202 show an inverse relationship of their respective diversity, 2) they can be regarded to have
 203 utilized the same resources, and 3) both groups evolved in allopatry before dispersal of one
 204 group into the other's range (Krause, 1986). All those points cannot be conclusively shown for
 205 teleosts and belemnites. Although both groups show largely inverse diversity trends, low
 206 recorded diversity of teleosts from the Coniacian to Campanian (Fig. 3) is likely a sampling
 207 artifact (Guinot & Cavin, 2016). Belemnites were mesopredators, likely being restricted to a
 208 carnivorous diet (Hoffmann & Stevens, 2020), while teleosts during the Cretaceous display
 209 diverse feeding strategies (e.g., herbivores; Davesne et al., 2018). Both groups certainly did not
 210 evolve allopatrically, teleosts and belemnites are both known from the Triassic onward in the
 211 marine realm. It seems more plausible that higher eustatic sea level as well as high
 212 temperatures favored the radiation of teleosts during the mid-Cretaceous (Cavin et al., 2007)
 213 and they diversified into some of the niches earlier occupied by belemnite species. For
 214 example, the widespread aulopiform family Enchodontidae were medium-sized
 215 mesopredatory fishes. The often highly abundant type genus *Enchodus* originated in the latest
 216 Albian/Cenomanian and was a very common component of ichthyofaunas until the end of the
 217 Cretaceous (e.g., Fielitz & González-Rodríguez, 2010). A faunal replacement of belemnites by

218 crown-octobranchian and crown-decabracian coleoids likely also occurred during the mid-
219 Cretaceous (Iba et al., 2011; Tanner et al., 2017).

220 The Cenomanian decline of belemnites has been suggested to be the main factor in the
221 extinction of ichthyosaurs at the Cenomanian/Turonian boundary (Bardet, 1992). A similar
222 belemnite decline during the Toarcian was also suggested to have affected ichthyosaurs during
223 this time (Martin et al., 2012). Later studies, however, argued for an environmentally driven
224 extinction of ichthyosaurs during OAE2 (e.g., Fischer et al., 2016). A new appreciation of
225 Cretaceous ichthyosaur diversity and disparity also argues against an extinction of
226 ichthyosaurs due to the decline of belemnites. Several of the last ichthyosaurs belonged to the
227 apex predator or generalist niche and were not restricted to soft-bodied prey like belemnites
228 (e.g., Fischer, 2016).

229 **Conclusions**

230 The first cladistic phylogeny of the belemnites (Belemnitida) is presented. Belemnitida as a
231 monophyletic group is well supported but the usually applied dichotomous subdivision of all
232 belemnites into Belemnitina and Belemnopseina finds no support. A new subgroup, consisting
233 of a subset of the “belemnopseine” belemnites, the unranked Pseudoalveolata, is suggested
234 here.

235 Belemnite diversity was reduced sharply during the Aptian, afterwards only belemnites of the
236 Pseudoalveolata remained. In the late Albian and Cenomanian, the geographic distribution of
237 belemnites was reduced, after the middle Cenomanian the group persists only as the
238 Belemnitellidae of the Boreal Realm and Dimitobelidae of the Austral Realm. High sea-surface
239 temperatures, high sea-level, and phases of widespread anoxia during the mid-Cretaceous
240 seem to have resulted in their extinction and reduced distribution and diversity. The radiation
241 of teleost fishes during the mid-Cretaceous cannot be causally linked to the decline of

242 belemnites but some of the vacant mesopredator niches of belemnites might have been filled
243 by teleosts.

244 Belemnites, because of their high fossilization potential and often high abundance in the
245 marine fossil record, might be of key importance in tracking faunal changes of pelagic realm of
246 the Jurassic and Cretaceous. The present study is only a first step and a phylogeny based on
247 more taxa and characters is needed to further resolve their evolutionary history and
248 paleoecology.

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252 Figures

Figure 1: Five most parsimonious trees (MPTs) found. Aulacoceratids are in green, belemnites usually referred to the Belemnitina in red, to the Belemnopseina in blue.

Figure 2 Strict consensus tree of five MPTs. Aulacoceratids are in green, belemnites usually referred to the Belemnitina in red, to the Belemnopseina in blue. Bootstrap and jackknife support values are indicated above and below nodes, respectively.

Figure 3: Genus richness of belemnites and teleosts with paleotemperature and sea level. Diversity data for belemnites from Mutterlose (1988), Doyle (1992), Christensen (1997), Williamson & Henderson (2015), and for teleosts from the Paleobiology Database (<https://paleobiodb.org/navigator/#/7b512dac>). Simplified paleotemperature and eustatic seawater-level curves based on O'Brien et al. (2017) and Haq (2014).

Figure 4: Combinable components consensus tree with stratigraphic ranges of the analyzed aulacoceratid and belemnite genera (Stevens, 1964; Combémoré et al., 1981; Mutterlose, 1983; 1988; 1998; Doyle, 1987; Christensen, 1997; Schlegelmilch, 1998; Iba et al., 2012; Weis et al., 2012, 2015; Rogov et al., 2019; Mariotti et al., 2021).

257 **References**

- 258 Arratia, G., 2013. Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes
259 (Actinopterygii, Teleostei). *Journal of Vertebrate Paleontology* 33, 1–138.
260 doi:10.1080/02724634.2013.835642
- 261 Bauer, K.W., Bottini, C., Frei, R., Asael, D., Planavsky, N.J., Francois, R., McKenzie, N.R., Erba, E.,
262 Crowe, S.A., 2021. Pulsed volcanism and rapid oceanic deoxygenation during Oceanic
263 Anoxic Event 1a. *Geology*. <https://doi.org/10.1130/G49065.1>
- 264 Baraboshkin, E.J., Mutterlose, J., 2004. Correlation of the Barremian belemnite successions of
265 northwest Europe and the Ulyanovsk – Saratov area (Russian Platform). *Acta Geologica*
266 *Polonica* 54, 499-510.
- 267 Bardet, N., 1992. Stratigraphic evidence for the extinction of the ichthyosaurs. *Terra Nova* 4,
268 649–656.
- 269 Bottini, C., Mutterlose, J., 2012. Integrated stratigraphy of Early Aptian black shales in the
270 Boreal Realm: calcareous nannofossil and stable isotope evidence for global and regional
271 processes. *nos* 45, 115–137. <https://doi.org/10.1127/0078-0421/2012/0017>
- 272 Brazeau, M.D., 2011. Problematic character coding methods in morphology and their effects.
273 *Biological Journal of the Linnean Society* 104, 489–498. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8312.2011.01755.x)
274 [8312.2011.01755.x](https://doi.org/10.1111/j.1095-8312.2011.01755.x)
- 275 Cantalice, K.M., Than–Marchese, B.A., Villalobos–Segura, E., 2021. A new Cenomanian
276 acanthomorph fish from the El Chango quarry (Chiapas, south–eastern Mexico) and its
277 implications for the early diversification and evolutionary trends of acanthopterygians.
278 *Papers in Palaeontology* 7, 1699–1726. <https://doi.org/10.1002/spp2.1359>
- 279 Cavin, L., Forey, P.L., 2007. Using ghost lineages to identify diversification events in the fossil

- 280 record. *Biology Letters* 3, 201–204. doi:10.1098/rsbl.2006.0602
- 281 Cavin, L., Forey, P.L., Lécuyer, C., 2007. Correlation between environment and Late Mesozoic
- 282 ray-finned fish evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 245, 353–
- 283 367. doi:10.1016/j.palaeo.2006.08.010
- 284 Christensen, W.K., 1997. The Late Cretaceous belemnite family Belemnitellidae: Taxonomy and
- 285 evolutionary history. *Bulletin of the Geological Society of Denmark* 44, 59–88.
- 286 Christensen, W.K., 2002. Palaeobiology, phylogeny and palaeobiogeography of belemnoids and
- 287 related coleoids. *Berliner Paläobiologische Abhandlungen* 1, 18–21.
- 288 Combémoré, R., 1973. Les Duvaliidae (Pavlow) du cretace inferieur francais. Document des
- 289 laboratoires de geology de la faculte des sciences de Lyon 57, 131–186.
- 290 Combémoré, R., Christensen, W.K., Naidin, D.P., Spaeth, C., 1981. Les Bélemnites. *Cretaceous*
- 291 *Research* 2, 283–286.
- 292 Crame, J.A., Lomas, S.A., Pirrie, D., Luther, A., 1996. Late Cretaceous extinction patterns in
- 293 Antarctica. *Journal of the Geological Society, London* 153, 503–506.
- 294 Dauphin, Y., Williams, C.T., Barskov, I.S., 2007. Aragonitic rostra of the Turonian belemnite
- 295 *Goniocamax*: Arguments from diagenesis. *Acta Palaeontologica Polonica* 52, 85.
- 296 Davesne, D., Gueriau, P., Dutheil, D.B., Bertrand, L., 2018. Exceptional preservation of a
- 297 Cretaceous intestine provides a glimpse of the early ecological diversity of spiny-rayed
- 298 fishes (Acanthomorpha, Teleostei). *Scientific Reports* 8. [https://doi.org/10.1038/s41598-](https://doi.org/10.1038/s41598-018-26744-3)
- 299 [018-26744-3](https://doi.org/10.1038/s41598-018-26744-3)
- 300 Dornburg, A., Near, T.J., 2021. The Emerging Phylogenetic Perspective on the Evolution of
- 301 Actinopterygian Fishes. *Annual Reviews in Ecology and Evolution. Syst.* 52, annurev-
- 302 ecolsys-122120-122554. <https://doi.org/10.1146/annurev-ecolsys-122120-122554>

- 303 Doyle, P., 1987. The Cretaceous Dimitobelidae (Belemnitida) of the Antarctic Peninsula region.
304 Palaeontology 30, 147-177.
- 305 Doyle, P., 1992. A review of the biogeography of cretaceous belemnites. Palaeogeography,
306 Palaeoclimatology, Palaeoecology 92, 207–216. [https://doi.org/10.1016/0031-](https://doi.org/10.1016/0031-0182(92)90082-G)
307 [0182\(92\)90082-G](https://doi.org/10.1016/0031-0182(92)90082-G)
- 308 Erba, E., Duncan, R.A., Bottini, C., Tiraboschi, D., Weissert, H., Jenkyns, H.C., Malinverno, A.,
309 2015. Environmental consequences of Ontong Java Plateau and Kerguelen Plateau
310 volcanism. Geological Society of America Special Papers 511, SPE511-15.
- 311 Ernst, G., Schmid, F., Seibertz, E., 1983. Event-Stratigraphie im Cenoman und Turon von NW-
312 Deutschland. Zitteliana 19, 531-554.
- 313 Fielitz, C., González-Rodríguez, K.A., 2010. A new species of *Enchodus* (Aulopiformes:
314 Enchodontidae) from the Cretaceous (Albian to Cenomanian) of Zimapán, Hidalgo, México.
315 Journal of Vertebrate Paleontology 30, 1343–1351.
316 <https://doi.org/10.1080/02724634.2010.501438>
- 317 Fischer, V., 2016. Taxonomy of *Platypterygius campylodon* and the diversity of the last
318 ichthyosaurs. PeerJ 4, e2604. <https://doi.org/10.7717/peerj.2604>
- 319 Fischer, V., Bardet, N., Benson, R.B.J., Arkhangelsky, M.S., Friedman, M., 2016. Extinction of fish-
320 shaped marine reptiles associated with reduced evolutionary rates and global
321 environmental volatility. Nature Communications 7, 10825.
322 <https://doi.org/10.1038/ncomms10825>
- 323 Friedman, M., 2010. Explosive morphological diversification of spiny-finned teleost fishes in
324 the aftermath of the end-Cretaceous extinction. Proceedings of the Royal Society B:
325 Biological Sciences 277, 1675–1683. doi:10.1098/rspb.2009.2177

326 Friedman, M., Keck, B.P., Dornburg, A., Eytan, R.I., Martin, C.H., Hulse, C.D., Wainwright, P.C.,
327 Near, T.J., 2013. Molecular and fossil evidence place the origin of cichlid fishes long after
328 Gondwanan rifting. *Proceedings of the Royal Society B: Biological Sciences* 280,
329 20131733–20131733. doi:10.1098/rspb.2013.1733

330 Fuchs, D., 2012. The “rostrum”-problem in coleoid terminology – an attempt to clarify
331 inconsistencies. *Geobios* 45, 29–39. <https://doi.org/10.1016/j.geobios.2011.11.014>

332 Fuchs, D., 2019. Part M, Coleoidea, Chapter 23E: Systematic descriptions: Diplobelida. *Treatise*
333 Online 118.

334 Gale, A.S., Christensen, W.K., 1996. *Bulletin of the Geological Society of Denmark* 43, 68–77.

335 Goloboff, P.A., Catalano, S.A., 2016. TNT version 1.5, including a full implementation of
336 phylogenetic morphometrics. *Cladistics* 32, 221–238. <https://doi.org/10.1111/cla.12160>

337 Guinot, G., Cavin, L., 2016. ‘Fish’ (Actinopterygii and Elasmobranchii) diversification patterns
338 through deep time: ‘Fish’ diversification patterns through deep time. *Biological Reviews*
339 91, 950–981. <https://doi.org/10.1111/brv.12203>

340 Haq, B.U., 2014. Cretaceous eustasy revisited. *Global and Planetary Change* 113, 44–58.
341 <https://doi.org/10.1016/j.gloplacha.2013.12.007>

342 Hoffmann, R., Mutterlose, J., 2011. Stratigraphie und Cephalopodenfauna des Unter-Apt von
343 Alstätte (NRW). *Geologie und Paläontologie in Westfalen* 80, 43–59.

344 Hoffmann, R., Stevens, K., 2020. The palaeobiology of belemnites – foundation for the
345 interpretation of rostrum geochemistry. *Biological Reviews* 95, 94–123.
346 <https://doi.org/10.1111/brv.12557>

347 Huck, S., Stein, M., Immenhauser, A., Skelton, P.W., Christ, N., Föllmi, K.B., Heimhofer, U., 2014.
348 Response of proto-North Atlantic carbonate-platform ecosystems to OAE1a-related

349 stressors. Sedimentary Geology 313, 15–31.
350 <https://doi.org/10.1016/j.sedgeo.2014.08.003>

351 Hueter, A., Huck, S., Bodin, S., Heimhofer, U., Weyer, S., Jochum, K.P., Immenhauser, A., 2019.
352 Central Tethyan platform-top hypoxia during Oceanic Anoxic Event 1a. *Climate of the Past*
353 15, 1327–1344. <https://doi.org/10.5194/cp-15-1327-2019>

354 Iba, Y., Mutterlose, J., Tanabe, K., Sano, S., Misaki, A., Terabe, K., 2011. Belemnite extinction and
355 the origin of modern cephalopods 35 m.y. prior to the Cretaceous-Paleogene event.
356 *Geology* 39, 483–486.

357 Iba, Y., Sano, S., Mutterlose, J., Kondo, Y., 2012. Belemnites originated in the Triassic — A new
358 look at an old group. *Geology* 40, 911–914. doi:10.1130/G33402.1

359 Iba, Y., Sano, S., Mutterlose, J., 2014a. The Early Evolutionary History of Belemnites: New Data
360 from Japan. *PLOS ONE* 9, e95632.

361 Iba, Y., Sano, S., Rao, X., Fuchs, D., Chen, T., Weis, R., Sha, J., 2014b. Early Jurassic belemnites
362 from the Gondwana margin of the Southern Hemisphere–Sinemurian record from South
363 Tibet. *Gondwana Research*. doi:10.1016/j.gr.2014.06.007

364 Jeletzky, J.A., 1966. Comparative morphology, phylogeny, and classification of fossil Coleoidea.
365 The University of Kansas Paleontological Contributions 7, 162 pp.

366 Jenkyns, H.C., 2010. Geochemistry of oceanic anoxic events. *Geochemistry, Geophysics,*
367 *Geosystems*. 11, n/a–n/a. <https://doi.org/10.1029/2009GC002788>

368 Keupp, H., Fuchs, D., 2014. Different regeneration mechanisms in the rostra of aulacocerids
369 (Coleoidea) and their phylogenetic implications. *Göttingen Contributions to Geosciences*
370 77, 13–20.

371 Košťák, M., 2012. On the Turonian origin of the *Goniocamax-Belemnitella* stock (Cephalopoda,

- 372 Coleoidea). *Geobios* 45, 79–85. <https://doi.org/10.1016/j.geobios.2011.11.004>
- 373 Košťák, M., Wiese, F., 2008. Lower Turonian record of belemnite *Praeactinocamax* from NW
374 Siberia and its palaeogeographic significance. *Acta Palaeontologica Polonica* 53, 669–678.
- 375 Krause, D.W., 1986. Competitive exclusion and taxonomic displacement in the fossil record;
376 the case of rodents and multituberculates in North America. *Rocky Mountain Geology* 24,
377 95–117.
- 378 Lehmann, J., Friedrich, O., Von Barga, D., Hemker, T., 2012. Early Aptian bay deposits at the
379 southern margin of the Lower Saxony Basin: Integrated Stratigraphy, palaeoenvironment
380 and OAE1a. *Acta Geologica Polonica* 62, 35–62. [https://doi.org/10.2478/v10263-012-](https://doi.org/10.2478/v10263-012-0002-2)
381 0002-2
- 382 Mariotti, N., Pignatti, J., Riegraf, W. 2021. Part M, Coleoidea, Chapter 23E: Systematic
383 descriptions: Diplobelida. *Treatise Online* 148.
- 384 Martin, J.E., Fischer, V., Vincent, P., Suan, G., 2012. A longirostrine *Temnodontosaurus*
385 (Ichthyosauria) with comments on Early Jurassic ichthyosaur niche partitioning and
386 disparity. *Palaeontology* 55, 995–1005. doi:10.1111/j.1475-4983.2012.01159.x
- 387 Matschiner, M., 2019. Gondwanan vicariance or trans-Atlantic dispersal of cichlid fishes: a
388 review of the molecular evidence. *Hydrobiologia* 832, 9–37.
389 <https://doi.org/10.1007/s10750-018-3686-9>
- 390 Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J.,
391 Cramer, P.S., Christie-Blick, N., Pekar, S.F., 2005. The Phanerozoic record of global sea-level
392 change. *Science* 310, 1293–1298.
- 393 Mutterlose, J. 1983. Phylogenie und Biostratigraphie der Unterfamilie Oxyteuthinae
394 (Belemnitida) aus dem Barreme (Unter-Kreide) NW-Europas. *Palaeontographica Abt. A*

395 180, 1-90.

396 Mutterlose, J., 1988. Migration and Evolution Patterns in Upper Jurassic and Lower Cretaceous
397 Belemnites. In: Wiedmann, J. & Kullmann, J. (eds.), *Cephalopods – Present and Past*,
398 Schweizerbart'sche Verlagsbuchhandlung, 525-537.

399 Mutterlose, J., 1998. The Barremian–Aptian turnover of biota in northwestern Europe:
400 evidence from belemnites. *Palaeogeography, Palaeoclimatology, Palaeoecology* 144, 161–
401 173.

402 Mutterlose, J., Baraboshkin, E.J., 2003. Taxonomy of the Early Cretaceous belemnite species
403 *Aulacoteuthis absolutiformis* (Sinzow, 1877) and its type status. *Berliner Paläobiologische*
404 *Abhandlungen* 3, 179-187.

405 Mutterlose, J., Pinckney, G., Rawson, P.F., 1987. The belemnite *Acroteuthis* in the *Hibolites* beds
406 (Hauterivian-Barremian) of north-west Europe. *Palaeontology* 30, 635-645.

407 Near, T.J., Eytan, R.I., Dornburg, A., Kuhn, K.L., Moore, J.A., Davis, M.P., Wainwright, P.C.,
408 Friedman, M., Smith, W.L., 2012. Resolution of ray-finned fish phylogeny and timing of
409 diversification. *Proceedings of the National Academy of Sciences* 109, 13698–13703.
410 <https://doi.org/10.1073/pnas.1206625109>

411 Nelson, J. S., Grande, T. C., Wilson, M. V. 2016. *Fishes of the World*. John Wiley & Sons.

412 O'Brien, C.L., Robinson, S.A., Pancost, R.D., Sinninghe Damsté, J.S., Schouten, S., Lunt, D.J.,
413 Alsenz, H., Bornemann, A., Bottini, C., Brassell, S.C., Farnsworth, A., Forster, A., Huber, B.T.,
414 Inglis, G.N., Jenkyns, H.C., Linnert, C., Littler, K., Markwick, P., McAnena, A., Mutterlose, J.,
415 Naafs, B.D.A., Püttmann, W., Sluijs, A., van Helmond, N.A.G.M., Vellekoop, J., Wagner, T.,
416 Wrobel, N.E., 2017. Cretaceous sea-surface temperature evolution: Constraints from TEX₈₆
417 and planktonic foraminiferal oxygen isotopes. *Earth-Science Reviews* 172, 224–247.

- 418 <https://doi.org/10.1016/j.earscirev.2017.07.012>
- 419 O'Dor, R.K., Webber, D.M., 1986. The constraints on cephalopods: why squid aren't fish.
420 Canadian Journal of Zoology 64, 1591–1605.
- 421 Packard, A., 1972. Cephalopods and fish: the limits of convergence. Biological Reviews 47, 241-
422 307.
- 423 Rogov, M.A., Shchepetova, E.V., Ippolitov, A.P., Seltser, V.B., Mironenko, A.A., Pokrovsky, B.G.,
424 Desai, B.G., 2019. Response of cephalopod communities on abrupt environmental changes
425 during the early Aptian OAE1a in the Middle Russian Sea. Cretaceous Research 96, 227–
426 240. <https://doi.org/10.1016/j.cretres.2019.01.007>
- 427 Schlegelmilch, R., 1998. Die Belemniten des suddeutschen Jura. Ein Bestimmungsbuch für
428 Geowissenschaftler und Fossiliensammler. Gustav Fischer Verlag, 151 pp.
- 429 Schwarzhans, W., 2018. A review of Jurassic and Early Cretaceous otoliths and the
430 development of early morphological diversity in otoliths. Neues Jahrbuch für Geologie und
431 Paläontologie 287, 75–121. <https://doi.org/10.1127/njgpa/2018/0707>
- 432 Stevens, G.R., 1964. The belemnite genera *Dicoelites* Boehm and *Prodicoelites* Stolley.
433 Palaeontology 7, 606-620.
- 434 Stevens, K., 2017. Calcitic skeletons of recent and fossil Coleoidea: Biological, environmental,
435 or diagenetic control? PhD thesis, Bochum. 185 pp. [http://hss-opus.ub.ruhr-](http://hss-opus.ub.ruhr-unibochum.de/opus4/frontdoor/index/index/docId/5374)
436 [unibochum.de/opus4/frontdoor/index/index/docId/5374](http://hss-opus.ub.ruhr-unibochum.de/opus4/frontdoor/index/index/docId/5374)
- 437 Stevens, K., Mutterlose, J., Schweigert, G., 2014. Belemnite ecology and the environment of the
438 Nusplingen Plattenkalk (Late Jurassic, southern Germany): evidence from stable isotope
439 data. Lethaia n/a-n/a. <https://doi.org/10.1111/let.12076>
- 440 Stevens, K., Griesshaber, E., Schmahl, W., Casella, L.A., Iba, Y., Mutterlose, J., 2017. Belemnite

- 441 biomineralization, development, and geochemistry: The complex rostrum of *Neohibolites*
 442 *minimus*. Palaeogeography, Palaeoclimatology, Palaeoecology 468, 388–402.
 443 <https://doi.org/10.1016/j.palaeo.2016.12.022>
- 444 Stolley E. 1911. Beitrage zur Kenntnis der Cephalopoden der norddeutschen unteren Kreide, I. Die
 445 Belemniten der norddeutschen unteren Kreide, 1. Die Belemniten des norddeutschen Gaults
 446 (Aptiens und Albiens). Geologische und Palaontologische Abhandlungen, Band 10, Heft 3.
- 447 Stoyanova-Vergilova, M., 1970. Les Fossiles de Bulgarie, IVa Cretace inferieur, Belemnitida [in
 448 Bulgarian]. Academie Bulgare des Sciences, 72 pp.
- 449 Tanner, A.R., Fuchs, D., Winkelmann, I.E., Gilbert, M.T.P., Pankey, M.S., Ribeiro, Â.M., Kocot, K.M.,
 450 Halanych, K.M., Oakley, T.H., da Fonseca, R.R., Pisani, D., Vinther, J., 2017. Molecular clocks
 451 indicate turnover and diversification of modern coleoid cephalopods during the Mesozoic
 452 Marine Revolution. Proceedings of the Royal Society B: Biological Sciences 284, 20162818.
 453 <https://doi.org/10.1098/rspb.2016.2818>
- 454 Weis, R., Mariotti, N., Di Cencio, A., 2015a. Systematics and evolutionary implications of Early
 455 Jurassic belemnites from the Peri-Mediterranean Tethys. Paläontologische Zeitschrift.
 456 <https://doi.org/10.1007/s12542-015-0265-5>
- 457 Weis, R., Dzyuba, O.S., Mariotti, N., Chesnier, M., 2015b. *Lissajousibelus* nov. gen., an Early
 458 Jurassic canaliculate belemnite from Normandy, France. Swiss Journal of Palaeontology
 459 134, 289–300. <https://doi.org/10.1007/s13358-015-0086-x>
- 460 Williamson, T., Henderson, R.A., 2015. *Pumiliobelus*, a new dwarf coleoid genus (Belemnoidea:
 461 Dimitobelidae) from the Cenomanian of Western Australia. Journal of Paleontology 89,
 462 183–188. <https://doi.org/10.1017/jpa.2014.15>
- 463 Zhu, K.-Y., Bian, Z.-X., 1984. Sinobelemnitidae, a new family of Belemnitida from the Upper

464 Triassic of Longmenshan, Sichuan. *Acta Palaeontologica Sinica* 23, 300-325.