1 **Bayesian inference reveals a complex evolutionary history of belemnites**

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3 **Authors:** Kevin Stevens[1]*, Alexander Pohle[2], René Hoffmann[1], and Adrian Immenhauser[1]

4 [1]Institute for Geology, Mineralogy, and Geophysics, Ruhr University Bochum, Germany

5 [2]Palaeontological Institute and Museum, University of Zurich, Switzerland

6 *corresponding author: kevin.stevens@rub.de

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9 **ABSTRACT**

10   Belemnites are an extinct group of Mesozoic coleoid cephalopods, common in Jurassic and

11 Cretaceous marine sedimentary rocks. Despite their significance, their total group phylogeny

12 has rarely been considered in recent decades. In contrast, most researchers restricted the

13 assignment of families to one of the two usually recognized subgroups, the Belemnitina and

14 the Belemnopseina. As for many fossil cephalopods, researchers have been reluctant to

15 employ modern phylogenetic methods to illuminate belemnites' evolutionary history.

16   To overcome the "dead end" of belemnite systematics, we performed the first tip-dated

17 Bayesian analysis of belemnite phylogeny. In our analysis, the Aulacoceratida are found as the

18 monophyletic sister group to belemnites. The Sinobelemnitidae are resolved as paraphyletic

19 and fall outside the Belemnitina and Belemnopseina, which make up the remaining

20 belemnites. Belemnitina is restricted to Jurassic species with generally no or apical furrows.

21 Holcobelidae are the earliest branching Belemnopseina. Cylindroteuthids *sensu lato* (including

22 Oxyteuthidae) are nested within Belemnopseina, contrary to the common hypothesis placing

23 them within the Belemnitina. Duvaliidae and Dicoelitidae are recovered as members of the

24 Belemnopseina, but their precise relationship has to be evaluated based on more taxa and

25 additional characters. We introduce the well-supported unranked clade Pseudoalveolata,

26 which includes Dimitobelidae, Belemnitellidae, and members of the paraphyletic

27 "Belemnopseidae".

28   The phylogeny presented here, based on reproducible and quantitative methods, contrasts

29 with the usually applied authoritative "stratophenetic" approach to belemnite systematics,

30 based on the overemphasis of single characters. This result is considered the basis for future

31 studies on belemnite phylogeny, allowing for a rigorous testing of evolutionary hypotheses.

32 **PLAIN LANGUAGE SUMMARY**

33   Belemnites were common extinct cephalopods that were closely related to today's squid

34   and cuttlefish. The most common fossil remains of belemnites are bullet-shaped calcitic

35   "cones" (rostrum) that cover their internal shells. Belemnites' evolutionary history is not well

36   known. Our study revealed an evolutionary tree of belemnites based on the statistical analysis

37   of morphological features of the rostrum and calibrated to the known geological ages of the

38   studied belemnite species. This approach was for the first time applied to belemnites and

39   changed several aspects that were believed about their evolution.

INTRODUCTION

40

41 Belemnites (Belemnitida) are an extinct group of stem-decabrachian coleoids (e.g., Fuchs et

42 al., 2013; Hoffmann and Stevens, 2020). They are characterized by a calcitic rostrum, which is

43 by far the most commonly preserved part of their internal shell. In this paper, the terms

44 belemnites and Belemnitida are used only for these calcite-rostrum-bearing species. This

45 definition excludes groups like the Belemnoteuthida and Diplobelida, sometimes referred to

46 as belemnites. The paraphyletic assemblage of Belemnitida, Aulacoceratida, Belemnoteuthida,

47 and Diplobelida is referred to as "belemnoids" in lieu of a proper understanding of their

48 interrelationships at present (Hoffmann and Stevens, 2020). Diplobelida probably represent

49 close relatives of crown-Decabrachia (Fuchs, 2019; Fuchs et al., 2013). Fuchs et al. (2013)

50 regarded belemnites as sister to a group consisting of crown Decabrachia, the stem-

51 decabrachian *Longibelus*, and the Diplobelida. In a cladistic analysis, Sutton et al. (2015) found

52 the belemnite *Hibolithes* closely related to the coleoid genera *Phragmoteuthis* and

53 *Belemnoteuthis*, nested within the Decabrachia crown group.

54 The relationship of the rostrum-bearing Aulacoceratida with other "belemnoid" groups, is

55 at present also unclear (Keupp and Fuchs, 2014). Aulacoceratids have aragonitic rostra (also

56 called "telum"; see Jeletzky, 1966) and differ in other morphological aspects from belemnites

57 (e.g., Jeletzky, 1966; Mariotti et al., 2021), but their aragonitic rostrum likely represents the

58 ancestral rostrum structure of coleoids.

59 The internal phylogenetic relationships of belemnites are even less clear than their

60 relationship to other coleoids. Early subdivisions of belemnites relied on general external

61 characteristics, mostly on the number and position of furrows, e.g., the classification of Werner

62 (1913). Abel (1916) subdivided all belemnites into the families "Clavirostridae" and

63 "Conirostridae" due to their early ontogenetic development. The definitions used nowadays

64 for belemnite families go back to Stolley's (1919) and Naef's (1922) classifications. Jeletzky's

65   (1966) proposal of subdividing the calcite-rostrum bearing belemnites into apically furrowed

66   Belemnitina and alveolar furrowed Belemnopseina has been largely followed by subsequent

67   workers and has been virtually the only applied subdivision of belemnites higher than the

68   family level since.

69   Recognition of the alveolar furrowed Triassic-Early Jurassic Sinobelemnitidae as true

70   belemnites (Zhu and Bian, 1984; Iba et al., 2012; Niko and Ehiro, 2022) has significantly altered

71   views on belemnite phylogeny. Apart from the Sinobelemnitidae, belemnites are exclusively

72   known from the earliest Jurassic onwards. Earlier hypotheses of belemnite phylogeny focused

73   on the well-known European fossil record of the group that suggested their origin during the

74   Hettangian in the diminutive and relatively character-poor genera *Schwegleria* and *Nannobelus*,

75   which both lack alveolar furrows. By the Early Jurassic, belemnites had reached a cosmopolitan

76   distribution and relatively high diversity and abundance (e.g., Iba et al., 2014a, 2014b; Weis et

77   al., 2015a). Although affected by second-order extinction events (e.g., Dera et al., 2016; Neige et

78   al., 2021; De Baets et al., 2021), belemnites continued to be diverse during the Jurassic and early

79   Early Cretaceous (e.g., Schlegelmilch, 1998; Mutterlose, 1988, 1998; Iba et al., 2011), with the

80   two last occurring, disjunctively distributed families, the Boreal Belemnitellidae and the Austral

81   Dimitobelidae, finally becoming extinct at the K/Pg-boundary (e.g., Doyle, 1992; Christensen,

82   1997; Iba et al., 2011).

83   The evolutionary history of belemnites as a whole has rarely been studied since Jeletzky

84   (1966). While several authors speculated about the interrelationships of belemnite families

85   (e.g., Christensen, 1997; Iba et al., 2012; Weis et al., 2012), there has been no study of their

86   phylogenetic relationships based on modern phylogenetic methods. This pattern reflects a

87   general tendency of researchers studying fossil cephalopods in the past (Neige et al., 2007;

88   Bardin et al., 2014; Pohle et al., 2022).

89   This paper presents the first quantitative approach towards belemnite phylogeny based on

90   Bayesian inference. The dichotomous subdivision of all belemnites into Belemnitina and

91   Belemnopseina, as these groups are usually defined, is not supported by these results. Our

92   findings challenge usual assumptions about the evolution of belemnites and identify parts of

93   the belemnite phylogenetic tree that still lack resolution.

94

95   **METHODS**

96   We selected 24 belemnite species, representative of the stratigraphic range, geographic

97   distribution, and diversity of the whole group (Table 1) and scored them for 29 rostrum

98   characters (Fig. 1; Supplementary Files 1, 2). Three aulacoceratid genera (including one

99   putative genus) were also included. Although other fossil "belemnoid" coleoid groups are

100   likely more closely related to the Belemnitida than aulacoceratids (e.g., Diplobelida,

101   Belemnoteuthida), these do not have proper rostra (*sensu* Fuchs, 2012) and so do not

102   contribute to the resolution of internal relationships of belemnites, whose phylogeny is here

103   inferred based on rostrum characters only. For the vast majority of belemnites, the rostrum is

104   the only known part (e.g., Hoffmann and Stevens, 2020) mimicking the situation for

105   conodonts, where inferences of their phylogenetic relationships must also be based on

106   conodont element data only (e.g., Donoghue, 2001; Bai et al., 2022). Morphological data comes

107   from several published sources and our own observations (Table 1). The terminology of

108   belemnite morphology follows Hoffmann and Stevens (2020) and Stevens et al. (2022). The

109   character matrix was compiled with Mesquite version 3.7 (Maddison and Maddison, 2021).

110   Coding practice follows suggestions by Brazeau (2011) for morphological character coding.

111   We used Bayesian tip-dating, which has become increasingly popular in recent years for

112   phylogenetic inference from morphological data for diverse extinct groups of invertebrates,

113   including cephalopods (e.g., Wright, 2017; Paterson, 2019; Pohle et al., 2022). The analyses

114   were performed in BEAST 2.6.7 (Bouckaert et al., 2019) using the fossilized birth-death model

115   as a tree prior (Stadler, 2010; Gavryushkina et al., 2014; Heath et al., 2014) and the

116   parametrization of net diversification rate, turnover and sampling proportion (Heath et al.,

117   2014). Morphological character evolution was modeled with the Mkv model, including

118   invariant site correction (Lewis, 2001). Characters were partitioned according to their

119   number of states, except for character 13 ("Doppellinien" type); all characters were binary.

120   The exchangeability rates were set to 1.0 for binary characters and 1.5 for the single three-

121   state character to prevent the artificial upweighting of multistate characters (King et al.,

122   2017), although this is naturally expected to have a minimal impact on the analyses. We

123   furthermore accounted for heterogeneous rates across sites with two discretized gamma

124   shape rate categories. Although usually four or more rate categories are employed in

125   morphological datasets for this purpose (Harrison and Larsson, 2015), we used only two

126   categories due to the small number of characters and states. Tip dates were fixed to the

127   midpoint between the first and last occurrence date of the corresponding species. First and

128   last occurrence dates are based on the literature and are calibrated to the ICS 2020 age model

129   (Supplementary File 3; Gradstein et al., 2020). We used a strict morphological clock with a

130   lognormally distributed prior (mean = 0.1, standard deviation = 1.25). We placed an

131   exponential prior on the origin (mean = 10 my, offset = 253.1 my), limiting the youngest

132   possible origin date to the age of the oldest taxon of the analysis. This approach avoids

133   unrealistically old estimates while not imposing an overly informative prior. The prior on

134   diversification rate was set to an exponential distribution (mean = 1.0), and the turnover prior

135   to a uniform distribution between 0.0 and 1.0. For the sampling proportion, we used a uniform

136   prior with an upper limit of 0.15, which we justify by a very rough estimate of the number of

137   belemnite species in the Palaeobiology Database (PBDB), which resulted in c. 200 species.

138   Although this number likely underestimates the true number of belemnite species by some

139   margin due to the incompleteness of both the fossil record and the PBDB, it represents a

140   useful estimate to provide an absolute upper limit for sampling rate, as it assigns zero

141   probability to any values above 0.15 (corresponding to the ratio between taxa used in the

142   analysis and approximate total number of known species). Lastly, we enforced a monophyletic

143   constraint on the Belemnitida (without the Sinobelemnitidae). We justify this constraint by

144   the strong prior expectation that this group is monophyletic (however, note that this does not

145   preclude potential paraphyletic relationships with respect to other groups such as

146   Diplobelida, Phragmoteuthida, or crown-Decabrachia). The analysis was run for two separate

147   runs of the MCMC algorithm, each with 10 000 000 generations sampling every 10 000

148   generations and 10% of the samples discarded as burn-in. Convergence was checked using

149   Tracer (Rambaut et al., 2018). The tree files were combined in LogCombiner (Bouckaert et al.,

150   2019) and the Maximum Clade Credibility tree was generated with TreeAnnotator, but using

151   the older BEAST version 1.10.4 (Suchard et al., 2018) because, in contrast to TreeAnnotator in

152   BEAST 2.6.7, it treats sampled ancestors as belonging to the same clade, which results in

153   underestimated posterior probabilities (Barido-Sottani et al., 2020). The xml script to run the

154   analysis in BEAST, the resulting combined log and tree files and the annotated summary tree

155   are contained in Supplementary File 4.

156

157   **RESULTS**

158   The parameter estimates of the tip-dated analyses are listed in Table 2. Although these

159   parameters were not a focus of our current study, and more extensive model testing should be

160   carried out before drawing any definite conclusions, they provide some insights. According to

161   the estimated sampling rate (95% HPD interval between 0.015 and 0.15 with 27 included

162   species), we would expect a total number of belemnite and aulacoceratid species that existed

163   until the end of the Cretaceous to be somewhere between approximately 180 and 1 800.

164   Although this is a rather large credible interval, it appears to be a reasonable estimate that

165 could be refined by adding more species or occurrence data. The omission of the diplobelids

166 and phragmoteuthids, which probably belong to the same clade, may also have caused slightly

167 biased estimates. Furthermore, refined models with variable rates through time may also

168 improve these estimates. The age of the last common ancestor (origin parameter) of

169 belemnites and the aulacoceratids included here was estimated to lie within the Permian,

170 which roughly agrees with previous hypotheses (e.g., Jeletzky, 1966; Kröger et al., 2011).

171 The topology of the maximum clade credibility tree (Fig. 2) reveals several well-supported

172 clades, although there are uncertainties in several areas of the tree. The placement of

173 *Palaeobelemnopsis sinensis* within the Aulacoceratida is moderately well supported (posterior

174 probability = PP = 0.69) as sister to the *Atractites alpinus* and *Aulacoceras sulcatum* clade.

175 Furthermore, there is high support for including the sinobelemnitids within the Belemnitida

176 (PP = 0.79), although Sinobelemnitidae itself is paraphyletic. Within the Belemnitida, there is

177 weak support for a group containing mostly Jurassic taxa traditionally recognized as part of

178 the Belemnitina (PP = 0.53), including *Schwegleria feifeli*, *Passaloteuthis bisulcata*, *Acrocoelites*

179 *oxyconus*, *Megateuthis gigantea*, as well as *Lissajousibelus harleyi*, which was so far of

180 uncertain placement inside Belemnitida. Sister to this clade is a larger group containing the

181 remaining belemnites (PP= 0.67). Within this latter clade, several subclades displayed

182 relatively high support: the sister group relationship between *Holcobelus munieri* and

183 *Calabribelus pallinii* (PP = 0.79), a large clade containing belemnitids that share a

184 pseudoalvelous (PP = 0.98); the same clade with *Belemnopsis apiciconus* as sister group to the

185 latter is moderately supported (PP = 0.64). The clade containing *Praeactinocamax plenus,*

186 *Gonioteuthis quadrata, Belemnitella propinqua* and *B. mucronata* is only weakly supported (PP

187 = 0.44). Other clades received low to moderate support. Among these, we recovered a

188 monophyletic clade containing *Cylindroteuthis puzosiana*, *Aulacoteuthis ernsti*, and *Oxyteuthis*

189 *brunsvicensis* (PP = 0.68), which formed a weakly supported monophyletic clade (PP = 0.25)

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190   together with *Duvalia* and *Dicoelites* (PP = 0.57). Furthermore, we recovered a polyphyletic

191   *Neohibolites* with *N. minimus* forming a monophyletic clade with *Dimitobelus diptychus* (PP =

192   0.39) and *N. ewaldi* as sister to *Mesohibolites minaret* (PP = 0.2).

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194   **DISCUSSION**

195   Due to the shared regeneration pattern and growth mode of Xiphoteuthidae (in the

196   phylogeny represented by *Atractites alpinus*) and belemnites, Keupp and Fuchs (2014)

197   suggested aulacoceratid paraphyly. On the other hand, Jeletzky (1966) argued for

198   aulacoceratid monophyly, going so far as to view the group as an independent offshoot of

199   bactritid cephalopods, leaving no descendants. Doyle et al. (1994) favored the derivation of

200   belemnites from within the Aulacoceratida potentially via the Phragmoteuthida.

201   Aulacoceratida are here recovered as a monophyletic group and sister to belemnites, with the

202   Permian *Palaeobelemnopsis sinensis* confirmed as a member of the Aulacoceratida. However,

203   since we only included a limited number of aulacoceratids in our analysis, it is still possible

204   that total group Aulacoceratida is paraphyletic, also with respect to other groups of early

205   coleoids such as the Phragmoteuthida.

206   Since Jeletzky (1966), all belemnites were usually divided into two suborders; Belemnitina

207   and Belemnopseina, with members of the former group considered ancestral to the latter.

208   Under this traditional scheme, Belemnitina groups taxa with apical furrows and

209   Belemnopseina taxa with alveolar furrows. Problematic under the

210   Belemnitina/Belemnopseina-scheme is that the earliest belemnites of the Sinobelemnitidae

211   are considered to be Belemnopseina with a gap of ca. 25 Ma between the youngest

212   Sinobelemnitida and remaining Belemnopseina (Iba et al., 2012). At least one of the two

213   sinobelemnitids in the current analysis, on the other hand, forms the sister group to the

214   remaining belemnites (Fig. 2). This result is in better agreement with the fossil record than the

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215   earlier hypothesis. It casts doubt on the homologization of dorsal alveolar furrows in

216   belemnites, which was discussed as a potential uniting character of the Sinobelemnitidae with

217   the Duvaliidae or Dicoelitidae (Iba et al., 2012). Still, a well-resolved position of the

218   Sinobelemnitidae and clarification of their mono- or paraphyly will require a detailed study of

219   this still sparsely known group and a better sampled Triassic fossil record of belemnites in

220   general.

221   The species *Lissajousibelus harleyi* displays a ventral furrow in addition to dorsolateral

222   apical furrows and was considered close to Belemnopseina by Weis et al. (2015b). In the

223   present analysis, *L. harleyi* was found to be closely related to typical Belemnitina. Our Bayesian

224   approach demonstrates how the relationship of belemnite taxa that do not easily fit the

225   Belemnitina/Belemnopseina-scheme of Jeletzky (1966) can be resolved quantitatively by

226   taking into account the maximally inclusive morphological and stratigraphic evidence.

227   Belemnitina as defined herein is recovered as a monophyletic group with a likely origin in the

228   Late Triassic but otherwise restricted to the Jurassic (Figs. 2 and 3). A close relationship

229   between these taxa was already suggested by Stolley (1919), who grouped them into his

230   family "Polyteuthidae". This new definition includes at least the likely paraphyletic

231   "Passaloteuthidae" and the Megateuthidae (Acrocoelitidae); it remains to be investigated in

232   which way other Jurassic families not considered in the present analysis (e.g., Hastitidae,

233   Salpingoteuthidae) are related to this group.

234   The Holcobelidae, Duvaliidae, and Dicoelitidae have an uncertain phylogenetic placement

235   (e.g., Stolley, 1911a, 1911b; Stevens, 1964; Jeletzky, 1966; Combémorel, 1973; Weis et al.,

236   2012). Our results place the Holcobelidae as the earliest branching Belemnopseina. This

237   leaves it ambiguous whether their ventral furrow that does not reach the alveolus represents

238   the ancestral state of the Belemnopseina or if this character represents a secondary

239   development from an alveolar furrow reaching the alveolus as is seen in typical

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240   "Belemnopseidae". In our tree, the placement of Duvaliidae as sister to Dicoelitidae finds

241   moderate support, but the placement of this clade itself has only weak support (Fig. 2). The

242   Duvaliidae share with the Dicoelitidae the presence of a dorsal alveolar furrow. However, a

243   belemnopsein ventral alveolar furrow is also developed in the Dicoelitidae. *Duvalia grasiana*

244   has recently been shown to display more organic-rich primary rostrum calcite than other

245   belemnites (Stevens et al., 2022). A similar detailed description of the microstructure of other

246   duvaliids and potentially related forms might reveal the phylogenetic position of this

247   enigmatic group in future studies with more certainty.

248   The monophyletic clade containing the Oxyteuthidae as sister to *Cylindroteuthis puzosiana*

249   confirms earlier thoughts on their phylogenetic relationships (e.g., Mutterlose, 1983).

250   However, in contrast to these earlier hypotheses, we recovered the Cylindroteuthidae *sensu*

251   *lato* clade within the Belemnopseina instead of within the Belemnitina. Still, the problem of

252   the phylogenetic placement and evolution of Cylindroteuthidae and Oxyteuthidae needs

253   further focused analyses, especially for Boreal belemnites of the Jurassic-Cretaceous

254   transition, which will also have to include closely related species of the Pachyteuthidae. Our

255   analysis suggests homology of the ventral furrow present in many Cylindroteuthidae *sensu*

256   *lato,* not with the apical ventral furrow as is typical for the Megateuthidae/Acrocoelitidae, but

257   with the belemnopsein ventral furrow. This hypothesis contrasts with the "stratophenetic"

258   reasoning of the independent evolution of a ventral furrow in the genus *Aulacoteuthis*

259   (Mutterlose and Baraboshkin, 2003; Baraboshkin and Mutterlose, 2004).

260   A name is suggested here for a newly identified and well-supported clade inside the

261   Belemnopseina, the unranked Pseudoalveolata (see Appendix; PP=0.98; Fig. 2). The

262   Pseudoalveolata is characterized by the synapomorphy of pseudoalveolus formation, a

263   secondary alveolus-deepening, developing by dissolution/erosion of anterior organic-rich

264   rostrum sections (Stevens et al., 2022). The pseudoalveolus is further characterized by a well-

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265   mineralized '"spike" projecting anteriorly toward the protoconch (*Nadelspitze* of Stolley,

266   1911a). *Hibolithes* has here been recovered as the earliest branching pseudoalveolate

267   belemnite. Pseudoalveolus types have been considered of great importance in the phylogeny

268   of the Belemnitellidae (e.g., Košťák, 2012), but contrary to suggestions by Dauphin et al.

269   (2007) and Košťák and Wiese (2008), there is no conclusive evidence for the anterior rostrum

270   of pseudoalveolate belemnites being of primarily aragonitic composition, as it likely consisted

271   of calcite with primarily high organic contents (see Stevens et al., 2017; 2022).

272   The two species of *Neohibolites* analyzed herein (*N. ewaldi* and *N. minimus*) are not

273   recovered as sister species. This indicates the possibly polyphyletic or paraphyletic nature of

274   *Neohibolites*, a genus which has long been seen as ancestral to the two only belemnite families

275   left after the Cenomanian, the Belemnitellidae and Dimitobelidae, (e.g., Mutterlose, 1998).

276   Future studies focusing on the origin of Belemnitellidae and Dimitobelidae might shed more

277   light on the exact origins of these two last surviving belemnite groups and their origins in the

278   paraphyletic "Belemnopseidae". "Belemnopseidae" has long been recognized as paraphyletic

279   with respect to the Belemnitellidae and Dimitobelidae (e.g., Jeletzky, 1966; Mutterlose, 1988).

280   However, a new phylogenetic definition of the family containing all belemnites closer to

281   *Belemnopsis* than to the Pseudoalveolata seems possible. This would require a more thorough

282   sampling of the diverse "belemnopseid" taxa of the earliest Cretaceous and a thorough

283   revision of not only the genus *Belemnopsis* but also *Hibolithes*, encompassing detailed revision

284   of the diverse *Belemnopsis* species of the Austral Realm (e.g., Stevens, 1965; Challinor, 1990)*.

285   Based on the unclear and absent types for both genera (e.g., Combémorel and Howlett, 1993;

286   Mitchell, 2015), the assignment of species to either genus was often based on superficial

287   morphological assessment. We here confirm that there is no pseudoalveolus formation in the

288   type species of *Belemnopsis*, *B. apiciconus*. Pseudoalveolus formation had already been

289   suggested as a differentiating character of the genera *Belemnopsis* and *Hibolithes* by Stolley

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290   (1911a) but was unfortunately not followed on by later authors.

291   The tip-dated Bayesian analysis confirms earlier ideas that the epirostrum, a "tertiary"

292   rostrum formation (Fuchs, 2012), which is developed only in some belemnites, represents a

293   parallelism and does not indicate a close relationship (Bandel and Spaeth, 1988; Stevens et al.,

294   2017). Epirostra are present in the analyzed species *Megateuthis gigantea*, *Holcobelus munieri*,

295   *Calabribelus pallinii*, and *N. minimus*, found on disparate parts of our tree (Fig. 2).

296   In our proposed systematic framework (Fig. 3), we regard the potentially paraphyletic

297   Sinobelemnitidae as the earliest branching belemnites. The remainder of the belemnites still

298   falls into two large monophyletic clades, the Belemnitina and Belemnopseina, to preserve the

299   current taxonomy as far as possible. We consider the Cylindroteuthidae *sensu lato*, Duvaliidae,

300   and Dicoelitidae more derived than the Holcobelidae inside the Belemnopseina but otherwise

301   of uncertain position with regard to the *Belemnopsis* + Pseudoalveolata clade.

302   The presented topology represents only a first step towards a well-resolved phylogeny of

303   all belemnites. To achieve further resolution, it will likely be necessary to detect and evaluate

304   further microstructural and geochemical data of several belemnite taxa and incorporate more

305   taxa and characters into the analysis. Furthermore, well-preserved specimens from Konservat-

306   Lagerstätten may provide additional valuable insights into the variability of soft-part anatomy,

307   statoliths, radulae, hooks, or jaws within belemnites (e.g., Klug et al., 2010; Fuchs and

308   Hoffmann, 2017), potentially adding other characters to include into phylogenetic analysis.

309   This would also allow for a more inclusive phylogenetic analysis involving non-rostrum

310   bearing "belemnoids" to resolve the decabrachian crown and stem groups.

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312   **CONCLUSIONS**

313   The first tip-dated analysis of belemnite (Belemnitida) phylogeny is presented. Our results

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314   suggest that the usually applied dichotomous subdivision of all belemnites into Belemnitina

315   and Belemnopseina based only on the presence of apical *versus* alveolar furrows needs some

316   adjustment. We consequently suggest the subdivision of all belemnites, except the potentially

317   paraphyletic and early branching Sinobelemnitidae, into newly phylogenetically defined

318   Belemnitina and Belemnopseina. Holcobelidae are the earliest branching Belemnopseina,

319   Duvaliidae and Dicoelitidae are confirmed as Belemnopseina but are still of uncertain

320   placement inside this group. A major change involves the transfer of the Cylindroteuthidae

321   (including Oxyteuthidae) from the Belemnitina to the Belemnopseina. A new well-supported

322   subgroup of the Belemnopseina, the unranked Pseudoalveolata, is suggested here, including a

323   phylogenetic definition and the suggestion of a potential synapomorphy.

324   Because of their high fossilization potential and often high abundance in the marine fossil

325   record, belemnites are particularly important in tracking faunal changes of the Jurassic and

326   Cretaceous pelagic realms. The present study is only a first step; further analyses based on

327   more taxa and characters, including detailed microstructural analyses of the rostra, are

328   needed to further resolve more details of the belemnites' evolutionary history. Applying

329   quantitative and reproducible phylogenetic methodology in contrast to earlier approaches

330   relying on authoritative overemphasis of single characters will lay a solid foundation for the

331   future study of belemnites.

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CAPTIONS

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).

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.

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.
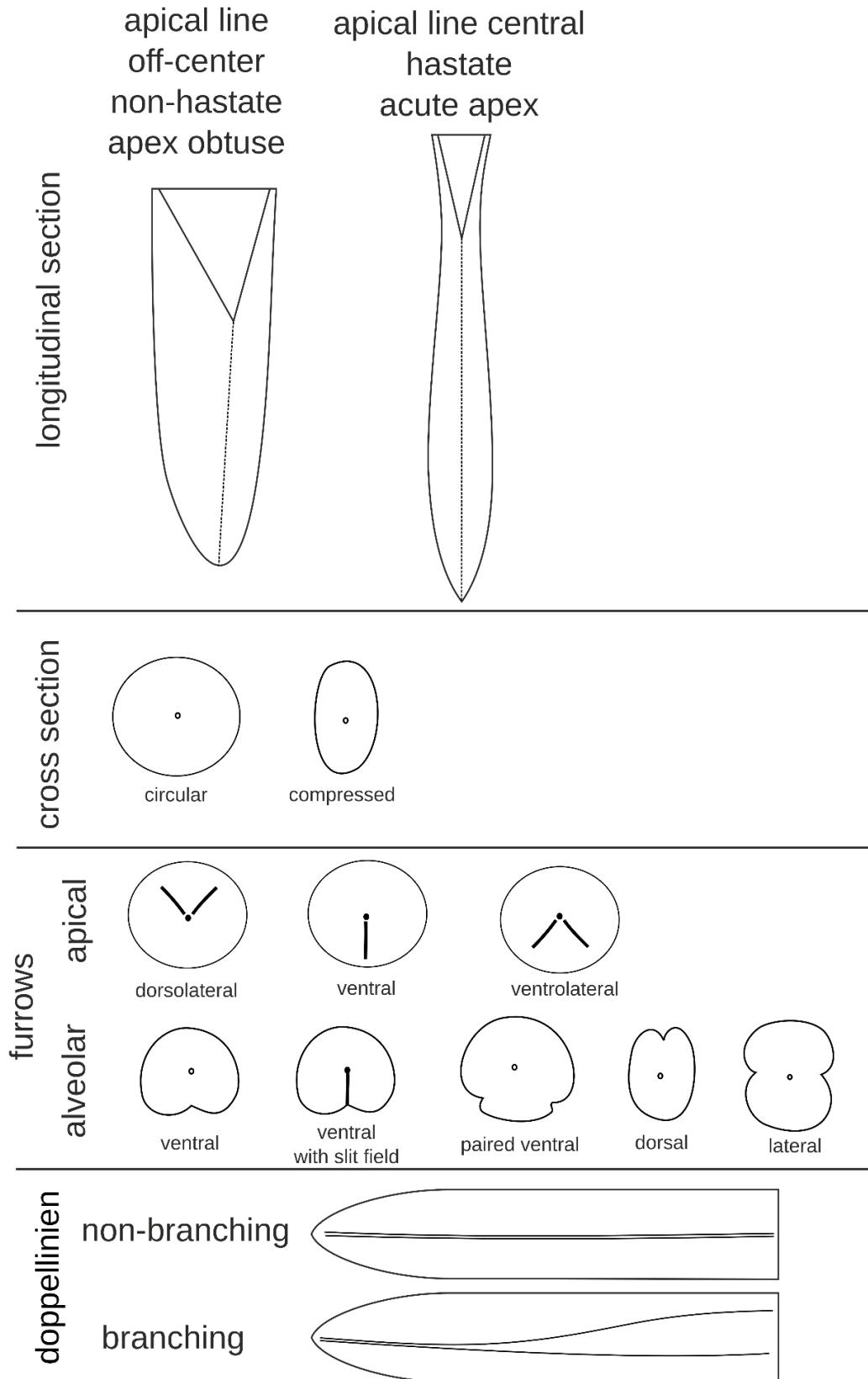
334   **FIGURES**

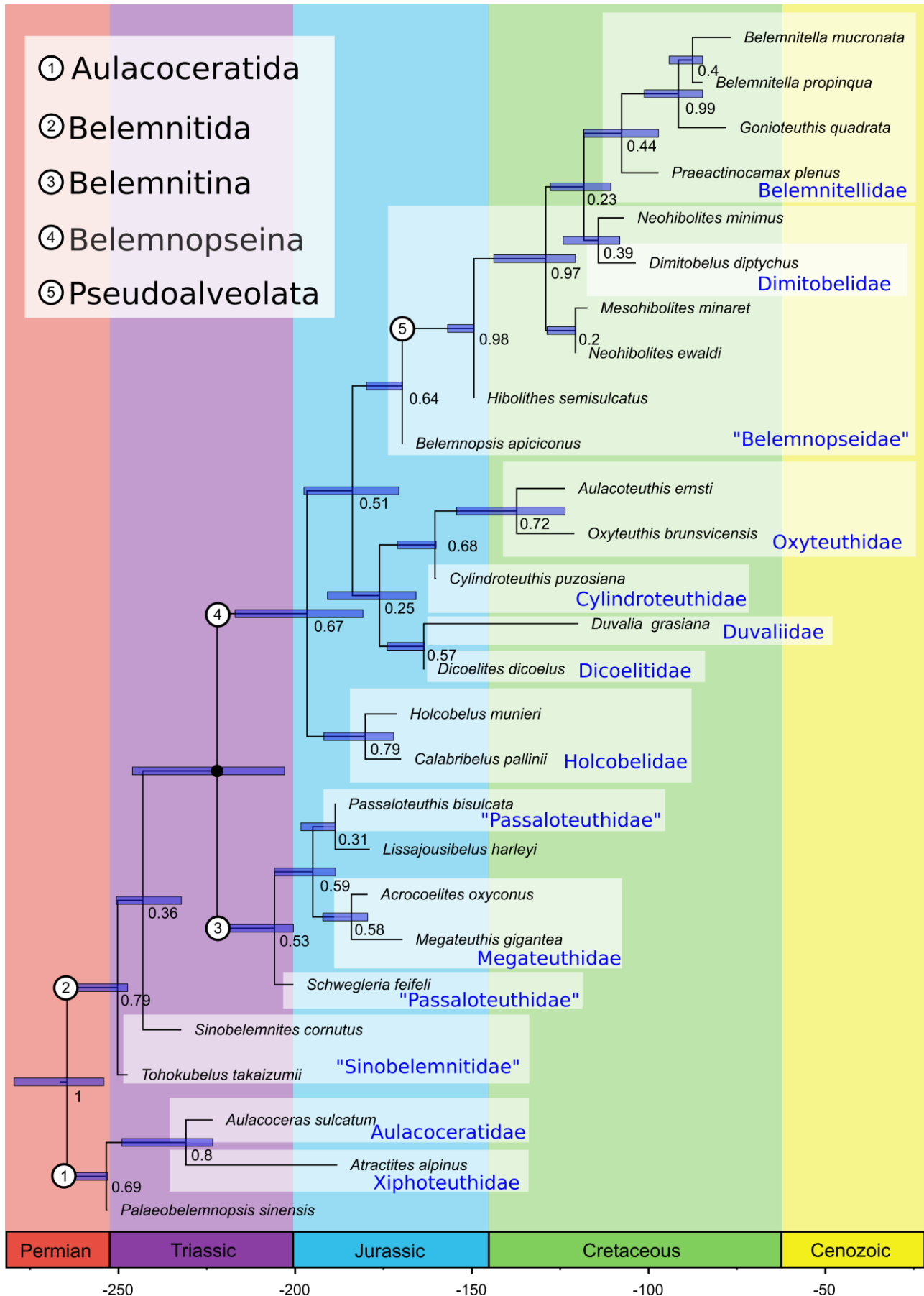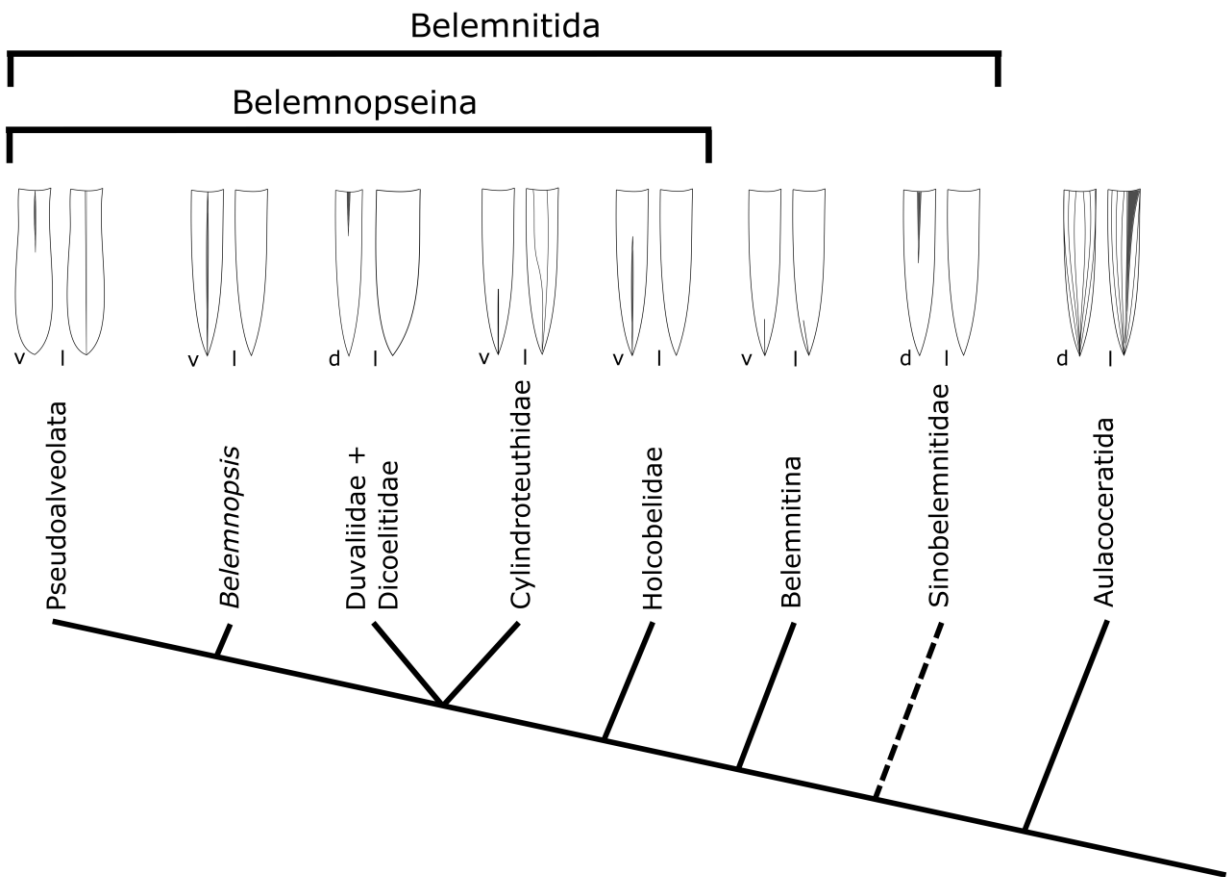**FIGURE 1.**

FIGURE 2.

FIGURE 3.

335

336 **TABLES**

337 **TABLE 1.** Overview of species used in the analysis. Assignment to suborders is here based on

338 previous taxonomic concepts, which may differ from the results obtained here. For more

339 details, see supplementary material.

Species	(Sub-) order	Age	Main sources
Atractites alpinus von Gümbel, 1861	Aulacoceratida	Early Jurassic	Jeletzky, 1966; Mariotti et al., 2021
Aulacoceras sulcatum von Hauer, 1860	Aulacoceratida	Late Triassic	Jeletzky, 1966; Mariotti et al., 2021
Acrocoelites oxyconus (Hehl in von Zieten, 1831)	Belemnitina	Early Jurassic	Schlegelmilch, 1998
Aulacoteuthis ernsti Mutterlose and Baraboshkin, 2003	Belemnitina	Early Cretaceous	Mutterlose, 1983; Mutterlose and Baraboshkin, 2003
Cylindroteuthis puzosiana (d'Orbigny, 1842)	Belemnitina	Late Jurassic	Schlegelmilch, 1998
Megateuthis gigantea (von Schlotheim, 1820)	Belemnitina	Middle Jurassic	Schlegelmilch, 1998, own data
Oxyteuthis brunsvicensis (Strombeck, 1861)	Belemnitina	Early Cretaceous	Stolley, 1911b; Mutterlose, 1983
Passaloteuthis bisulcata	Belemnitina	Early Jurassic	Schlegelmilch,

20

(Blainville, 1827)			1998
Schwegleria feifeli (Schwegler, 1939)	Belemnitina	Early Jurassic	Schlegelmilch, 1998
Belemnitella mucronata (von Schlotheim, 1813)	Belemnopseina	Late Cretaceous	Christensen, 1997
Belemnitella propinqua (Moberg, 1885)	Belemnopseina	Late Cretaceous	Christensen,
Belemnopsis apiciconus (Blainville, 1827)	Belemnopseina	Middle Jurassic	Schlegelmilch, 1998
Calabribelus pallinii Weis et al., 2012	Belemnopseina	Middle Jurassic	Weis et al., 2012
Dicoelites dicoelus Boehm, 1906	Belemnopseina	Late Jurassic	Stevens, 1964
Dimitobelus diptychus (McCoy, 1867)	Belemnopseina	Early Cretaceous	Whitehouse, 1924; Williamson, 2006
Duvalia grasiana (Duval-Jouve, 1841)	Belemnopseina	Early Cretaceous	Stolley, 1911a; Stoyanova-Vergilova, 1970; Combémorel, 1973; own data
Gonioteuthis quadrata (Blainville, 1827)	Belemnopseina	Late Cretaceous	Ernst, 1964; Christensen 1997

Hibolites semisulcatus (zu Münster, 1830)	Belemnopseina	Late Jurassic	Schlegelmilch, 1998; own data
Holcobelus munieri (Eudes-Deslongchampes, 1878)	Belemnopseina	Middle Jurassic	Jeletzky, 1966; Weis et al., 2012
Lissajousibelus harleyi (Mayer, 1866)	Belemnopseina	Early Jurassic	Weis et al., 2015b
Mesohibolites minaret (Raspail, 1829)	Belemnopseina	Early Cretaceous	Stoyanova-Vergilova,1970
Neohibolites ewaldi (Strombeck, 1861)	Belemnopseina	Early Cretaceous	Stolley, 1911a; own data
Neohibolites minimus (Miller, 1826)	Belemnopseina	Early Cretaceous	Stolley, 1911a; Spaeth, 1971; Stevens et al., 2017
Palaeobelemnopsis sinensis Chen, 1982	Aulacoceratida incertae sedis	Late Permian	Mariotti et al., 2021
Praeactinocamax plenus (Blainville, 1827)	Belemnopseina	Late Cretaceous	Christensen, 1997
Sinobelemnites cornutus Zhu and Bian 1984	Belemnopseina	Late Triassic	Zhu and Bian 1984
Tohokubelus takaizumii Niko and Ehiro, 2022	Belemnopseina	Early Triassic	Niko and Ehiro 2022

340 **TABLE 2.** Results of the parameter estimates. Abbreviations: stdev = standard deviation, HPD

341 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

342

343

APPENDIX

345 *Phylogenetic Definition of Pseudoalveolata*

346 **Pseudoalveolata** unranked K. Stevens, A. Pohle, and R. Hoffmann, new clade name.

347 Phylogenetic definition: the least inclusive clade containing the Belemnitellidae Pavlow, 1914,

348 Dimitobelidae Whitehouse, 1924, and the species *Hibolithes semisulcatus* (zu Münster, 1830),

349 *Neohibolites ewaldi* (Strombeck, 1861), *N. minimus* (Miller, 1826), and *Mesohibolites minaret*

350 (Raspail, 1829). Etymology: derived from the belemnite morphological term pseudoalveolus,

351 itself derived from Greek pseúdō, meaning "to lie" or "to deceive", and alveolus, from Latin,

352 meaning a small cavity. Reference phylogeny: Fig. 2. Diagnosis: In belemnite morphological

353 terminology, the alveolus is the approximately cone-shaped cavity of the rostrum, which

354 contains the phragmocone. If the alveolus is secondarily enlarged by abrasion or dissolution of

355 the anterior part of the rostrum due to an anterior primarily porous and organic-rich

356 composition of the rostrum (e.g., Stolley, 1911a; Ernst, 1964; Stevens et al., 2022), the

357 resulting secondary deepening is termed a pseudoalveolus. Anterior primarily porous and

358 organic-rich rostra, which might result in a pseudoalveolus, accordingly represent the

359 synapomorphy of the Pseudoalveolata.

360

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