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1 **The Paris Biota decapod (Arthropoda) fauna and the diversity of**  
2 **Triassic decapods**

3  
4 Christopher. P. A. Smith<sup>1</sup>, Sylvain Charbonnier<sup>2</sup>, James F. Jenks<sup>3</sup>, Kevin G. Bylund<sup>4</sup>, Gilles  
5 Escarguel<sup>5</sup>, Nicolas Olivier<sup>6</sup>, Emmanuel Fara<sup>1</sup>, Arnaud Brayard<sup>1</sup>

6  
7 <sup>1</sup>Biogéosciences, UMR CNRS 6282, Université Bourgogne Franche-Comté, 21000 Dijon,  
8 France <christopher.smith@u-bourgogne.fr>

9 <sup>2</sup>Muséum national d'Histoire naturelle, CR2P, UMR 7207, CNRS, Sorbonne Université, 75005  
10 Paris, France

11 <sup>3</sup>West Jordan, UT 84084, USA

12 <sup>4</sup>Spanish Fork, UT 84660, USA

13 <sup>5</sup>LEHNA, UMR 5023, CNRS, ENTPE, Université Claude Bernard Lyon 1, F-69622,  
14 Villeurbanne, France

15 <sup>6</sup>LMV, Université Clermont Auvergne, CNRS, IRD, 63000 Clermont-Ferrand, France

16  
17 **Abstract.**—We describe here the early Spathian (Early Triassic) Paris Biota decapod fauna  
18 from the western USA basin. This fauna contains two taxa of Aegeridae (Dendobranchiata),  
19 namely *Anisaeger longirostrus* n. sp. and *Aeger* sp. that are the oldest known  
20 representatives of their family, thus extending its temporal range by 5 Myr back into the  
21 Early Triassic. This fauna also includes two representatives of Glypheida (Pleocyemata)  
22 with *Litogaster turnbullensis* Schram, 1971 and *Pemphix krumenackeri* n. sp., comforting  
23 for the former, and extending for the latter, the temporal range of their respective  
24 superfamily back to the Early Triassic. Overall, the Paris Biota decapods are some of the

25 oldest known representatives of Decapoda, filling in an important gap in the evolutionary  
26 history of this group, especially during the Triassic that marks the early diversification of  
27 this clade. Additionally, we overview and compile all known Triassic decapods, which  
28 leads to the revision of four species of Middle and Late Triassic Aegeridae, and to a revised  
29 family assignment of a Middle Triassic Glypheida. Based on this refined dataset, we also  
30 investigate decapod diversity throughout the Triassic. We show that the apparent increase  
31 in decapod taxonomic richness is probably driven by the heterogeneity of the fossil record  
32 and/or sampling effort, and that the decapod alpha diversity is actually relatively high as  
33 soon as the Early Triassic and remains rather stable throughout the Triassic.

34

35 UUID: <http://zoobank.org/References/0f435f27-1767-473d-955c-57fe869faa0f>

36

## 37 **Introduction**

38

39 The Paris Biota is an exceptional early Spathian (Early Triassic) marine assemblage (Brayard  
40 et al., 2017) discovered in the Thaynes Group (*sensu* Lucas et al., 2007) within the northern and  
41 western parts of the western USA basin (Smith et al., 2021). It appears to be the oldest known  
42 diversified and complex Triassic marine assemblage following the Permian/Triassic boundary  
43 (PTB; ~252 Ma). Dated from immediately after the Smithian/Spathian boundary (~249.2 Ma;  
44 Widmann et al., 2020), it challenges the often assumed scenario of a global delayed and slow  
45 post-PTB marine biotic recovery (*e.g.*, Erwin, 1998; Sahney and Benton, 2008; Song et al.,  
46 2011, 2018; Chen and Benton, 2012; Benton et al., 2013). This assemblage is all the more  
47 remarkable as the Smithian-Spathian transition corresponds to the most severe environmental  
48 perturbations documented for the Early Triassic (Tozer, 1982; Dagys, 1988; Hallam, 1996;  
49 Payne, 2004; Brayard et al., 2006; Romano et al., 2013; Jattiot et al., 2016; Goudemand et al.,

2019; Leu et al., 2019). The Paris Biota offers a unique opportunity to study one of the most important faunal shift known: the transition between the Paleozoic and the Modern evolutionary faunas, which is assumed to have happened around the PTB (Sepkoski, 1981). The Paris Biota is composed of a mixture of long-term survivors and newly-evolved taxa. It comprises almost all the clades of the Modern evolutionary fauna. It yielded algae, sponges (Botting and Brayard, 2019), brachiopods, bivalves, echinoderms (Saucède et al., 2019; Thuy et al., 2019), cephalopods (Doguzhaeva et al., 2018; Brayard et al., 2019), vertebrate remains and coprolites (Romano et al., 2019), and arthropods (Lerner et al., 2017; Charbonnier and Brayard, 2019; Laville et al., 2021). Among arthropods, many well-preserved decapods (an order of crustaceans characterized, among others, by the presence of 5 pairs of walking appendages), were uncovered. This is of major importance as they represent some of the earliest representatives of their order.

Only three decapod taxa are reported so far from the Paleozoic: (i) *Aciculopoda mapesi* Feldmann and Schweitzer, 2010 that was described based on a unique specimen from southcentral Oklahoma, USA, and which is the only known Paleozoic Dendobranchiata (Feldmann and Schweitzer, 2010); (ii) *Palaeopalaemon newberryi* (Whitfield, 1880), also from the late Devonian of northeast Ohio, South New York state, central Kentucky and southeast Iowa, USA and that corresponds to the oldest Pleocyemata documented (Schram et al., 1978); and (iii) *Eryma antiquum* (Birshtein, 1958), from the Late Permian of Ukhta region, Siberia (Schram, 1980), which is the oldest Erymidae reported, but whose systematic position above the superfamily rank remains uncertain (Devillez and Charbonnier, 2017). The Early Triassic fossil record of decapods is also very scarce. It is limited to an isolated specimen reported from the early Spathian at Bear Lake Hot Springs, Idaho, USA, designated by Schram (1971) as *Litogaster turnbullensis*, and the poorly age-constrained Dienerian-Smithian decapod-rich fossil sites from the Ambilobé region, NW Madagascar (Besairie, 1932; Marramà et al., 2017;



75 Laville et al., 2021), that yield three species of Penaeoidea: *Ifasya madagascariensis* (Van  
76 Straelen, 1933), *Ifasya straeleni* Garassino and Teruzzi, 1995, and *Ambilobeia karojo*  
77 Garassino and Pasini, 2002.

78 The Paris Biota decapod fauna includes two genera of Aegeridae which is a family  
79 regarded as a potential stem-group of Penaeoidea (Burkenroad, 1963, 1983; Tavares and  
80 Martin, 2010), *i.e.*, the oldest of the two Dendobranchiata superfamilies, the other one being  
81 Sergestoidea whose oldest representative is *Paleomattea deliciosa* Maisey and Carvalho, 1995  
82 from the Early Cretaceous of the Santana Formation, Brazil. It also includes representatives of  
83 two superfamilies of Glypheida (Pleocyemata), extending for one, and confirming for the other,  
84 their temporal range back to the Early Triassic. These new findings significantly increase the  
85 current knowledge of Early Triassic decapods by doubling the number of known taxa (from 3  
86 to 6 species) for this interval. Additionally, we overview in this work all known Triassic  
87 decapods, with a special emphasis on Dendobranchiata, as well as their taxonomic assignments.  
88 This leads to the revision of four species of Middle and Late Triassic Aegeridae, and to a revised  
89 family assignment of a Middle Triassic Glypheida. Based on this revised dataset of Triassic  
90 decapods, we investigate their early diversification after the PTB mass extinction. We further  
91 discuss our observation with regards to the ongoing debate of the accuracy and reliability of  
92 macroevolutionary signals derived from current online databases, especially concerning the  
93 post-PTB biotic recovery.

94

## 95 **Geological setting**

96

97 The Paris Biota has been documented in 5 different sites (Brayard et al., 2017; Smith et al.,  
98 2021), all from the northern and western parts of the western USA basin (Fig.1). Two of these  
99 sites (NoName and Immigrant Canyon) are located in northeastern Nevada; the three others

100 (Paris Canyon, Stewart Canyon and Georgetown) are located in southeastern Idaho. At each  
101 site, fossils were collected from exposures of the Lower Triassic Thaynes Group (*sensu* Lucas  
102 et al., 2007) that is mainly characterized by alternating limestones and shales of Smithian-  
103 Spathian age which corresponds to relatively shallow, epicontinental marine depositional  
104 environments (*e.g.*, Caravaca et al., 2018). During the Early Triassic, the western USA Basin  
105 was located at a near-equatorial latitude on the western margin of the Pangea *i.e.*, the eastern  
106 coast of the Panthalassa Ocean (Fig.1. 2). Biostratigraphy in the region is well constrained by  
107 Smithian and Spathian ammonoid assemblages that have recently been partly revised within  
108 southeastern Idaho by Guex et al. (2010), Jenks et al. (2013) and Brayard et al. (2019). With  
109 the exception of those of the Immigrant Canyon site (Smith et al., 2021), all decapod specimens  
110 were collected from early Spathian beds, corresponding to the *Bajarunia-Tirolites-Albanites*  
111 beds (Brayard et al., 2019). Immigrant Canyon fossils are from slightly younger fossiliferous  
112 levels belonging to the *Prohungarites* and *Neopopanoceras* beds of middle-late Spathian age  
113 (Smith et al., 2021).

114

## 115 **Material and methods**

116

117 The Paris Canyon locality remains by far the most sampled site from which the Paris Biota has  
118 been documented (Smith et al., 2021). Indeed, two thirds of the Paris Biota fossils come from  
119 this site. Therefore, most of the decapod specimens studied here are from Paris Canyon.  
120 Additionally, the Paris Canyon decapod specimens are slightly better preserved *i.e.*, more  
121 complete than those from the other sites, and have the advantage of being preserved as calcium  
122 phosphate (Iniesto et al., 2019), which tends to well react under UV illumination, facilitating  
123 anatomical observations. The specimens from Georgetown are also preserved in calcium

124 phosphate whereas those from NoName, Stewart Canyon, and Immigrant Canyon are  
125 carbonaceous.

126 The systematic work was established based on the best preserved specimens that we  
127 refer to as the “illustrated material”. However, other specimens that are referred to as  
128 “additional material” were also examined. Several specimens can occur on the same slab, and  
129 occasionally accumulate in mass *i.e.*, tens of specimens on the same slab. In such cases, the  
130 specimen repository numbers finish by an additional letter to specify which specimen of the  
131 slab is referred to.

132 The specimens were examined under natural light, and under UV illumination using a  
133 Vilber Lourmat VL-115.L lamp with a wavelength of 365 nm in the dark. Photographs were  
134 taken using a Nikon D750 camera coupled to a AF-S VR Micro-Nikkor 105mm f/2.8G IF-E  
135 lens. The brightness and contrast of each picture was optimized to highlight some anatomical  
136 parts using imageJ 1.52s and the auto “Brightness/Contrast...” tool. Unless specified otherwise,  
137 the line drawings were realized by the first author.

138 *Repositories and institutional abbreviations.*—All the studied specimens are held in the  
139 collections of the Université de Bourgogne, Géologie Dijon, France (UBGD).

140

## 141 **Systematic paleontology**

142

143 **Phylum** ARTHROPODA Latreille, 1829

144 **Subphylum** CRUSTACEA Brünnich, 1772

145 **Class** MALACOSTRACA Latreille, 1802

146 **Subclass** EUMALACOSTRACA Grobben, 1892

147 **Superorder** EUCARIDA Calman, 1904

148 **Order** DECAPODA Latreille, 1802

149                                   **Suborder** DENDROBRANCHIATA Spence Bate, 1888

150                                   **Superfamily** PENAEOIDEA Rafinesque, 1815

151                                   **Family** AEGERIDAE Burkenroad, 1963

152

153    *Included genera.*—*Aeger* Münster, 1839; *Acanthochirana* Strand, 1928; *Anisaeger* Schweitzer  
154    et al., 2014.

155

156    *Emended diagnosis by Schweitzer et al. (2014).*—Carapace with long or short rostrum  
157    compressed laterally, with one subrostral spine or with several suprarostal and sometimes  
158    postrostral spines or no rostral spines at all; hepatic spine present; scaphocerite long; antennular  
159    flagellae short or long, basal articles not extending anteriorly more than one-third the length of  
160    the carapace; antennar flagellae long; third maxilliped long, usually longer than or as long as  
161    pereiopods, with multiple long, thin spines perpendicular to long axis; pereiopods ranging from  
162    overall long to overall short; pereiopods 1–3 chelate, may be spinose, 1 to 3 increasing in length  
163    posteriorly; pleonal somite 1 overlapping somite 2, somite 1 shorter than other somites; pleura  
164    rounded, may be spined or serrate; pleopods with two multiarticulate flagella each; exopodite  
165    of uropod usually with diaeresis; telson with at least one pair of movable spines, may have  
166    marginal setae distally.

167    *Remarks.*—The Aegeridae family was erected by Burkenroad (1963) and initially only included  
168    *Aeger* and *Acanthochirana*. Nonetheless, until Schweigert (2001) revised *Aeger tipularius*  
169    (Schlothheim, 1822), the type species of *Aeger*, and assigned it to Aegeridae, most authors  
170    continued to assign *Acanthochirana* and *Aeger* to Penaeidae (*e.g.*, Förster, 1967; Glaessner,  
171    1969; Förster and Crane, 1984; Garassino and Teruzzi, 1990). A few years later, Feldmann et  
172    al. (2007) also confirmed the placement of *Acanthochirana* within Aegeridae as previously

173 suggested by Etter (2004). Finally, Schweitzer et al. (2014) added the genera *Anisaeger* and  
174 *Distaeger* to Aegeridae.

175 Careful examination of high-resolution pictures (Supplementary file 1; courtesy Shixue  
176 Hu and Carrie Schweitzer) of the holotype of *Distaeger prodigiosus* (Middle Triassic, China)  
177 lead us to modify its placement within Aegeridae. Indeed, the initially described pediform third  
178 maxilliped with propodus presenting scalloped upper and lower margins is most likely a first  
179 pereiopod showing a strong terminal chela with index and dactylus of equal size. Second and  
180 third pereiopods are also chelate. The reinterpretation of the hypertrophied third maxilliped as  
181 a chelate first pereiopod and the well-developed pereiopods of *Distaeger* still suggest a  
182 placement within Penaeoidea but in a different family than Aegeridae.

183 The family Aegeridae has undergone multiple diagnosis modifications during the last  
184 two decades, as new species and genera were erected. Given the unclear, yet potentially basal  
185 phylogenetic positioning of this family as suggested by several authors (Burkenroad, 1963,  
186 1983; Tavares and Martin, 2010), and its being as an early member of the Modern Evolutionary  
187 Fauna (Sepkoski, 1981) following the PTB biotic crisis, it is crucial to correctly define the  
188 taxonomical limits of this family. The diagnosis remains too poorly restrictive considering the  
189 important intra-family morphological variability and in particular within *Aeger*. Nonetheless,  
190 the main characteristics of Aegeridae, that differentiate them from other penaeoids, are the  
191 presence of a very long antennal flagellum, long pereiopods and a hypertrophied spinose or  
192 setose third maxilliped at least as long as the pereiopods.

193

194 **Genus ACANTHOCHIRANA** Strand, 1928

195 1862 *Acanthochirus* Oppel, p. 97-98.

196 1928 *Acanthochirana* Strand, p. 40: *nomen novum* pro *Acanthochirus*.

197

198 *Type species.*—*Udora cordata* Münster, 1839 (partim) by subsequent designation of Glaessner  
199 (1929).

200 *Other species.*—Triassic: *Acanthochirana norica* (Pinna, 1974) n. comb; *Acanthochirana*  
201 *spinifera* (Schweitzer et al., 2014) n. comb.; *Acanthochirana triassica* Garassino, 2013. Post-  
202 Triassic : *Acanthochirana angulata* Opperl, 1862; *Acanthochirana cordata* (Münster, 1839)  
203 (junior synonym: *Acanthochirus longipes* Opperl, 1862); *Acanthochirana krausei* (Förster,  
204 1967b); *Acanthochirana liburiaensis* Garassino, Audo, Charbonnier & Schweigert in Bravi et  
205 al., 2014; *Acanthochirana smithwoodwardi* (Van Straelen, 1940) (junior synonym:  
206 *Acanthochirus cenomanicus* Glaessner, 1945).

207 *Emended diagnosis by Charbonnier et al. (2017).*—Rostral carina with spines pointing forward;  
208 smooth rostrum, spineless; one epigastric spine in the third anterior of dorsal margin; weak  
209 cervical groove, not joined to dorsal margin; oblique branchiocardiac groove joined to hepatic  
210 groove at level of strong hepatic spine; short hepatic groove backward directed; cephalic region  
211 with postorbital spine; hypertrophied Mxp3 with rows of movable spines; branch-like Mxp3  
212 dactylus; chelate P1-P3; achelate P4-P5; uropodal exopod without diaeresis.

213 *Remarks.*—*Acanthochirana* is placed within Aegeridae based on the presence of a hepatic spine,  
214 a hypertrophied Mxp3 with rows of movable spines, and chelate P1-P3. Additionally,  
215 *Acanthochirana* exhibits a cervical, a branchiocardiac and a hepatic groove. It also has a long  
216 scaphocerite and very long antennal flagellum, which are common features in Aegeridae.  
217 *Acanthochirana* can be distinguished from other Aegeridae based on its characteristic rostrum,  
218 usually moderately long, that presents multiple basal dorsal teeth. This genus also exhibits a  
219 distinctive spinose Mxp3 that is hypertrophied, but just moderately longer than the pereopods,  
220 and with a branch-like dactylus, unlike that of *Aeger* that is considerably longer than the  
221 pereopods, or that of *Anisaeger* that has an acuminate (brush tip shaped) dactylus and that is

222 not (or only very thinly) setose. When identifiable, *Acanthochirana* carapace grooves are also  
223 discriminant.

224

225 *Acanthochirana norica* (Pinna, 1974) new combination

226 1974 *Antrimpos noricus*, Pinna, p. 14-20, pl. 2-11, figs.4-8.

227 1976 *Antrimpos noricus*, Pinna, p. 34, pl. 1, figs.1-2; pl. 3, fig.2.

228 1990 *Antrimpos* sp., Dalla Vecchia, 1990, p. 131, photo 37.

229 1991 *Antrimpos* sp., Dalla Vecchia, 1991, p. 26.

230 1996 *Antrimpos noricus*, Garassino et al., p. 30-31.

231

232 *Holotype*.—Almost complete individual (n° 3380) from the *Zambelli Rocco* collection  
233 repositated at the *Museo civico di Scienze Naturali di Bergamo, Italy*. The specimen was collected  
234 near the village of Cene (Val Seriana, Bergamo, Italy) in the Norian Zorzino Limestone  
235 Formation (Pinna, 1974).

236 *Original diagnosis by Pinna (1974; translated from Italian and simplified based on the*  
237 *description of the holotype)*.—Rather elongated rostrum with two suprarostal teeth and no  
238 infrarostal teeth; an antennal angle rather acute bearing an antennal spine; the presence of  
239 supraorbital and hepatic spines; a gastro-frontal groove from which a gastro-orbital groove  
240 departs dorsoventrally towards the hepatic spine; and an hepatic groove under the hepatic spine  
241 and that bends forward and downwards towards the pterygostomial angle; antennae very robust;  
242 antennal flagella very long; scaphocerite well developed; Mxp3 well developed with propodus,  
243 carpus and merus carrying two rows of dense and robust spines along their anterior and  
244 posterior margin; P1-P3 chelate; P4-P5 achelate; s1-s3 increasing in length with rounded pleura;  
245 s4-s5 axially keeled; s6 elongated, longer than high; pl1-pl5 of considerable size; pl1 often  
246 transformed in petasma; pl2-pl5 composed of subrectangular basipodite which bear two very

247 long flagella; telson triangular; uropod rounded; uropodal endopod slightly longer than exopod,  
248 both far exceeding length of telson.

249 *Emended diagnosis by Pinna (1976; translated from Italian; partial modification of his original*  
250 *diagnosis following the discovery of additional better preserved specimens).*—The posterior  
251 margin of the carapace is slightly more sinuous than previously reconstructed as the lower part  
252 projects backwards in a more markedly way; the rostrum also possesses a series of suprarostal  
253 teeth arranged along the entire central portion of the rostrum, and a well-developed infrarostal  
254 tooth in the apical position, additionally to the two proximal suprarostal teeth previously  
255 recognized. The uropodal exopod is much longer than the endopod and presents a diaeresis.

256 *Remarks.*—*Antrimpos noricus* was first described by Pinna (1974) based on 149 specimens  
257 from the Norian (Upper Triassic) of Cene (Lombardy, Italy). The author provided a thorough  
258 study including a full description of the holotype, a reconstruction of the species, and a  
259 discussion on its ontogenetic variations and its exuvia. Later, Pinna (1976) described 34  
260 specimens from the Norian (Upper Triassic) of Valvestino, a neighbouring locality in  
261 Lombardy. Despite the presence of new characters (*i.e.*, posterior margin of the carapace  
262 slightly more sinuous; additional suprarostal teeth and a well-developed infrarostal teeth;  
263 uropodal exopod much longer than endopod; uropodal exopod with diaeresis), he ascribed these  
264 specimens to *Antrimpos noricus*, considering that observed differences between the Cene and  
265 the Valvestino specimens were of taphonomic origin, the Valvestino specimens being better  
266 preserved. Garassino et al. (1996) later described nine specimens from Rio Seazza (Preone,  
267 Italy), one specimen from Caprizzi (Socchieve, Italy), and one specimen from Forni di Sopra  
268 (Udine, Italy), all Norian in age. Based on the similarities between these specimens and the  
269 specimens from Valvestino, they ascribed them to *Antrimpos noricus*. However, they raised the  
270 hypothesis of the existence of two distinct taxa. Unfortunately, the illustrations provided by  
271 Pinna (1974, 1976) and Garassino et al. (1996) are not sufficient to clarify this matter. However,



272 they are sufficient to identify a well-developed scaphocerite, a very long antennal flagellum, a  
273 well-developed spinose Mxp3, and chelate P1–P3 increasing in length posteriorly. These  
274 characters are diagnostic of Aegeridae and therefore we proposed to assign *Antrimpos noricus*  
275 to this family. Additionally, based on the holotype and its associated original description,  
276 *Antrimpos noricus* presents a moderately long rostrum with basal infrarostral teeth, a short  
277 hepatic groove, a hepatic spine, a postorbital spine (initially interpreted as supraorbital spine),  
278 a short cervical groove (initially interpreted as gastro-orbital groove) and a Mxp3 spinose and  
279 rather robust that is about as long as the pereopods. These features are typical of  
280 *Acanthochirana*, supporting the new combination *Acanthochirana norica* (Pinna, 1974). This  
281 taxon is easily distinguishable from other *Acanthochirana* species as it is the only known  
282 member of its genus to have two basal suprarostal teeth and an antennal spine.

283

284 *Acanthochirana spinifera* (Schweitzer et al., 2014) new combination

285 2014 *Anisaeger spiniferus* Schweitzer et al., p. 464-466, figs.8-9.

286

287 *Holotype*.—Complete specimen (LPI-40455) from the Anisian Luoping Biota, Yunnan  
288 Province, China and repositated at the Chengdu Institute of Geology and Mineral Resources,  
289 Chengdu, Sichuan Province, China.

290 *Original diagnosis by Schweitzer et al. (2014)*.—Carapace with slender, postorbital spine  
291 triangular, hepatic spine needle-like; rostrum elongate bearing three suprarostal and one  
292 subrostral spine; pleura smooth, with dorsal keel on somite 6; pleura of somites 4–6 with serrate  
293 posterior margins.

294 *Remarks*.—This species was initially attributed to *Anisaeger* as Schweitzer et al. (2014) erected  
295 the later based on *An. spiniferus* and the type species *An. brevirostrus*. The main arguments  
296 used to erect *Anisaeger* and to attribute *An. spiniferus* to it were the size of the pereopods that

297 was interpreted as distinctively smaller than those found in other genera of Aegeridae, and the  
298 only very moderately longer Mxp3 in comparison to the pereopods. In *Aeger*, the pereopods  
299 are distinctively long, and the Mxp3 is significantly more developed and longer than them.  
300 However, in *Acanthochirana* the size of the pereopods and the difference in size between them  
301 and the Mxp3 is much lesser and therefore similar to that observed in *Anisaeger*. Such  
302 characteristics are therefore no longer sufficient to discriminate *Anisaeger*.

303 The postorbital spine of *An. spiniferus*, and its short cervical groove inclined  
304 anteroventrally at about 45° with a hepatic needle-like spine at its base, are shared  
305 cephalothoracic features with many *Acanthochirana* species. Additionally, *An. spiniferus* has a  
306 long rostrum with multiple basal and proximal suprarostralspines and one subrostral spine. The  
307 subrostral spine may be interpreted as corresponding to *Aeger*. However, neither do the  
308 carapace features, nor the cephalothoracic appendages corroborate such interpretation. In  
309 contrast, if not for the subrostral spine, *An. spiniferus* rostrum is reminiscent of the rostrum in  
310 *Acanthochirana*.

311 Based on the shared characters between *An. spiniferus* and *Acanthochirana* species, we  
312 propose the new combination. *Acanthochirana spinifera* (Schweitzer et al., 2014). This taxon  
313 differs from the other *Acanthochirana* species by its subrostral spine. It also exhibits a s4-s6  
314 with dorsal margin distinctively serrated and a dorsally-keeled s6.

315

316 **Genus AEGER** Münster, 1839

317 1839 *Aeger* Münster, p. 64-65.

318

319 *Type species*.—*Macrourites tipularius* Schlotheim, 1822, by subsequent designation of Woods  
320 (1925).

321 *Other species.*—Triassic: *Aeger gracilis* Förster and Crane, 1984; *Aeger lehmanni* (Langenhan,  
322 1910); *Aeger luxii* Huang et al., 2013; *Aeger straeleni* Glaessner, 1930. Post-Triassic: *Aeger*  
323 *brevirostris* Van Straelen, 1923; *Aeger brodiei* Woodward, 1888; *Aeger elegans* Münster, 1839;  
324 *Aeger elongatus* Garassino and Teruzzi, 1990; *Aeger foersteri* Garassino and Teruzzi, 1990;  
325 *Aeger franconicus* Förster, 1980; *Aeger hidalguensis* Feldmann et al., 2007; *Aeger insignis*  
326 Oppel, 1862; *Aeger laevis* (Blake, 1876); *Aeger libanensis* Roger, 1946; *Aeger macropus*  
327 Garassino and Teruzzi, 1990; *Aeger marderi* Woodward, 1866a; *Aeger muensteri* Garassino  
328 and Teruzzi, 1990; *Aeger robustus* Garassino and Teruzzi, 1990; *Aeger rostrospinatus*  
329 Garassino and Teruzzi, 1990; *Aeger spinipes* (Desmarest, 1817).

330 *Emended diagnosis by Charbonnier et al. (2017).*—Rostrum with one infrarostral spine;  
331 cervical groove steeply inclined, not joined to the dorsal margin, joined to antennal groove;  
332 oblique and sinuous branchiocardiac groove, crossing all the carapace from the posterior margin  
333 to the hepatic region; convex hepatic groove joined anteriorly to cervical groove and posteriorly  
334 to branchiocardiac groove; short inferior groove backward directed, not joined to ventral  
335 margin; hypertrophied Mxp3 with rows of movable spines; branch-like Mxp3 dactylus; chelate  
336 P1-P3 with chelae bearing movable spines on outer margins; achelate P4-P5, smooth; uropodal  
337 exopod with diaeresis.

338 *Remarks.*—*Aeger* is by far the most diverse genus among the family Aegeridae (Schweitzer et  
339 al., 2010). It is distinguishable from the other genera of the family by its characteristic third  
340 maxillipeds that are distinctively longer than the pereopods and that bear long movable spines.  
341 Additionally, it has a specific rostrum that is variable in length and with variable suprarostal  
342 spines depending on the species, but always with a single infrarostral spine.

343

344 *Aeger* sp.

345 Figures 2-3

346 2017 Caridean shrimp Brayard et al., p. 4, fig. 4.F; fig. 6.D-F; fig. S19.C-I; fig. S20.D.

347 2021 Penaeoid shrimp Smith et al., p. 2-3, fig. 3B-C.

348

349 *Description.*—Carapace.—Carapace seemingly thin, subtriangular. Posterior margin thinly  
350 rimed and strongly convex postero-ventrally, covering s1. Dorsal margin straight along the  
351 cardiac and gastric regions, and presenting a lump towards the frontal region above the orbital  
352 notch that may host a postrostral spine. Straight ventral margin. Anterior margin with a well-  
353 pronounced orbital notch, and a distinct antennal notch terminated ventrally by a sharp  
354 pterygostomial spine pointing outwards in adult specimens. Rostrum very long and granular,  
355 presenting multiple tubercle-like marks, with a single small infrarostral spine. Steeply inclined  
356 cervical groove, forming a strong angle half way through, as it starts posteriorly parallel to  
357 dorsal margin and ends anteriorly parallel to the orbital notch. Long and sinuous  
358 branchiocardiac groove joining cervical groove anteriorly in the antennal region of the  
359 carapace. Short hepatic groove steeply inclined in antennal region, not joined to cervical or  
360 branchiocardiac groove. Postorbital spine present.

361 Pleon.—s1-s6 smooth. s1-s3 roughly the same height although gradually longer posteriorly. s1-  
362 s2 with sinuous posterior margins and s2 also with a sinuous anterior margin. Tergopleuron of  
363 s2 slightly front-turned. s3 is the highest and longest somite and is subtriangular with a rounded  
364 termination. s4-s5 suboval with a rounded termination, higher than long, and of the same length  
365 although s4 is higher than s5. s4-s5 anterior margin slightly convex with posterior margin  
366 slightly concave and presenting an axial notch. s6 elongated, longer than high, subrectangular  
367 and axially keeled. s6 ventral margin thinly rimed. Telson badly preserved in all studied  
368 specimens.

369 Cephalic appendages.—Antennular peduncle barely perceptible and only a small piece of thin  
370 antennular flagellum identified. Antenna with rather long peduncle composed of three segments

371 increasingly thinner and longer distally. Antennal flagellum multi-articulated, incomplete but  
372 seemingly very long. Pointed scaphocerite, straight and potentially slightly curved upwards.  
373 Thoracic appendages.—Although not well preserved, they seem rather long and slender.  
374 *Pleonal appendages.* Pairs of pleopods moderately long, ovoid, fan-like. No traces of pleopod  
375 flagella. First pair distinctively bigger than the others, possibly petasma. No uropods preserved.  
376 Internal structures.—Multiple specimens (UBGD30558 and some of the additional material)  
377 exhibit remains of the digestive track throughout the pleon. The intestine extends parallel to the  
378 median line, slightly dorsally from s1 to s6 and terminates posteriorly just beneath the telson.  
379 *Illustrated material.*—UBGD30558, UBGD30555a, UBGD30553a and UBGD294002 from  
380 Paris Canyon, Idaho, USA (early Spathian, Early Triassic).  
381 *Additional material.*—the majority of the specimens on slabs UBGD30553, UBGD30635 from  
382 Paris Canyon, Idaho, USA (early Spathian, Early Triassic); UBGD33011BIS [not  
383 “UBGD33011” as mentioned in Smith et al., 2021] and UBGD294003 from Georgetown  
384 locality, Idaho, USA (early Spathian, Early Triassic).  
385 *Measurements.*—Available in Table 1.  
386 *Remarks.*—The large majority of the sampled specimens are small (2-3 cm), rather stocky and  
387 occur in mass (over 30 specimens on a 35cm x 35 cm slab). They present cephalic structures  
388 diagnostic of *Aeger* (e.g., cervical groove steeply inclined, not joined to the dorsal margin,  
389 joined to antennal groove that in our specimens is most probably mingled with the anterior  
390 section of the branchiocardiac groove; oblique and sinuous branchiocardiac groove; hepatic  
391 groove; postorbital spine). Unfortunately, the lack of complete rostrum and cephalothoracic  
392 appendages prevents identification at the species level.  
393 One specimen (UBGD294002), much larger but poorly preserved, is also ascribed to *Aeger* sp.  
394 It consists of an isolated and incomplete carapace. Based on the preservation state of the  
395 posterior part of the carapace, this specimen probably corresponds to an exuvia. Nonetheless,

396 the rostrum is partially preserved and appears to be elongated, granular and with only one  
397 isolated infrarostral spine, which is reminiscent of the rostrum of *Aeger*.

398 To avoid any overestimation of the diversity, and given that we suspect the two distinct  
399 morphs (small stocky vs large with infrarostral spine) may represent two different ontogenetic  
400 stages of the same taxon, we choose to ascribe both morphs to *Aeger sp.* pending the find of  
401 additional material. The genus *Aeger* was until now known from the Middle Triassic (Anisian  
402 Luoping Biota; Huang et al., 2013) to the Late Cretaceous (Cenomanian and Santonian Lebanon  
403 Konservat-Lagerstätten; Charbonnier et al., 2017). These specimens therefore represent the  
404 oldest known occurrence of *Aeger*, extending its range by about 5 Myr into the early Spathian  
405 (Early Triassic).

406

407 **Genus ANISAEGER** Schweitzer et al., 2014

408 2014 *Anisaeger* Schweitzer et al., p. 459-461.

409

410 *Type species.*—*Anisaeger brevirostrus* Schweitzer et al., 2014, by original designation. The  
411 name *An. brevispinus* [sic] is used several times in the figure captions corresponding to  
412 illustrations of *An brevirostrus* provided by Schweitzer et al. (2014). This is obviously a  
413 misspelling.

414 *Other species.*—Triassic: *Anisaeger longirostrus* n. sp.; *Anisaeger atavus* (Bill, 1914) n. comb.;  
415 *Anisaeger crassipes* (Bronn, 1858) n. comb.

416 *Original diagnosis by Schweitzer et al. (2014).*—Carapace small to moderate size, laterally  
417 compressed; rostrum short, upturned, and lacking spines to long, upturned, and bearing  
418 suprarostal and subrostral spines. Pleon with smooth terga and generally rounded pleural  
419 terminations; somites 5 and 6 axially keeled. Telson sharply pointed, with or without articulated  
420 spines. Uropodal exopod without diaeresis. Third maxilliped relatively short, setose or spinose.

421 Pereiopods generally short; pereiopods 1–3 with small chelae. Pleopods with a pair of annulated  
422 terminal processes.

423 *Emended diagnosis (present work).*—Rostrum of variable length, from moderately short (equal  
424 to the length of the eye), to very long (length of the carapace); smooth rostrum without spines;  
425 cephalothorax with hepatic and postorbital spines; s1 narrower and shorter than s2, with a strong  
426 anteriorly incurved ventral termination; s6 longer than the others, and dorsally keeled;  
427 hypertrophied third maxilliped just slightly longer than pereiopods with an acuminate dactylus;  
428 all pereiopods developed and of medium length; pereiopods not setose or spinose; P1–P3  
429 chelate; P4 and P5 achelate. Pleopods with a pair of annulated terminal processes.

430 *Remarks.*—The placement of *Anisaeger* within Aegeridae is based on the presence of a hepatic  
431 spine, a long scaphocerite, a long antennal flagellum, well-developed third maxillipeds and  
432 pereiopods, chelate pereiopods 1 to 3, and pleopods composed of two multi-articulated flagella  
433 each. As mentioned previously, *Anisaeger* was erected based on *An. brevirostrus* (type species)  
434 and *An. spiniferus*. These two taxa are significantly different (*e.g.*, respectively a short smooth  
435 rostrum *vs* a long rostrum with multiple basal teeth and one subrostral spine, and smooth  
436 posterior margin of s4–s6 *vs* a serrated posterior margin of s4–s6). They thus do not pertain to  
437 the same genus. *An. spiniferus* is assigned to *Acanthochirana* (see section on this genus), and  
438 based on observations made on *An. longirostrus* nov. sp, and on *An. brevirostrus*, we provide  
439 herein a new diagnosis for *Anisaeger*.

440         Additionally, *Anisaeger* was up till now only reported from the Middle Triassic of South  
441 China (Luoping Biota, Anisian; Schweitzer et al., 2014). Our revision shows that this genus  
442 was also present in the Middle and Late Triassic of Europe (Anisian of France and Carnian of  
443 Austria; Bronn, 1858; Bill, 1914). The specimens from the Paris Biota described below not only  
444 extend the temporal range by 5 Myr the genus into the early Spathian (Early Triassic), but also  
445 considerably extend its spatial distribution into the eastern Panthalassa.

446

447

*Anisaeger atavus* (Bill, 1914) new combination

448

Supplementary file 2

449

1914 *Penaus atavus* Bill, p. 305-308, pl. 11, fig. 3; pl. 12, fig. 4.

450

1971 *Antrimpos atavus* Gall, p. 50-52, pl. 12, figs. 1-3.

451

2010 *Antrimpos atavus* Schweitzer et al., p. 9.

452

453 *Neotype*.—Holotype destroyed. Neotype designated by Gall (1971): almost complete specimen  
454 (PEN 1) from the Anisian *Grès à meules* Formation, France, and repositied in the Grauvogel-  
455 Gall collection at the Ecole et Observatoire des Sciences de la Terre, Strasbourg, France.

456 *Emended diagnosis by Gall (1971; translated from French)*.—Crustacean with a narrow and  
457 elongated body, laterally compressed, generally fossilized in the dorso-ventral position. Thin  
458 and smooth cephalothoracic carapace, bearing 3 pairs of short grooves (cervical, hepatic and  
459 branchiocardiac) and two pairs of spines in the anterior region. It is extended in front by a long  
460 and pointed rostrum, adorned with a few dorsal teeth in the large specimens. Abdomen longer  
461 than the cephalothorax, formed of 6 segments, the last of which is about twice as long as it is  
462 height. Triangular telson, finished in a point. Short antennae formed by two unequal rami.  
463 Antennae with a long multi-jointed whip and a broad scale with the outer edge differentiated  
464 into a thorn. Third maxilliped with stiff bristles. Slender and smooth thoracic legs, the first three  
465 ending in a claw. Abdominal appendages unknown. Strongly chitinized uropods; the exopodite  
466 is articulated.

467 *Remarks*.—*Penaus atavus* was described based on eight specimens from the Upper  
468 Buntsandstein (Middle Triassic) *Grès à Voltzia* Formation (Bill, 1914). These specimens were  
469 described as having very long antennal flagellum, hypertrophied third maxillipeds that were  
470 spinose or setose (as evidenced by pits along the appendages), chelate pereopods 1 to 3, and



471 with a first pleonal somite shorter than the others. Bill (1914) attributed these specimens to the  
472 Penaeidae mainly on the basis of the chelae observed on the first three pereiopods.  
473 Unfortunately, all specimens originally housed at the University of Strasbourg were destroyed  
474 by fire in 1967. Gall (1971) later erected a neotype after examining over a hundred specimens  
475 also sampled from the *Grès à Voltzia* Formation. Considering the characters described by Bill  
476 (1914), he established a new diagnosis accompanied by a schematic reconstruction in which  
477 the species is described with cervical, hepatic and branchiocardiac grooves, two spines in the  
478 anterior part of the carapace, a dorsally keeled s6 longer than high, and a long rostrum with  
479 basal spines on the largest specimens. The illustrations provided by Bill (1914) and Gall (1971)  
480 do not allow to confirm the presence of basal spines on the rostrum. Without any justification,  
481 the species was assigned to the “wastebasket” genus *Antrimpos* by Gall (1971).

482         Given the distinctive hypertrophied setose third maxilliped, this species should be  
483 regarded as an Aegeridae. Additionally, the presence of (i) two anterior spines on the carapace  
484 that most probably correspond to the hepatic and postorbital spines, (ii) the branchiocardiac  
485 cervical and hepatic grooves, (iii) the s6 dorsally keeled, and (iv) the hypertrophied third  
486 maxilliped as long as the pereiopods, suggest it belongs to *Anisaeger*. We therefore propose the  
487 new combination *Anisaeger atavus*. *Anisaeger atavus* (Bill, 1914) differs from other *Anisaeger*  
488 species by the presence of a third maxilliped of the same length as the pereiopods, thinly setose,  
489 and that is terminated by a straight sharp dactylus.

490

491                                   *Anisaeger longirostrus* new species

492   Figures 4-6

493 2017 Penaeoid shrimp Brayard et al., p. 4, fig. 6.C; fig. S20.A,E.

494

495 *Type material.*—The holotype is UBGD294000 and paratypes include, UBGD30559,  
496 UBGD294001 and UBGD294004 from Paris Canyon, Idaho, USA (early Spathian, Early  
497 Triassic); UBGD33022BIS [not “UBGD33022” as mentioned in Smith et al., 2021] from  
498 NoName locality, Nevada, USA (early Spathian, Early Triassic).

499 *Type locality.*—Paris Biota of Paris Canyon, southeastern Idaho and NoName, northeastern  
500 Nevada, USA.

501 *Type age.*—Early Spathian, Early Triassic.

502 *Diagnosis.*—Carapace with a very long spineless rostrum; postorbital spine present; cervical  
503 groove inclined and terminated by an hepatic spine; long oblique branchiocardiac groove; well  
504 pronounced orbital notch; third maxilliped smooth and slightly longer than pereopods;  
505 acuminate dactylus of third maxilliped; pereopods 1–3 with moderate sized chelae; s1 narrower  
506 and shorter than s2, with a strong anteriorly incurved ventral termination; s3 higher than others  
507 and triangular; lateral keel on s5 and s6. Uropodal exopod with diaeresis.

508 *Description.*—Carapace.—Thin subrectangular carapace, narrower anteriorly than dorsally,  
509 with straight ventral margin, and dorsal margin gently arched. Anterior margin with well  
510 pronounced orbital notch and distinct antennar notch, both notches being separated by a sharp  
511 protuberance and possibly even an antennar spine. Thinly rimed posterior margin, ventrally  
512 rounded and slightly concave dorsally. Smooth and long rostrum, straight or slightly upturned  
513 and without spines. Small postorbital spine pointing anteriorly. Short inclined cervical groove  
514 terminated anteriorly by a hepatic spine. Long and shallow branchiocardiac groove.

515 *Pleon.*—s1-s6 tergopleura smooth with a thin rim on the external margin. Terga of s1 to s4  
516 smooth, and with a thin dorsal carina on s5 and s6. s1 higher than long, narrower and shorter  
517 than s2, with tergopleuron strongly concave anteriorly, ending with a sharp to narrowly rounded  
518 extremity, and with a convex to slightly sinuous posterior margin. s2 higher than long, rather  
519 triangular with anterior margin of tergopleuron straight or slightly concave, posterior margin

520 straight, and a rounded termination. s3 is higher and longer than the others, triangular, and  
521 overlapping s2. s4 is ovoid with a rounded end, about the same dimension as s2 with an anterior  
522 margin slightly convex and a posterior margin slightly concave with an axial notch. s5 is the  
523 smallest, slightly higher than long, with a convex anterior margin, a concave posterior margin  
524 also presenting an axial notch, and a rounded termination. s6 is elongated, longer than high,  
525 subrectangular. s5 and s6 show traces of an axial keel. Straight, triangular and elongated telson,  
526 about as long as s6 and sharply terminated.

527 Cephalic appendages.—No clear remains of antennular peduncle. Antennulae with two, thin,  
528 long multi-articulated flagella (~length of the carapace). Antenna composed of a smooth  
529 elongated peduncle with three elongated segments slightly thinner and gradually longer distally.  
530 Antennal flagellum multi-articulated and very long. Scaphocerite composed of two distinct  
531 parts: a spine that is rigid, and a blade that is thinner. The spine is straight, long, extending  
532 beyond antenna basal elements and with a sharp distal extremity. The blade is rather smooth,  
533 ovoid with a rounded termination, wide, and extending above the scaphocerite spine.

534 Thoracic appendages.—Maxillipeds 1 and 2 not preserved. Mxp3 smooth, well developed,  
535 moderately longer than the pereopods. Mxp3 carpus and propodus slender and very elongated,  
536 roughly equally long. Mxp3 dactylus large and acuminate. Pereopods moderately long, slender  
537 and smooth. P1–P3 gradually longer posteriorly and with moderate sized chelae. P4 and P5  
538 achelate.

539 Pleonal appendages.—Protopodite of pleopods moderately long, ovoid to slightly triangular,  
540 preserved in pairs. No remains of pleopod flagella. First pair of pleopods distinctively bigger  
541 than others in some specimens, potentially petasma. Rounded to subtriangular uropodal  
542 basipodite. Uropodal exopod and endopod ovoid with smooth lateral margins, and rounded  
543 distal margins. Uropodal exopod slightly shorter or the same length as the telson, and slightly

544 longer than uropodal endopod, both uropodal exopod and endopod present marks of  
545 longitudinal streaks. Uropodal exopod with diaeresis.

546 Internal structures.—Several specimens exhibit remains of digestive system. Even part of the  
547 stomach, located in the hepatic region, is occasionally preserved (Fig.6. 4-5). The digestive  
548 tractus extends anteriorly in the carapace to the hepatic region, horizontally and axially. It  
549 extends parallel to median line, slightly dorsally throughout the pleon and terminates posteriorly  
550 just beneath the telson.

551 *Etymology*.—The specific epithet refers to the elongated rostrum.

552 *Additional material*.—UBGD294005a, UBGD294005b, UBGD294005c, UBGD294006,  
553 UBGD30553b, UBGD30555b, UBGD294007 and UBGD294008 from Paris Canyon, Idaho,  
554 USA (early Spathian, Early Triassic).

555 *Measurements*.—Available in table 2.

556 *Remarks*.—The specimens exhibit spineless, well developed thoracic appendages, long  
557 scaphocerites, and third maxillipeds moderately longer than the pereopods. These characters  
558 are diagnostic of Aegeridae. With their moderately long thoracic appendages, these specimens  
559 differ from *Aeger* species that bear very long ones, and very well developed third maxillipeds,  
560 usually spinose or setose. The long and spineless rostrum of these specimens also distinguishes  
561 them from *Acanthochirana*. The only other Aegeridae presenting a spineless rostrum is  
562 *Anisaeger*.

563         Sampled specimens are flattened but abundant, allowing to distinguish recurrent  
564 anatomical features from simple compression artefacts. These features are the inclined cervical  
565 groove, the long and oblique branchiocardiac groove, and the hepatic and postorbital spines.  
566 Hepatic and postorbital spines as well as a shallow cervical groove were also identified in *An.*  
567 *brevirostrus*, but no branchiocardiac carina were reported so far from the latter. However, this  
568 difference should be taken with caution as it may result from a taphonomic bias *i.e.*, the

569 compression of the carapace may have erased some cephalic features. There are, however, other  
570 features differentiating the two species. The rostrum of *An. longirostrus* n. sp. is very long (table  
571 2) whereas it is never much longer than the eyestalks in *An. brevirostrus*. *An. brevirostrus* also  
572 exhibits setal pits on the third maxilliped whereas *An. longirostrus* n. sp. does not present any  
573 setose or spinose thoracic appendages, implying that if setose or spinose were present, they  
574 were very thin. Finally, the third maxilliped of *An. longirostrus* n. sp. is much slenderer than  
575 that of *An. brevirostrus*, and terminated by an acuminate dactylus.

576

577 *Anisaeger crassipes* (Bronn, 1858) new combination

578 1858 *Aeger crassipes* Bronn, p. 26-30, pl. 5, figs. 1-2 [not pl. 4, fig. 5].

579 1928 ?*Aeger crassipes* Van Straelen, p. 497.

580 1930 *Antrimpos crassipes* Glaessner, p. 139-140, pl. 6, fig.1; pl. 10, fig. 4.

581 1965 *Antrimpos crassipes* Glaessner, p. 112, fig. 1.

582 2010 *Antrimpos crassipes* Schweitzer, p. 9.

583 2016 *Antrimpos crassipe* Hyžný and Zorn, p. 137, pl. 14, fig. 1.a-c.

584 in press “Genus? *crassipes*” Hyžný and Garassino, p. 1-17, figs. 1-4.

585

586 *Type material*.—Syntypes figured by Bronn (1858: pl. 5, figs.1, 2, not pl. 4, fig.5) and from the  
587 Carnian Raibl Formation, Italy, possibly lost.

588 *Emended diagnosis by Glaessner (1930; translated in modern terms)*.—Carapace and rostrum  
589 poorly preserved; s1-s3 with rounded tergopleura; s4 and s5 with subtriangular tergopleura; s6  
590 longer than the others; s5 and s6 with median lateral keel; telson as long as s6; uropods third  
591 longer than telson, with longitudinal carina; very long multi-articulated antennal flagellum; oval  
592 scaphocerite; third maxilliped with foliole-shaped dactylus; P1–P3 with elongate chelae; P3

593 longest that P1 and P2; short P4, P5 achelate; pleopods with exopodite and endopodite of same  
594 length; first pleopods arched and heavily calcified (petasma).

595 *Remarks.*—*Aeger crassipes* was described based on four specimens from the Carnian Raibl  
596 Formation, Italy (De Zanche et al., 2000). As specified by Bronn (1858), the specimens are  
597 poorly preserved, complicating their identification. None the less, he identified five pairs of  
598 pereopods and long antennae. Additionally, he also noticed a long third maxilliped that he  
599 identified as a 6th pair of pereopods. Based on the similarities of its overall shape, the antennae,  
600 the thoracic appendages, and the uropods, Bronn (1858) assigned these specimens to *Aeger*.  
601 Finally, based on the rather robust P4 and P5 differing from those of other *Aeger* species that  
602 are usually filiform, he erected *Aeger crassipes*. Later, Glaessner (1930) revised this species  
603 based on 23 specimens, also from the Raibl Formation, and among which six exhibited the  
604 carapace and pleon, and three also presented pereopods. He described a triangular foliole-  
605 shaped dactylus for the third maxillipeds that are long, and three anterior pairs of pereopods  
606 that are chelate, the third pair of pereopods being the longest. The apparent absence of traces  
607 of setose or spinose on the third maxillipeds was mentioned by Glaessner (1930). He also  
608 provided a species reconstruction in which the rostrum is long and spineless. Considering that  
609 this species presents the general characteristics of Penaeoidea but not those of *Aeger*, and  
610 finding more shared features with *Antrimpos* than with *Aeger*, Glaessner (1930) proposed the  
611 new combination *Antrimpos crassipes* (Bronn, 1858). Schweitzer (2010) followed this opinion.  
612 Nowadays however, *Antrimpos* is considered as a “wastebasket” taxon (e.g., Garassino and  
613 Teruzzi, 1995; Garassino et al., 2013; Robalino et al., 2016). Finally, Hyžný and Garassino (in  
614 press) restudied the original material of Bronn (1858) and Glaessner (1930). After not being  
615 able to identify any important diagnostic character that would support an attribution to one of  
616 the two genera *Aeger* or *Antrimpos*, they suggested to place this taxon in open nomenclature as

617 “Genus? *crassipes* (Bronn, 1858)”. However, they did not consider an attribution to any other  
618 genera.

619 After examination of the illustrations in Bronn (1858) and Glaessner (1930), we identified the  
620 presence of well-developed third maxillipeds, at least as long as the pereiopods, P1–P3 chelate  
621 with the third pair longer than the others, very long antennal flagellum, and pleopods with two  
622 multi-articulated flagella each. These characters suggest that *Antrimpos crassipes* should be  
623 reassigned to Aegeridae. Additionally, given the presence of a spineless rostrum, Mxp3 about  
624 as long as the pereiopods that themselves are moderately long, the absence of traces of setose  
625 or spinose on the Mxp3 that are terminated by an acuminate dactylus, and the s1 narrower and  
626 shorter than s2 with a strong anteriorly incurved ventral termination, we argue for an assignment  
627 to *Anisaeger*. *Anisaeger crassipes* (Bronn, 1858) n. comb. differs from *Anisaeger brevispinus*  
628 by its long rostrum, and the seemingly smooth Mxp3. *Anisaeger crassipes* also shows relatively  
629 robust thoracic appendages among which the P1-P3 are terminated by relatively big chelae,  
630 contrary to *Anisaeger longirostrus* n. sp. in which the thoracic appendages are rather slender  
631 and the P1-P3 only exhibit moderate sized chelae.

632

633 **Suborder** PLEOCYEMATA Burkenroad, 1963

634 **Infraorder** GLYPHEIDEA Winkler, 1882

635 **Superfamily** GLYPHEOIDEA Winkler, 1882

636 **Family** LITOGASTRIDAE Karasawa et al., 2013

637 **Genus** *LITOGASTER* Meyer, 1847

638 1847 *Litogaster* Meyer, p. 137.

639

640 *Type species*.—*Litogaster obtusa* Meyer, 1844, by monotypy (junior synonym: *Litogaster*  
641 *ornata* Meyer, 1851).

642 *Other species.*—Triassic: *Litogaster durlachensis* (Förster, 1967a); ?*Litogaster keuperinus*  
643 Kuhn, 1939; *Litogaster limicola* (König, 1920); ?*Litogaster luxoviensis* Etallon, 1859;  
644 *Litogaster tiefenbachensis* Assmann, 1927; *Litogaster tuberculata* Assmann, 1927; *Litogaster*  
645 *turnbullensis* Schram, 1971.

646 *Emended diagnosis by Charbonnier et al. (2013).*—Subcylindrical carapace, laterally  
647 compressed; spatulate, spineless rostrum; cephalic region with longitudinal inflected carinae;  
648 very deep cervical groove, steeply inclined, ventrally joined to antennal groove, delimiting  
649 relatively narrow cephalic region; ventral margin of antennal-ptyergostomial region slightly  
650 convex; antennal groove rounded ventrally; deep, narrow postcervical groove, dorsally  
651 incurved, not joined to dorsal margin but joined ventrally to branchiocardiac groove, forming  
652 elongate and narrow lobe; very short cardiac groove, slightly convex posteriorly; intercervical  
653 groove absent; deep, narrow branchiocardiac groove, dorsally incurved, joined to dorsal margin  
654 of carapace; deep hepatic groove, semicircular at intersection with branchiocardiac groove and  
655 straight before joining cervical groove; inflated adductor muscle insertion area; deep inferior  
656 groove, convex posteriorly, joined to hepatic groove.

657

658 *Litogaster turnbullensis* Schram, 1971

659 *Figures 7-8*

660 1971 *Litogaster turnbullensis* Schram, p. 534-537, figs. 1-3.

661 2004 *Litogaster turnbullensis* Amati et al., p. 150, 155, fig. 2.2.

662 2010 Schweitzer et al., p. 19.

663 2013 Karasawa et al., p. 79.

664 2013 Charbonnier et al., p. 229-230, figs. 495-496.

665



666 *Type material*.—Holotype by monotypy (FMNH PE 16215) from the Early Triassic, Upper  
667 Siltstone Member of the Thaynes Formation of locality NW1/4, NW1/4, S 19, T. 15 S., R 45  
668 E, on the top of a ridge about  $\frac{3}{4}$  miles east of Hot Springs, Bear Lake, Idaho, United States of  
669 America.

670 *Original diagnosis by Schram (1971)*.—Decapod of moderate size; rostrum short and spatulate;  
671 carapace granulose in texture; postcervical and branchiocardiae grooves parallel and gently  
672 directed posteriad; doublure on posterior margin of carapace; abdominal terga smooth; telson  
673 subrectangular; exopod of uropod with diaeresis.

674 *Emended diagnosis (present work)*.—Subcylindrical carapace granulose in texture, with a short  
675 spatulate rostrum without spines; distinct orbital notch; well pronounced antennal and orbital  
676 carina; antennal groove weakly rounded ventrally, forming flat antennal lobe and joined to  
677 rimmed ventral margin of cephalic region; postcervical and branchiocardiae grooves parallel  
678 and gently directed posteriorly; subchelate P1-P3; P1 merus with dorsal and ventral spiny  
679 margins; P3 merus with spiny ventral margin; abdominal terga smooth; s2-s6 terga with median  
680 raised longitudinal carina; subrectangular telson rounded distally; uropodal endopod and exopod  
681 as long as telson, with strong median longitudinal carina; exopod of uropod with diaeresis.

682 *Description*.—Carapace.—Laterally compressed, subcylindrical carapace (UBGD30557: CL=  
683 16.31 mm, CH= 6.9 mm); short, spineless rostrum; distinct orbital notch; cephalic region with  
684 two tuberculated carinae, slightly raised; orbital and gastro-orbital carinae distinct, approaching  
685 each other distally; deep, straight cervical groove, intercepting dorsal midline at *ca* 80° angle;  
686 cervical groove ventrally joined to antennal groove, delimiting narrow cephalic region; ventral  
687 margin of antennal-ptyergostomial region slightly convex; antennal groove weakly rounded  
688 ventrally, forming flat antennal lobe and joined to rimmed ventral margin of cephalic region;  
689 weak postcervical groove, incurved dorsally, not joined to dorsal margin but joined ventrally to  
690 branchiocardiac groove, forming elongate, narrow lobe; very short cardiac groove, interrupted

691 before joining dorsal midline; weak branchiocardiac groove, incurved dorsally, reaching dorsal  
692 midline at about 70° angle; hepatic groove, semicircular at intersection with branchiocardiac  
693 groove and straight before joining cervical groove; inferior groove not visible; raised adductor  
694 muscle insertion area. Ornamentation of carapace: all regions finely tuberculated.

695 Cephalic appendages.—Poorly preserved, only a fragment of probable antennal flagellum is  
696 visible.

697 Thoracic appendages.—Subchelate P1, largest and stoutest; cylindrical P1 merus with spiny  
698 dorsal and ventral margins; tronconical P1 carpus as long as high; subrectangular P1 propodus,  
699 at least two times as long as high; P1 dactylus large, elongate and distally curved; subchelate  
700 P2-P3; P3 merus with spiny ventral margin; achelate P4-P5 more slender than P1-P3.

701 Pleon.—s1 shorter than others; subrectangular s2-s5, equal in size, with smooth terga and  
702 mucronate tergopleura; subrectangular s6 shorter than previous ones, with triangular  
703 tergopleura; s2-s6 terga with median raised longitudinal carina; subrectangular telson with  
704 rounded distal extremity, marked with faint median and lateral longitudinal carinae.

705 Pleonal appendages.—Uropodal endopod and exopod as long as telson, with strong median  
706 longitudinal carina; uropodal exopod with straight diaeresis.

707 *Illustrated material.*—Three specimens from the Paris Biota (from Paris Canyon, Idaho, USA):  
708 UBGD30557 is a subcomplete specimen preserved in left lateral view showing a disarticulation  
709 between the carapace, the pleon, the endophragmal skeleton and the pereopods, which suggests  
710 a probable exuvia origin; UBGD30560 is a subcomplete specimen preserved in dorso-ventral  
711 position; UBGD30548 is an isolated pleon preserved in dorsal view.

712 *Measurements.*—Available in Table 3.

713 *Remarks.*—The three new specimens sampled from the Paris Biota show diagnostic characters  
714 of *Litogaster* such as the carapace groove pattern with the postcervical and branchiocardiac  
715 grooves joined ventrally, the short cardiac groove and the semicircular hepatic groove. The

716 subchelate P1-P3 are also very typical of *Litogaster*. The finely tuberculated ornamentation, the  
717 presence of a clear orbital notch, and the well-pronounced antennal and orbital carinae suggests  
718 a placement in *Litogaster turnbullensis*.

719

720 **Superfamily PEMPHICOIDEA** Van Straelen, 1928

721 **Family PEMPHICIDAE** Van Straelen, 1928

722

723 *Included genera*.—*Pemphix* Meyer, 1835; *Pseudopemphix* Wüst, 1903; *Oosterinkia*  
724 Klompmaker and Fraaije, 2011.

725

726 *Emended diagnosis* by Charbonnier *et al.* (2015).—Carapace with strongly inflated  
727 cephalothoracic regions; spatulate, dorsoventrally flattened rostrum; orbital, gastro-orbital and  
728 antennal ridges absent in cephalic region; gastro-orbital groove with two wide branches; very  
729 deep cardiac groove; postcervical and branchiocardiac directed toward the dorsal margin with  
730 angle c. 30° and converging dorsally but without dorsal connection; biconvex hepatic groove;  
731 subchelate pereopods 1 to 3; uropodal exopodite with straight diaeresis; subrectangular telson  
732 with rounded extremity.

733

734 **Genus PEMPHIX** Meyer, 1835

735 1835 *Pemphix* Meyer, p. 328.

736

737 *Type species*.—*Palinurus sueurii* Desmarest, 1817, by subsequent designation of Glaessner  
738 (1929).

739 *Other species*.—Triassic: *Pemphix malladai* Via, 1971; *Pemphix silesiacus* Assmann, 1927;  
740 *Pemphix sueurii* (Desmarest, 1817).

741 *Emended diagnosis by Feldmann et al. (2015).*—Subcylindrical carapace slightly compressed  
742 dorsoventrally, strongly sculptured by deep grooves; gastric, hepatic, meso- gastric,  
743 metagastric, and epibranchial regions well defined; cervical, postcervical, and branchiocardiac  
744 grooves well developed; long and spatulate rostrum lacking supra- and subrostral teeth but  
745 broadly rimmed; short antennules; long antennae with leaf-shaped scaphocerite; pereopod 1  
746 strongly developed and subchelate; pereopods 2-3 slender and subchelate; pereopods 4-5 with  
747 terminal dactylus; subrectangular pleonal somites with wide articulating rings; tergopleura  
748 blunt-triangular, directed posteriorly; subrectangular telson; exopodite with diaeresis.

749 *Emended diagnosis (present work).*—Carapace tuberculate with strongly inflated  
750 cephalothoracic regions; gastric, hepatic, meso- gastric, metagastric, and epibranchial regions  
751 well defined; spatulate rostrum, broadly rimmed; long antennae with leaf-shaped scaphocerite;  
752 short antennules; orbital, gastro-orbital and antennal ridges absent in cephalic region; gastro-  
753 orbital groove with two wide branches; very deep cardiac groove; postcervical and  
754 branchiocardiac directed toward the dorsal margin with angle ca 30° and converging dorsally  
755 but without dorsal connection; biconvex hepatic groove; subchelate pereopods 1 to 3;  
756 pereopod 1 strongly developed; pereopods 4-5 achelate; subrectangular pleonal somites;  
757 tergopleura blunt-triangular, directed posteriorly; uropodal exopodite with straight diaeresis;  
758 subrectangular telson with rounded extremity.

759

760 *Pemphix krumenackeri* new species

761 Figure 9

762

763 *Type material.*—Holotype by monotypy UBGD294009, subcomplete specimen from Paris  
764 Canyon, Idaho, USA (early Spathian, Early Triassic), preserved in dorso-ventral position,  
765 showing fragmentary carapace, complete pleon and tail fan.

766 Type locality.—Paris Canyon, southeastern Idaho, USA.

767 Type age.—Early Spathian, Early Triassic.

768 *Diagnosis.*—Carapace tuberculate with strongly inflated cephalothoracic regions; rostrum large  
769 and dorsoventrally flattened; very deep cervical groove; branchiocardiac grooves directed  
770 dorsally and converging close to postero-dorsal extremity; moderately biconvex hepatic  
771 groove; deep cardiac groove joined ventrally and slightly anteriorly to postcervical groove;  
772 cardiac groove cutting dorsal midline perpendicularly; strongly sculptured pleonal somites with  
773 one transversal groove interrupted by a short median carina on s2-s5 terga, and strong nodulose  
774 process rimmed by one triangular groove at the fold separating tergopleuron from tergum on  
775 s2-s5 tergopleura; telson with one pair of broad proximal tubercles; uropods as long as telson,  
776 with one longitudinal carina; uropodal exopod with straight diaeresis.

777 *Description.*—Carapace.—Carapace with originally strongly inflated cephalothoracic regions;  
778 rostrum not preserved, except the basis, broadly rimmed, suggesting a large, dorsoventrally  
779 flattened shape; very deep cervical groove; gastro-orbital groove poorly preserved, with two  
780 wide branches but only the dorsal one is well-visible; postcervical and branchiocardiac grooves  
781 directed toward the dorsal margin with an angle of  $\sim 30^\circ$  and converging posteriorly, but without  
782 dorsal connection; moderately biconvex hepatic groove; deep cardiac groove joined ventrally  
783 and slightly anteriorly to postcervical groove; cardiac groove cutting dorsal midline  
784 perpendicularly; ornamentation of carapace poorly preserved but remains of small tubercles are  
785 present on cephalic and branchial regions.

786 Pleon.—Pleon as wide as carapace; subrectangular s1, smaller than the others; s1 tergum with  
787 short transversal groove; s2-s5 of similar size and shape; s2-s5 terga with one transversal groove  
788 interrupted by a short median carina, s2-s5 tergopleura with one strong nodulose process  
789 rimmed by one triangular groove at the fold separating tergopleuron from tergum; s2-s5  
790 tergopleura acuminate; s6 tergum with median carina; s6 tergopleuron with one strong nodulose

791 process rimmed by incurved groove, at the fold separating tergopleuron from tergum;  
792 subrectangular telson with rounded extremity; telson with one pair of broad proximal tubercles.  
793 Pleonal appendages.—Pleopods not preserved; uropods as long as telson, with one longitudinal  
794 carina; uropodal exopod with straight diaeresis.

795 *Etymology*.—The specific epithet honours L. J. Krumenacker, first finder of the Paris Canyon  
796 fossiliferous site.

797 *Measurements*.—Available in Table 4.

798 *Remarks*.—This new taxon shows diagnostic characters of *Pemphix* Meyer, 1835 such as the  
799 carapace groove pattern (very deep cervical groove, parallel postcervical and branchiocardiac  
800 grooves, very deep cardiac groove cutting dorsal midline perpendicularly) and the originally  
801 strongly inflated regions of carapace (flattened on the fossil). Schweitzer et al. (2010) listed  
802 three species in *Pemphix*: *Pemphix sueurii* (Desmarest, 1817) from the Middle Triassic of  
803 France and Germany, *P. silesiacus* Assmann, 1927 from the Middle Triassic of Poland, and *P.*  
804 *malladai* Via, 1971 from the Middle Triassic of Spain. *Pemphix krumenackeri* n. sp. differs  
805 from the type species by its strongly sculptured pleonal somites (almost smooth, with wide  
806 articulating rings in *P. sueurii*). After Förster (1967), *Pemphix silesiacus* is very close to  
807 *P. sueurii* but much smaller and with a gastric region without strong sculpture. A potential  
808 synonymy between these two species was raised but not solved because only one of the 21  
809 original type specimens listed by Assmann (1927) was recovered and studied by Förster (1967).  
810 The poor preservation of *Pemphix malladai* Via, 1971 precludes any comparison with other  
811 Pemphicidae species and even raises the question of its placement within *Pemphix*. *Pemphix*  
812 *krumenackeri* n. sp. represent the oldest known *Pemphix* species, enlarging the temporal extent  
813 of the genus back to the Early Triassic, and extending its spatial range to the American  
814 continent.

815

816                               **Genus OOSTERINKIA** Klompmaker and Fraaije, 2011

817   2011   *Oosterinkia* Klompmaker and Fraaije, p. 6.

818

819   *Type species*.—*Oosterinkia neerlandica* Klompmaker and Fraaije, 2011, by monotypy.

820   *Emended diagnosis*.—As for type species by monotypy.

821

822                               *Oosterinkia neerlandica* Klompmaker and Fraaije, 2011

823

824   *Type material*.—Holotype by monotypy (MAB k2854) from the Anisian Quarry I of the  
825   *Winterswijk* quarry complex, eastern Netherlands. Stored at Oertijdmuseum De Groene Poort,  
826   Boxtel, Netherlands.

827   *Original diagnosis by Klompmaker and Fraaije (2011)*.—Cephalothorax cylindrical; triangular  
828   rostrum; median line present; intercalated plate on gastric part; strong cervical groove; small,  
829   faint postcervical groove parallels stronger branchiocardiac groove; cephalothorax partly  
830   smooth or pitted. Terga and epimeres pitted; epimeres with pointed, slightly posteriorly directed  
831   tip. Spade-shaped telson with longitudinal groove but without bristle structure; exopod with  
832   diaeresis.

833   *Emended diagnosis*.—Subcylindrical carapace slightly compressed dorsoventrally, sculptured  
834   by deep grooves; deep cervical groove; postcervical and branchiocardiac grooves directed  
835   toward the dorsal margin and converging dorsally but without dorsal connection; gastro-orbital  
836   groove with two wide branches; deep hepatic groove; gastric, hepatic, meso- gastric,  
837   metagastric, and epibranchial regions well defined; spatulate rostrum, dorsoventrally flattened,  
838   broadly rimmed; strong antenna with leaf-shaped scaphocerite; subrectangular pleonal somites  
839   with wide articulating rings; tergopleura blunt-triangular, directed posteriorly; subrectangular  
840   telson; exopodite with diaeresis.

841 *Remarks.*—*Oosterinkia* was placed among the Erymidae Van Straelen, 1925. However, after  
842 careful examination of the original figures, the carapace with inflated cephalothoracic regions,  
843 the spatulate rostrum (even if broken), the gastro-orbital groove with two wide branches, the  
844 postcervical and branchiocardiac directed toward the dorsal margin and converging dorsally  
845 but without dorsal connection, and the uropodal exopod with straight diaeresis are actually  
846 diagnostic characters of Pemphicidae (see diagnosis proposed by Charbonnier et al., 2015).  
847 *Oosterinkia* differs from *Pemphix* and *Pseudopemphix* by the absence of very deep cardiac  
848 groove, its less strongly inflated cephalothoracic regions (*e.g.*, cardiac region: short and raised  
849 in *Pemphix*, large and very raised in *Pseudopemphix*, large and flat in *Oosterinkia*), and its  
850 partially smooth or pitted carapace (strongly tuberculated in *Pemphix* and *Pseudopemphix*).

851

## 852 **Diversification trends data**

853

854 Following the taxonomical work, we listed all the Triassic decapods known to date (Table 5;  
855 Supplementary file 3). A total of 75 species were listed along with their age and location, going  
856 from the Olenekian (Smithian + Spathian substages of the Early Triassic) to the Rhaetian, and  
857 from all continents but Oceania and Antarctica. When taxa were reported from two closely-  
858 located sites and from the same age, they were grouped under the same locality name. For each  
859 listed taxon, the taxonomic and systematic validity was verified. Several taxonomic and  
860 systematic issues were raised, especially regarding Aegeridae. Therefore, when illustrations  
861 were sufficient to have solid arguments to reattribute the species, we did so, despite not having  
862 seen the type material, either because it has gone missing (*e.g.*, type specimens of *Penaeus*  
863 *atavus*, Bill, 1914 destroyed by fire) or it was not easily accessible. A first graphic  
864 representation of the decapod taxonomic richness is presented by epoch in Fig.10. 1 and by  
865 stage in Fig.10. 2. However, there is a strong correlation between the raw taxonomical richness



866 and the number of sites from which the taxa were reported (Fig.10. 3-4). In order to minimize  
867 a possible co-variance between the two latter, we also studied the mean of the observed alpha  
868 diversity of each site [ $\alpha_s$ ] per studied interval (Fig.10. 5-6). This mean [ $\alpha_m$ ] was calculated for  
869 each time interval following  $\alpha_m = \frac{\sum_{i=1}^S \alpha_s}{N}$ , where  $N$  is the number of sites  $S$  of the interval  
870 (Whittaker, 1960). This approach presents the advantage of being easily applicable to any  
871 dataset in which the sampling sites are reported. It is favored to other model-based approaches  
872 (*e.g.*, subsampling models, coverage-based models, rarefaction models) due to the limited size  
873 of the dataset. Such approach is all more important when the fossil record is highly  
874 heterogeneous (Fig.10. 3-4), as is the case for the Triassic (Muscente et al., 2017).

875

## 876 **Discussion**

877

878 *The Paris Biota decapods.*—The first field samplings of the Paris Biota yielded about 4550  
879 fossil specimens among which about 350 decapods (articulated + disarticulated; Smith et al.,  
880 2021). We can now assess that it comprises at least four species representing three superfamilies  
881 of Decapoda. In comparison, the renowned and well-studied Anisian Luoping Biota (> 18 500  
882 arthropods; Hu et al., 2011), that is often regarded as the first fully recovered marine fauna  
883 following the PTB crisis (Hu et al., 2011; Chen and Benton, 2012; Benton et al., 2013), hosts  
884 seven species of four different superfamilies of Decapoda (Feldmann et al., 2012; Huang et al.,  
885 2013; Schweitzer et al., 2014; Table 5; Supplementary file 3). Another well-known decapod  
886 rich Triassic formation, this time from Europe, is the Anisian Grès à Voltzia Formation that  
887 hosts five species of four different superfamilies.

888         The decapod assemblage of the Paris Biota is only the second Early Triassic decapod  
889 assemblage known to date. The other known Early Triassic decapod assemblage is from the  
890 Dienerian-Smithian of Ambilobé, ~150 km SW of Diego Suarez (Antsiranana), NW

891 Madagascar (Besairie, 1932). A total of three species of Penaeidae (*Ambilobeia karojo*  
892 Garrasino & Pasini, 2002; *Ifasia dagascariensis* (Van Straelen, 1933); *Ifasia straeleni*  
893 Garrasino & Teruzzi, 1995) have been reported from this area. In addition to the specimens  
894 from Madagascar, only a single other Early Triassic decapod was documented up till now, *i.e.*,  
895 *Litogaster turnbullensis* identified by Schram (1971) based on a single isolated specimen from  
896 the Thaynes Group of southeastern Idaho, USA. However, this specimen was found in a  
897 neighboring locality of Paris Canyon and is early Spathian in age. Therefore, this specimen is  
898 likely another component of the Paris Biota that is known to extend throughout the Northern  
899 part of the western USA basin (Smith et al., 2021). By doubling the number of known Early  
900 Triassic decapod taxa, the Paris Biota specimens significantly increase our knowledge on the  
901 diversity of this clade during this geological interval.

902         The two new Aegeridae taxa (*Aeger* sp. and *Anisaeger longirostrus* n. sp.) described in  
903 this work are both the earliest representatives of their respective genera and the earliest  
904 representatives of Aegeridae. They thus extend the temporal range of these genera and this  
905 family back into the Early Triassic (Fig.11). These occurrences of aegerids, 5 Myr older than  
906 previously reported, are all the more important as this family has been suggested to be a basal  
907 group within Penaeoidea (Burkenroad, 1963, 1983; Tavares and Martin, 2010). With the  
908 isolated Famennian (Devonian) specimen of *Aciculopoda mapesi* Feldmann & Schweitzer,  
909 2010 and the previously mentioned Malagasy Penaeidae for which the dating is rather poorly  
910 constrained (Marramà et al., 2017; Laville et al., 2021), the Paris Biota specimens represent  
911 some of the oldest occurrences of Dendobranchiata (Schram, 1977, 1980; Schram et al., 1978;  
912 Feldmann and Schweitzer, 2010). They therefore fill-in an important gap in the history of this  
913 group, from which present-day representatives are well studied for their economic interest  
914 (Farfante, 1988; Cervantes-Hernández et al., 2010; Robalino et al., 2016; Fernández de Alaiza  
915 García Madrigal et al., 2018), but whose origin remains elusive.

916 *Pemphix krumenackeri* n. sp. extends the temporal range of Pemphicoidea by over 2  
917 Myr, back into the Early Triassic (Fig.11), and enlarges its spatial distribution to the American  
918 continent, as up till now this family was only known from the Middle-Late Triassic of Europe  
919 (Amati et al., 2004; Karasawa et al., 2013; Schweitzer and Feldmann, 2014). The temporal  
920 extent of Glypheidea was thought to extend from the Early Triassic to nowadays. However,  
921 only one specimen (*L. turnbullensis* described by Schram in 1971) was reported from the Early  
922 Triassic, leaving some uncertainty as to the actual origin of this group. The co-occurrence of  
923 *Pemphix krumenackeri* n. sp. and *Litogaster turnbullensis* in the Paris Biota confirms the  
924 appearance and the diversification of Glypheidea as soon as the Early Triassic.

925 *Diversification trends during the Triassic.*—The decapods of the Paris Biota significantly  
926 increase the known diversity of Early Triassic decapods, and therefore provide new insights  
927 into the Triassic diversification of this clade. We discuss the latter using a compiled and revised  
928 list of Triassic decapods (Table 5; Supplementary file 3).

929 A first comparison can be made between our dataset and other available Triassic  
930 decapod datasets such as that of Paleobiology Database (PBDB; search “Decapoda, Triassic”,  
931 downloaded on June 18th, 2021; Table Supplementary file 4). At first, it appears like the two  
932 datasets are rather similar in terms of decapod taxonomic richness (PBDB: 63 species and 20  
933 higher rank taxa; Supplementary file 5; our dataset: 74 species including the 3 new ones from  
934 the Paris Biota). However, 29 taxa reported in our dataset (over 40% of the total, the newly  
935 described taxa excluded) do not occur in the PBDB dataset (Supplementary file 6), implying  
936 the latter is still incomplete. Additionally, a third of the species listed in the PBDB dataset are  
937 incorrectly recorded (Supplementary file 5). Most of these records concern the temporal range  
938 of taxa, as Jurassic, Cretaceous, and even Paleocene occurrences are registered as being Triassic  
939 (Supplementary file 5). Some other issues such as synonymy mistakes, invalid taxa, and even  
940 some microcoprolites registered as valid decapod species, have also been noticed

941 (Supplementary file 5). It thus appears that the PBDB Triassic decapod dataset is inappropriate  
942 to analyze the Decapoda diversity trends throughout the Triassic.

943         Based on our dataset at the epoch-scale, decapods apparently underwent an important  
944 diversification throughout the Triassic (Fig.10. 1). However, at the stage-scale (Fig.10. 2), this  
945 trend is more contrasted, with the Anisian and Norian being the most diverse stages. This  
946 differential pattern likely results from the heterogeneity of the decapod fossil record and  
947 sampling effort. Indeed, a very few sites have been intensively sampled comparatively to the  
948 majority of them (*e.g.*, in the south-west of Germany and the Guizhou province of China for  
949 the Anisian, and in the Italian Lombardy region for the Norian). Additionally, certain time  
950 intervals are much better represented than others, with more known fossiliferous localities.

951         Based on  $\alpha_m$ , the Triassic decapod diversification trend significantly differs from that  
952 observed on the raw richness at all taxonomic ranks (Fig.10). At the epoch-scale, whereas the  
953 taxonomical richness gradually increases (Fig.10. 1),  $\alpha_m$  at each taxonomical level remains  
954 rather constant throughout the Triassic (Fig.10. 6). At the stage-scale, whereas the Olenekian  
955 appears to be the poorest Triassic stage and the Anisian appears to be the richest (Fig.10. 2),  
956 the Olenekian exhibits  $\alpha_m$  comparable to that of the Anisian and lower than that of the Norian  
957 (Fig.10. 6). These differences illustrate how the heterogeneity of the fossil record can strongly  
958 bias observed diversity trends. The evolution of the apparent decapod mean alpha diversity ( $\alpha_m$ )  
959 throughout the Triassic (Fig.10. 5-6) can be interpreted in two ways:

960 (i) If considered that the taxonomy and systematics of Triassic decapods remain too amiss: then  
961 any apparent diversity trend should be considered hardly interpretable. The Triassic decapod  
962 taxonomy and systematic inaccuracy likely originate from the scarce occurrences of Triassic  
963 decapods that led to important knowledge gaps. Such poor fossil record is not specific to  
964 decapods (Twitchett, 2001; Muscente et al., 2017), implying that similar hiatus likely exist for  
965 other organisms.

966 (ii) If considered that the taxonomy and systematics of Triassic decapods are reliable and the  
967 data is accurate (such assumption can only be asserted after having carefully studied the  
968 corresponding literature): then no increase in alpha diversity is documented for the Triassic  
969 decapods (Fig.9. 5-6). Additionally, it appears that decapods were already well diversified as  
970 soon as the Early Triassic (at least relatively to what is actually known from the rest of the  
971 Triassic). This contrasts with the generally assumed model of a delayed post-PTB biotic  
972 recovery of Early Triassic marine organisms (*e.g.*, Chen and Benton, 2012).  
973 Ultimately, none of these interpretations supports a delayed post-PTB biotic recovery scenario  
974 for decapods.

975

## 976 **Conclusion**

977

978 The Paris Biota offers an exceptional window into Early Triassic marine ecosystems. This is  
979 all the more important as the Early Triassic is assumed to be the time interval during which the  
980 Modern evolutionary fauna took its rise, and thus, to be the scene of the diversification of many  
981 modern clades, including decapods (Sepkoski, 1981).

982         Among the Paris Biota Dendrobranchiata, *Aeger* sp. and *Anisaeger longirostrus* n. sp.  
983 extend by 5 Myr back into the Early Triassic the temporal range of their respective genera.  
984 Additionally, they represent the oldest known specimens of Aegeridae, also extending the  
985 temporal range of this family by 5 Myr back into the Early Triassic. In fact, if not for  
986 *Aciculopoda mapesi* Feldmann and Schweitzer, 2010 that was described based on a single  
987 poorly-preserved specimen, and the poorly age-constrained Malagasy specimens, the Paris  
988 Biota Aegeridae represent the oldest Dendrobranchiata currently known, thus providing a new  
989 anchor point for future studies on this group.

990           Regarding the Paris Biota Pleocyemata, the newly sampled specimens of *L.*  
991 *turnbullensis*, previously known from a single isolated and disarticulated specimen, confirm the  
992 existence of this taxon as soon as the Early Triassic, and more specifically, as soon as the early  
993 Spathian. *Pemphix krumenackeri* n. sp. represents the oldest known species of its genera, but  
994 also of the superfamily Pemphicoidea, extending their temporal ranges by about 2 Myr into the  
995 Early Triassic. In addition, *Pemphix krumenackeri* n. sp. is now the co-oldest Glypheidea  
996 known, with *L. turnbullensis*.

997           The co-occurrence of these decapods in the Paris Biota provides evidence for an early  
998 diversification of this group, as soon as the early Spathian. This is congruent with available  
999 decapod phylogenies and diversification models that argue for a Triassic diversification of these  
1000 groups (Gherardi et al., 2010; Lavalli and Spanier, 2010; Schweitzer and Feldmann, 2014;  
1001 Robalino et al., 2016; Wolfe et al., 2019). Besides, all the Paris Biota taxa extend the Triassic  
1002 spatial range of their respective genera and/or family (that were up to now only known from  
1003 Europe and Asia) to the American continent. This suggests transoceanic dispersals for these  
1004 taxa, which is a feature observed in other clades at least transiently during the Early Triassic:  
1005 ammonoids (Brayard et al., 2006; Jattiot et al., 2016), thylacocephalans (Laville et al., 2021),  
1006 marine vertebrates (Tintori et al., 2014). Another interpretation could lie in the incomplete  
1007 knowledge of an otherwise cosmopolitan decapod distribution during the Triassic.

1008           The description of the Paris Biota specimens also led to a taxonomic and systematic  
1009 revision of Triassic decapods, highlighting the significance of this biota in the debates on the  
1010 Early Triassic recovery and on the rise of the modern ecosystems. Using a refined dataset of  
1011 known Triassic decapod taxa that strongly differs from that of the PBDB, we showed that: (i)  
1012 the apparent increase in decapod taxonomic richness throughout the Triassic mainly results  
1013 from the heterogeneity of the fossil record and/or the sampling intensity; (ii) the Decapoda  
1014 alpha diversity was relatively high as soon as the Early Triassic; (iii) the Decapoda alpha

1015 diversity seems to have remained rather constant throughout the Triassic. A considerable  
1016 amount of sampling, taxonomic and systematic work on Triassic decapods remains to be done  
1017 if we are to understand the early diversification of decapods and the underlying processes.  
1018 However, we hope the present contribution will constitute one step further in that direction.

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1055 **Accessibility of supplemental data**

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1057 Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hmgqnk9jp>  
1058 [Supplementary data awaiting for acceptance on DRYAD. Therefore, the DOI link is not active  
1059 yet. Pending acceptance of Supplementary data, it is available at:  
1060 <https://datadryad.org/stash/share/OCIQZ98IIV-L59Rh48Y3vdyvJAERJS1M1PZICc6nffE> ]

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1539 **Figure caption**

1540

1541 **Figure 1:** Location of the sites from which the Paris Biota has been reported. (1) Present-day  
1542 map; (2) Early Triassic paleogeographic map; (3) Simplified map of northeastern Nevada; (4)  
1543 Simplified map of southeastern Idaho. Yellow rectangle indicates the location of the western  
1544 USA basin. Small red rectangles in (1) indicate the location of map (3) and (4). Stars indicate  
1545 the location of the sites from which the Paris Biota has been reported. IC: Immigrant Canyon;  
1546 NN: NoName; STW: Stewart Canyon; GT: Georgetown; PC: Paris Canyon, original site of the  
1547 Paris Biota. Maps, following Romano et al. (2012).

1548

1549 **Figure 2:** *Aeger* sp. (1-3) Right lateral view of specimen UBGD30555a; (4-6) Right lateral  
1550 view of specimen UBGD30558; (7-8) Left lateral view of specimen UBGD30553a. (1, 4, 7)  
1551 Line drawings; (2, 5, 8) Under UV illumination; (3, 6, 9) Under natural illumination.  
1552 Abbreviations: a - branchiocardiac groove; b<sub>1</sub> - hepatic groove; e<sub>1e</sub> - cervical groove; eskt -  
1553 endophragmal skeleton; hs - hepatic spine; on - optical notch; P - pereiopod; pl - pleopod; prs -  
1554 postrostral spine; ps - postorbital spine; r - rostrum; s - pleonal somite; t - telson. The beige  
1555 colour corresponds to digestive track traces. Scale is 1 cm.

1556

1557 **Figure 3:** *Aeger* sp. specimen UBGD294002. (1) Line drawing; (2) Under UV illumination; (3)  
1558 Under natural illumination; Abbreviations: a1 - antennula; a2 - antenna; on - optical notch; P -  
1559 pereiopod; pts - pterygostomial spine; r - rostrum; sc - scaphocerite; sp - subrostral spine. Scale  
1560 is 1 cm.

1561

1562 **Figure 4:** *Anisaeger longirostrus* n. sp. (1-3) Right lateral view of holotype, specimen  
1563 UBGD294000; (4-6) Left lateral view of specimen UBGD30559; (7-10) Dorsal view of

1564 paratype, specimen UBGD294001. (1, 4, 7) Line drawings ;(2, 5, 10) Under UV illumination;  
1565 (3, 6, 8, 9) Under natural illumination. Abbreviations: a - branchiocardiac groove; a2 - antenna;  
1566 as - antennal spine; bp - basipodite; di - diaeresis; e<sub>1</sub>e - cervical groove; en - endopodite; eskt -  
1567 endophragmal skeleton; ex - exopodite; hs - hepatic spine; mxp3 - third maxilliped; P -  
1568 pereiopod; pl - pleopod; ps - postorbital spine; r - rostrum; s - pleonal somite; sc - scaphocerite;  
1569 t - telson. Scale is 1 cm.

1570

1571 **Figure 5:** *Anisaeger longirostrus* n. sp. (1-3) Dorso-right lateral view of paratype, specimen  
1572 UBGD294004; (4-6) Left lateral view of specimen UBGD30553b; (7, 8) Left lateral view of  
1573 specimen UBGD294005c; (9-11) Right lateral view of paratype, specimen UBGD33022BIS.  
1574 (1, 4, 8, 9) Line drawings; (2, 5, 7, 10) Under UV illumination; (3, 6, 11) Under natural  
1575 illumination. Abbreviations: a - branchiocardiac groove; a1 - antennula; a2 - antenna; as -  
1576 antennal spine; crp - carpocerite; bas - basicerite; bp - basipodite; di - diaeresis; e<sub>1</sub>e - cervical  
1577 groove; eskt - endophragmal skeleton; hs - hepatic spine; mxp3 - third maxilliped; P -  
1578 pereiopod; pl - pleopod; ps - postorbital spine; r - rostrum; s - pleonal somite; sc - scaphocerite;  
1579 t - telson. Scale is 1 cm.

1580

1581 **Figure 6:** *Anisaeger longirostrus* n. sp. (1-3) Left lateral view of specimen UBGD294005a; (4-  
1582 6) Left lateral view of specimen UBGD294005b. (7-9) left lateral view of specimen  
1583 UBGD30555b; (10) Mirrored counter-impression of UBGD30555b. (1, 4, 7) Line drawings;  
1584 (2, 5, 9, 10) Under UV illumination; (3, 6, 8) Under natural illumination. Abbreviations: a -  
1585 branchiocardiac groove; as - antennal spine; bp - basipodite; di - diaeresis; en - endopodite; ex  
1586 - exopodite; P - pereiopod; pl - pleopod; r - rostrum; s - pleonal somite; sto - stomach traces; t  
1587 - telson. The beige colour corresponds to digestive track traces. Scale is 1 cm.

1588

1589 **Figure 7:** *Litogaster turnbullensis* Schram, 1971. Left lateral view of an exuvia, specimen  
1590 UBGD30557. (1) Line drawing; (2) Under natural illumination; (3) Under UV illumination.  
1591 Abbreviations: a - branchiocardiac groove; a2 - antenna; b - antennal groove; b<sub>1</sub> - hepatic  
1592 groove; c - postcervical groove; cd - cardiac groove; d - gastro-orbital carina; e<sub>1e</sub> - cervical  
1593 groove; i - inferior groove; mxp3 - third maxilliped; oc - orbital carina; P - pereopod; s - pleonal  
1594 somite; t - telson. Scale is 1 cm.

1595  
1596 **Figure 8:** *Litogaster turnbullensis* Schram, 1971. (1, 2) Dorsal view of UBGD30560; (3) Dorsal  
1597 view of specimen UBGD30548. (1, 3) Under natural illumination. (2) Under UV illumination.  
1598 Scale is 1 cm.

1599  
1600 **Figure 9:** *Pemphix krumenackeri* n. sp. Dorsal view of holotype, specimen UBGD294009. (1)  
1601 Line drawing (by Julien Devillez & Sylvain Charbonnier); (2) Under natural illumination; (3)  
1602 Under UV illumination. Abbreviations: a - branchiocardiac groove; b - antennal groove; b<sub>1</sub> -  
1603 hepatic groove; c - postcervical groove; cd - cardiac groove; di - diaeresis; en - endopodite; ex  
1604 - exopodite; r – rostrum; s - pleonal somite; t - telson. Scale is 1 cm.

1605  
1606 **Figure 10:** Triassic decapod diversity trends based on the newly compiled dataset. (1, 2)  
1607 Taxonomic richness; (3, 4) Number of sites from which Triassic decapods have been reported;  
1608 (5, 6) Mean of observed alpha diversity. (1, 3, 5) Per epoch; (2, 4, 6) Per stage.

1609  
1610 **Figure 11:** Updated stratigraphic ranges of the decapods studied here.

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1612  
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1614 **Tables**

1615

1616 **Table 1:** Measurements (in mm) of specimens of *Aeger* sp. When both left and right appendages  
1617 were measurable, both measures are given.

1618

1619 **Table 2:** Measurements (in mm) of specimens of *Anisaeger longirostrus* n. sp. When both left  
1620 and right appendages were measurable, both measures are given.

1621

1622 **Table 3:** Measurements (in mm) of specimens of *Litogaster turnbullensis*. When both left and  
1623 right appendages were measurable, both measures are given.

1624

1625 **Table 4:** Measurements (in mm) of specimens of *Pemphix krumenackeri* n. sp.. When both left  
1626 and right appendages were measurable, both measures are given.

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1628 **Table 5:** List of all valid Triassic decapod taxa known to date and their respective stratigraphic  
1629 range per series and stage. Classification is based on Schweitzer et al. (2010), Karasawa et al.  
1630 (2013), Devillez et al. (2019) and Audo et al. (2021).

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1639 **Supplementary Data**

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1641 **Supplementary file 1:** *Distaeger prodigosus* Schweitzer et al., 2014. (1) Right lateral view of  
1642 holotype, LPI-41666A. (2) Clos-up view of holotype first pereopod. (3) Line drawing of  
1643 holotype first pereopod. Abbreviations: c - carpus; da - dactilus; m - merus; P - pereopod; pr  
1644 - propodus. Scale is 1 cm.

1645

1646 **Supplementary file 2:** *Anisaeger atavus* (Bill, 1914) illustrated in Gall (1971). (1)  
1647 Reconstitution by Gall (1971). (2) Ventral view of the neotype designated by Gall (1971), Grès  
1648 à meules, Vilsberg, PEN 1. (2) Dorsal view of the specimen PEN 3 from the Grès à meules,  
1649 Vilsberg. (3) Dorsal view of the specimen PEN 2 from the Grès à meules, Bust.

1650

1651 **Supplementary file 3:** Compiled dataset of all known Triassic decapods.

1652

1653 **Supplementary file 4:** Paleobiology Database (PBDB) raw data downloaded on June 18th,  
1654 2021 using as search words: “Decapoda” and “Triassic”.

1655

1656 **Supplementary file 5:** List of Triassic decapods according to the Paleobiology Database  
1657 (PBDB; search “Decapoda, Triassic”, downloaded on June 18<sup>th</sup>, 2021) and associated summary  
1658 of the accuracy of each reported taxon. Duplicate of taxa reported from the same age and site  
1659 were dismissed. For each taxon, the epoch and/or stage, as well as the number of distinct  
1660 formations from which it was reported in the PBDB are also specified. When the misreport is  
1661 only minor (*i.e.*, it does not impact diversity estimates), the report is considered as valid.

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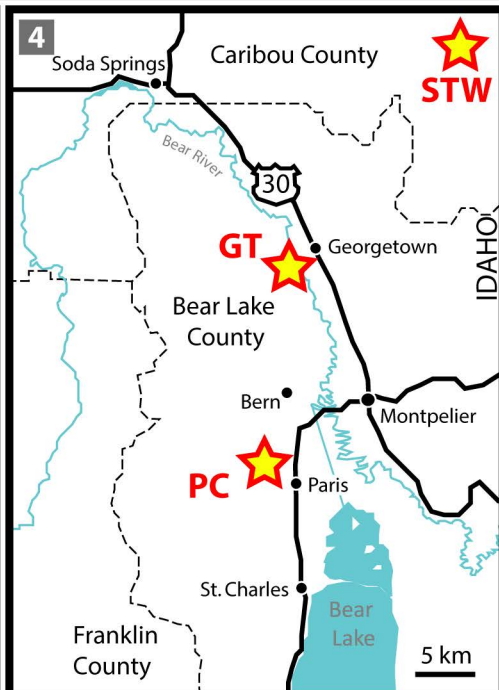
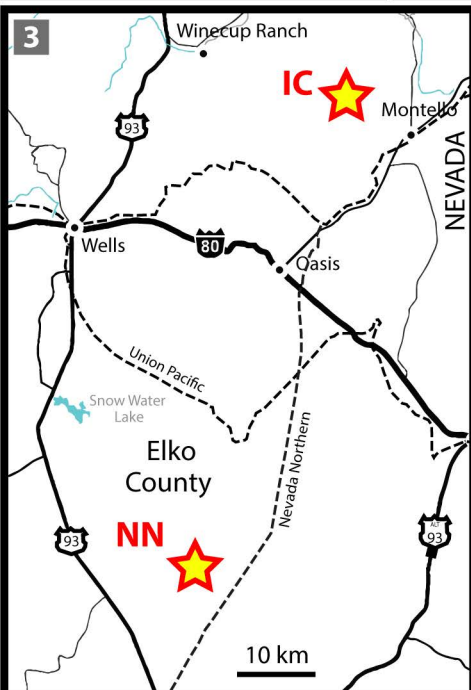
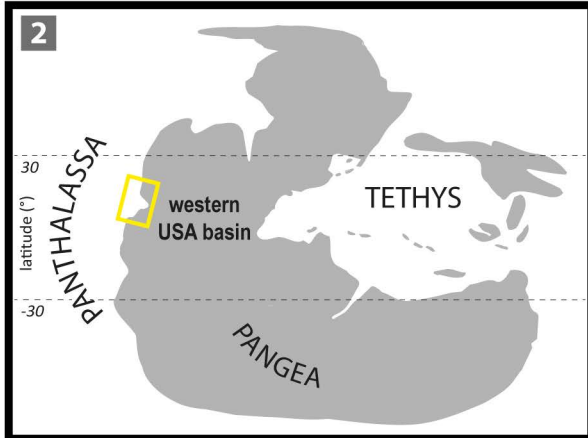
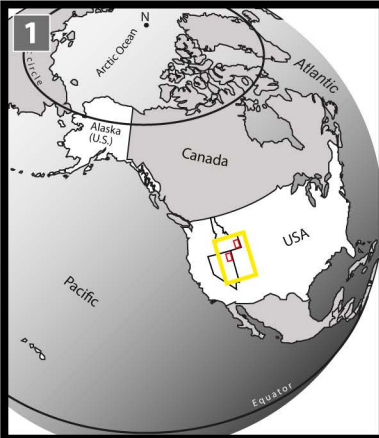


1663 **Supplementary file 6:** Summary of the Triassic decapods from the newly compiled dataset that  
1664 are also reported in the PBDB dataset. The taxa for which a new combination is proposed in  
1665 this work are indicated by a "\*".

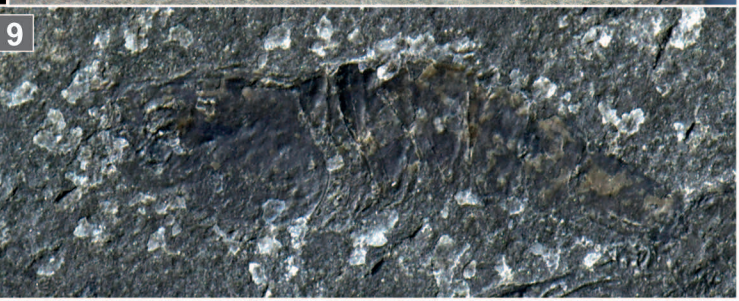
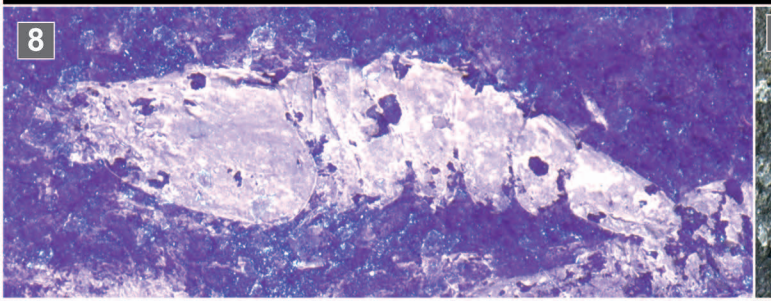
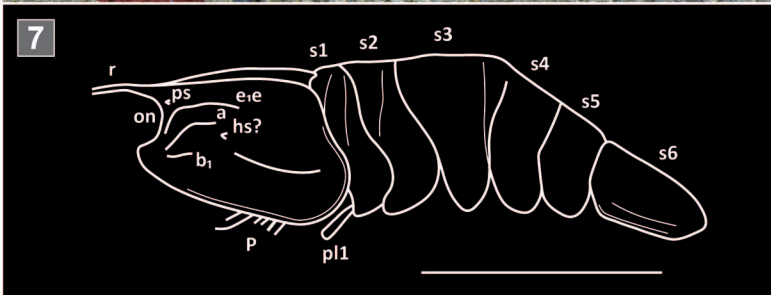
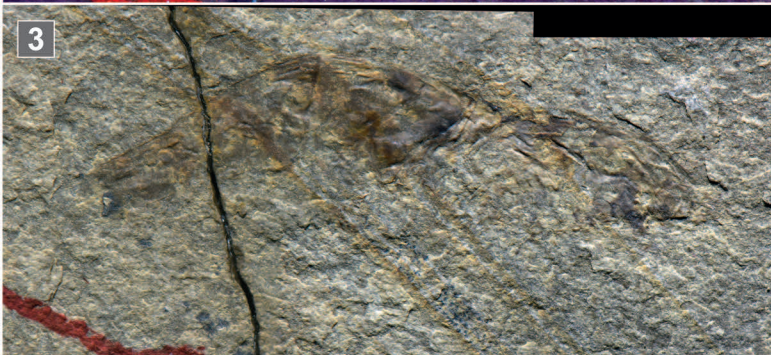
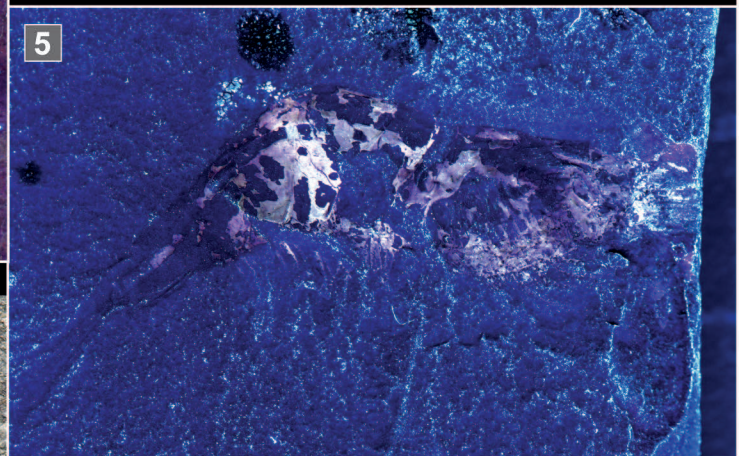
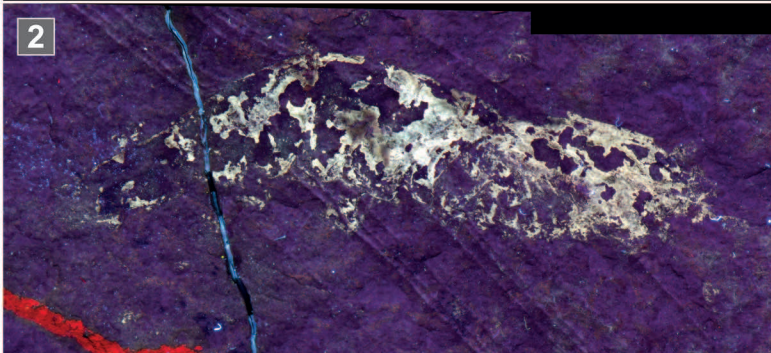
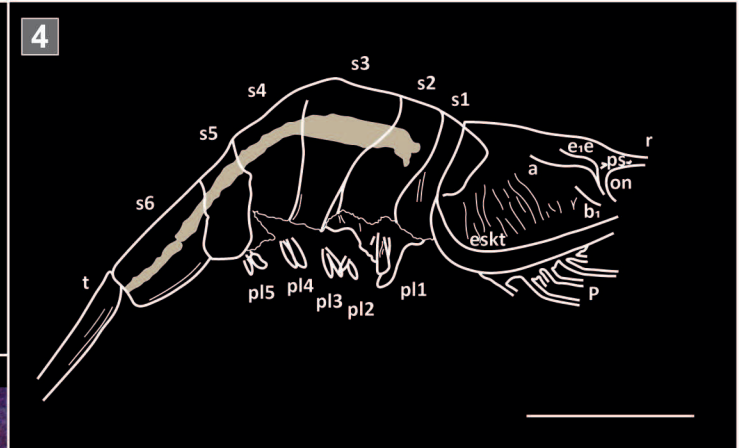
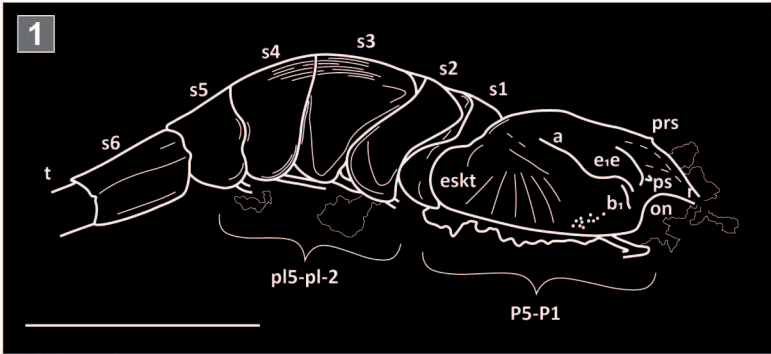
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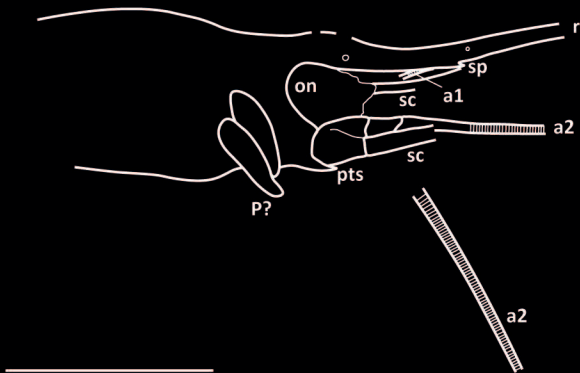




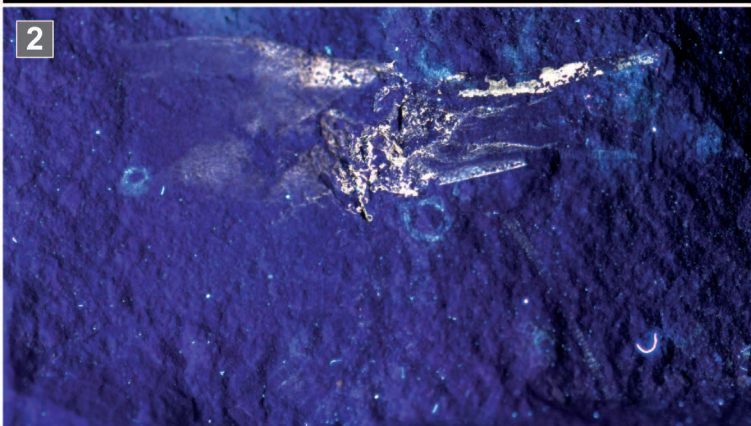




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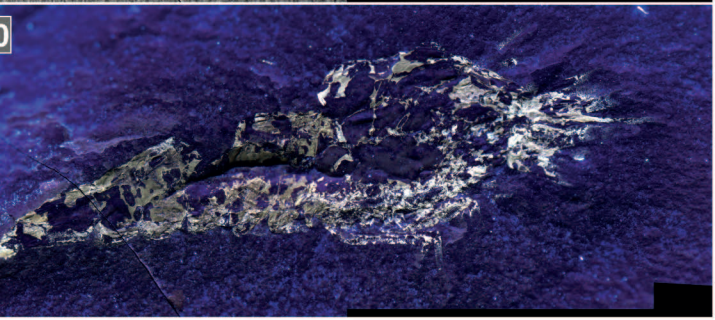
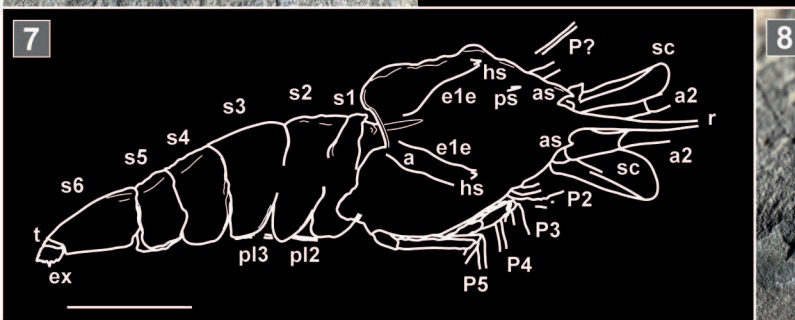
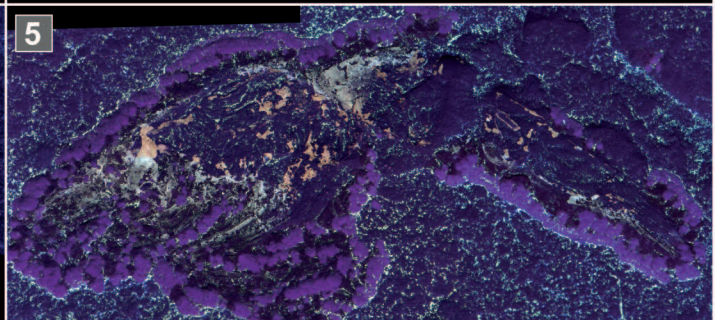
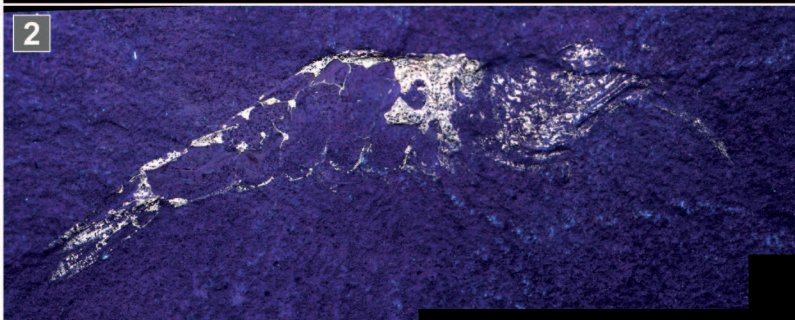
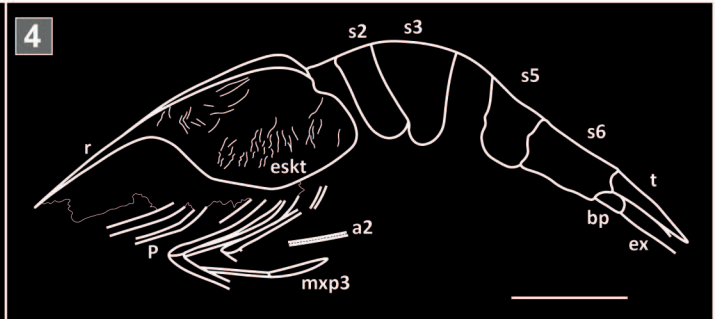
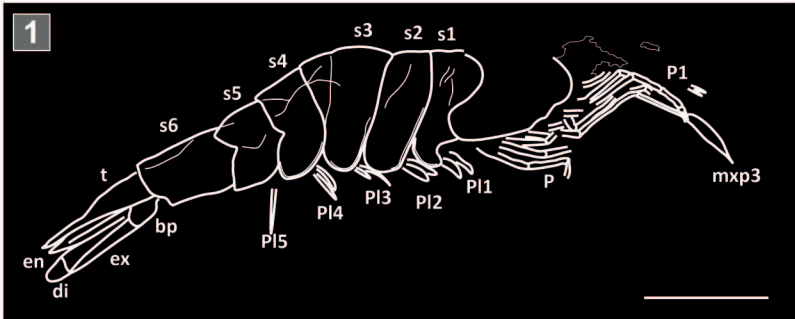
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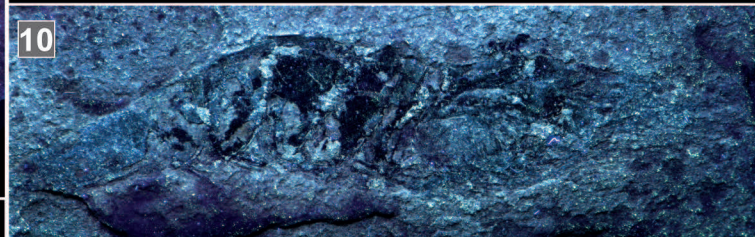
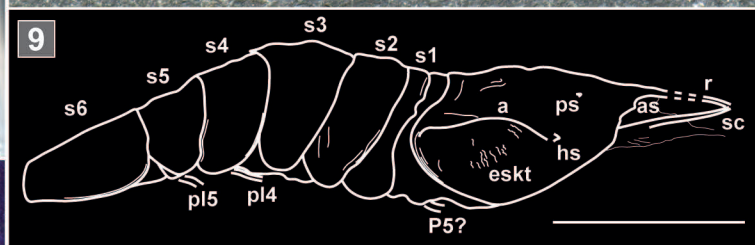
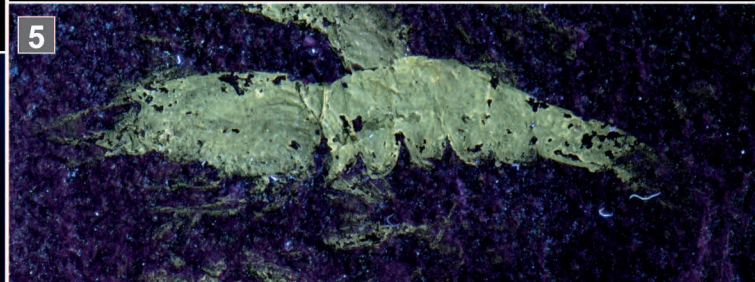
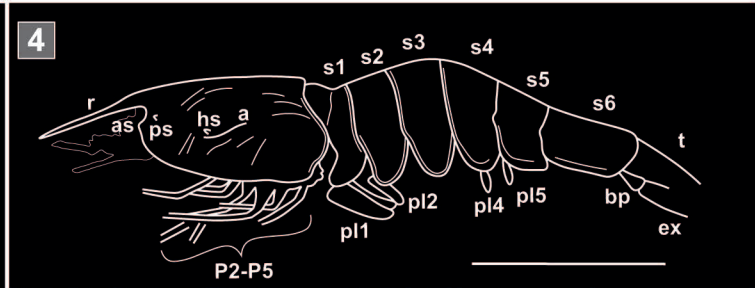
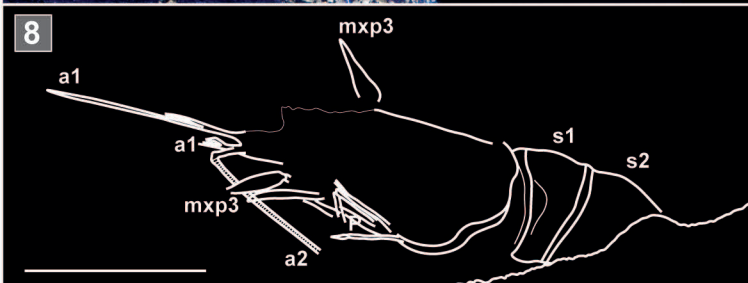
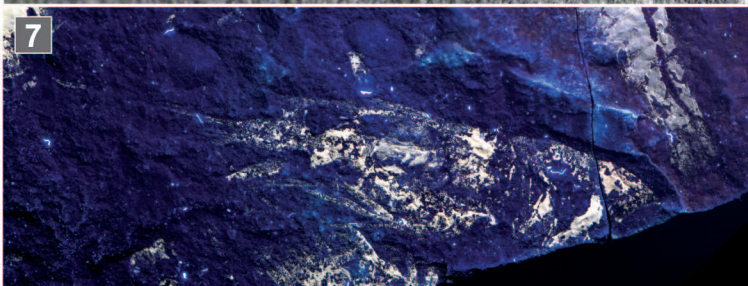
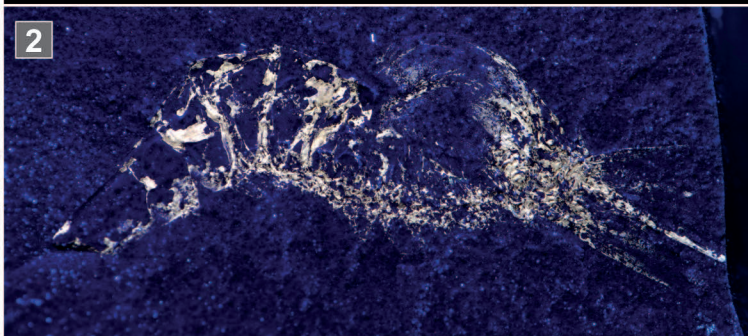
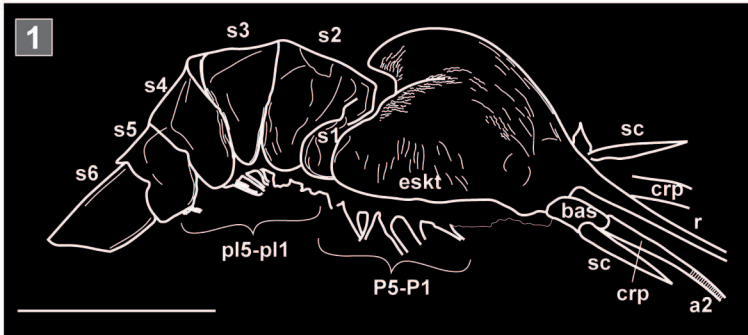
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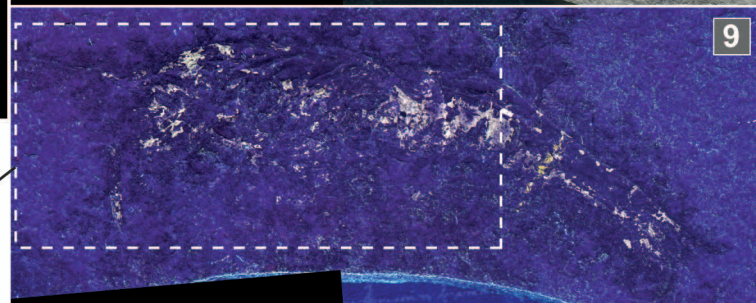
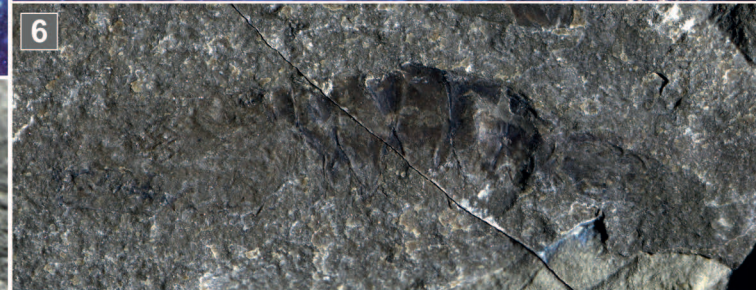
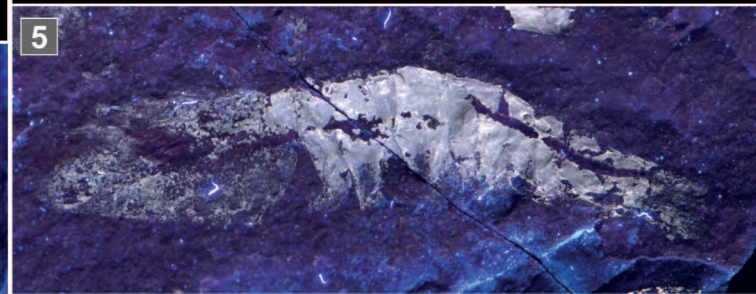
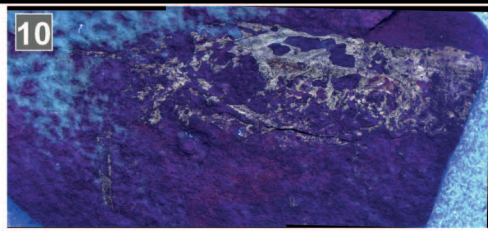
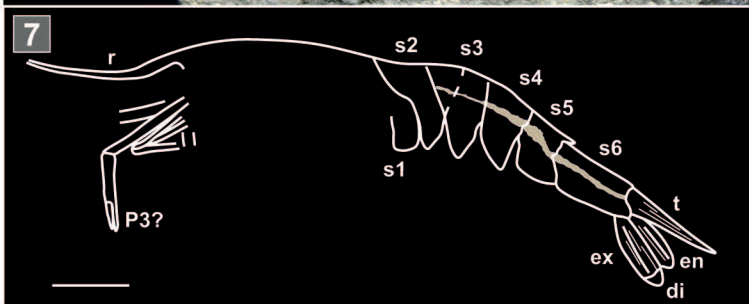
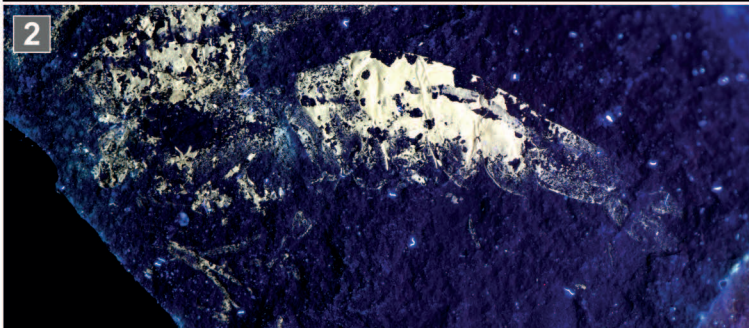
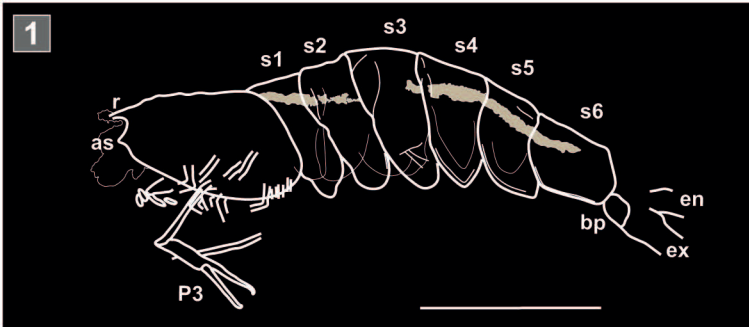














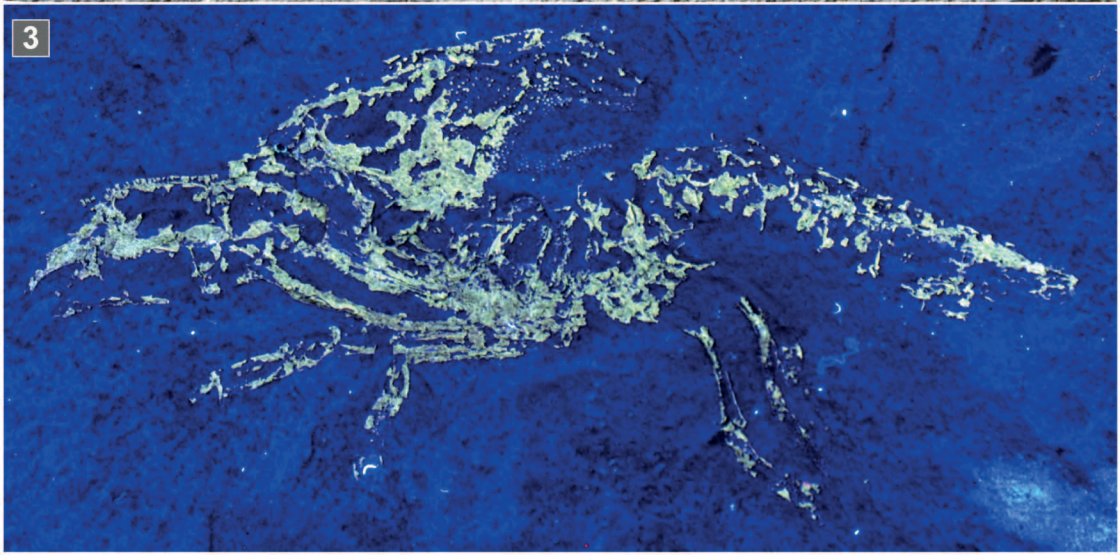
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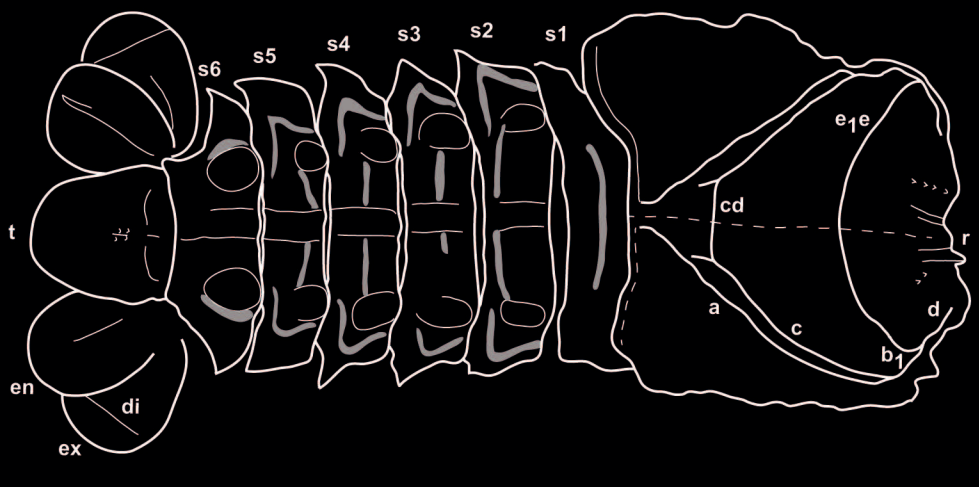




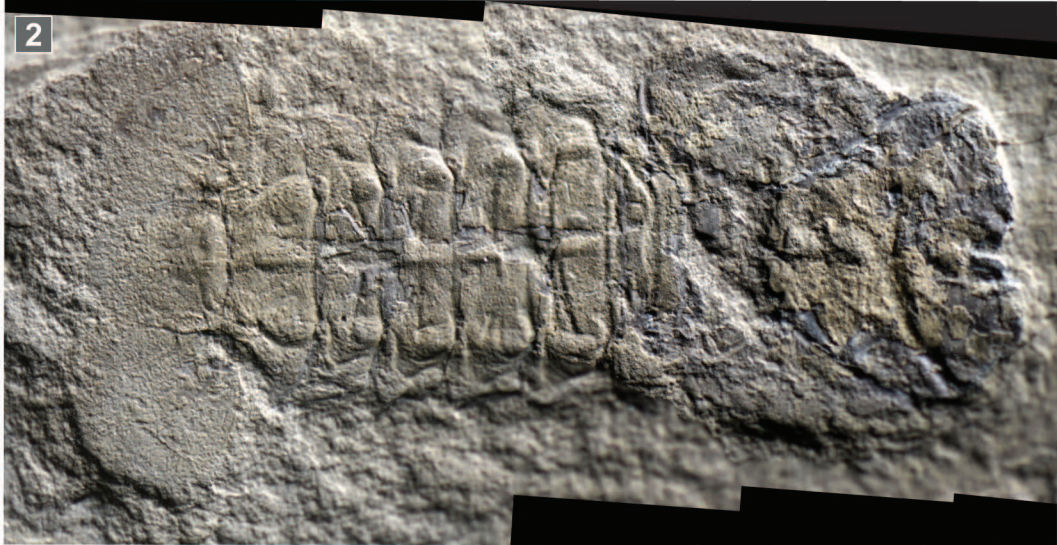




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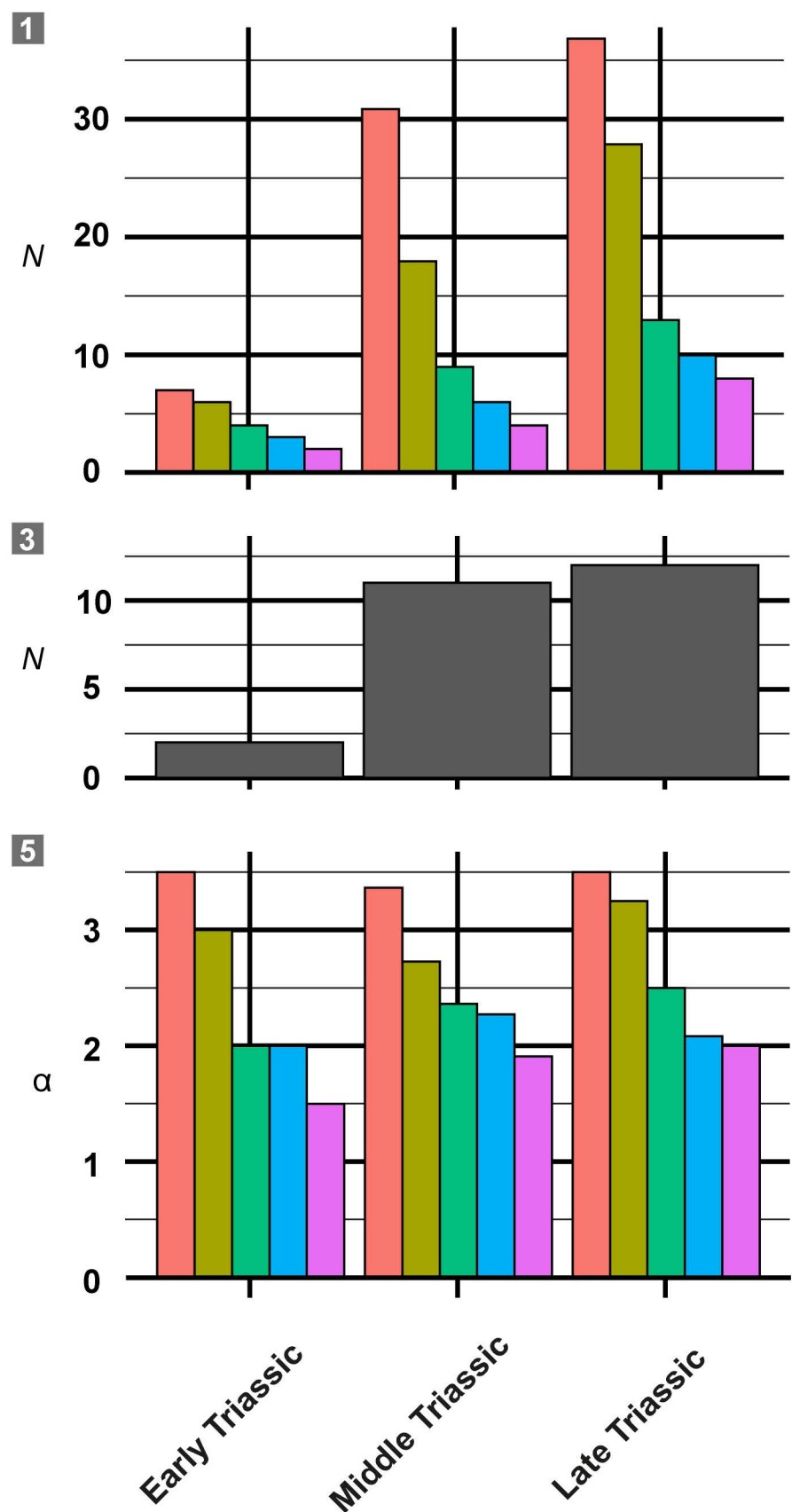
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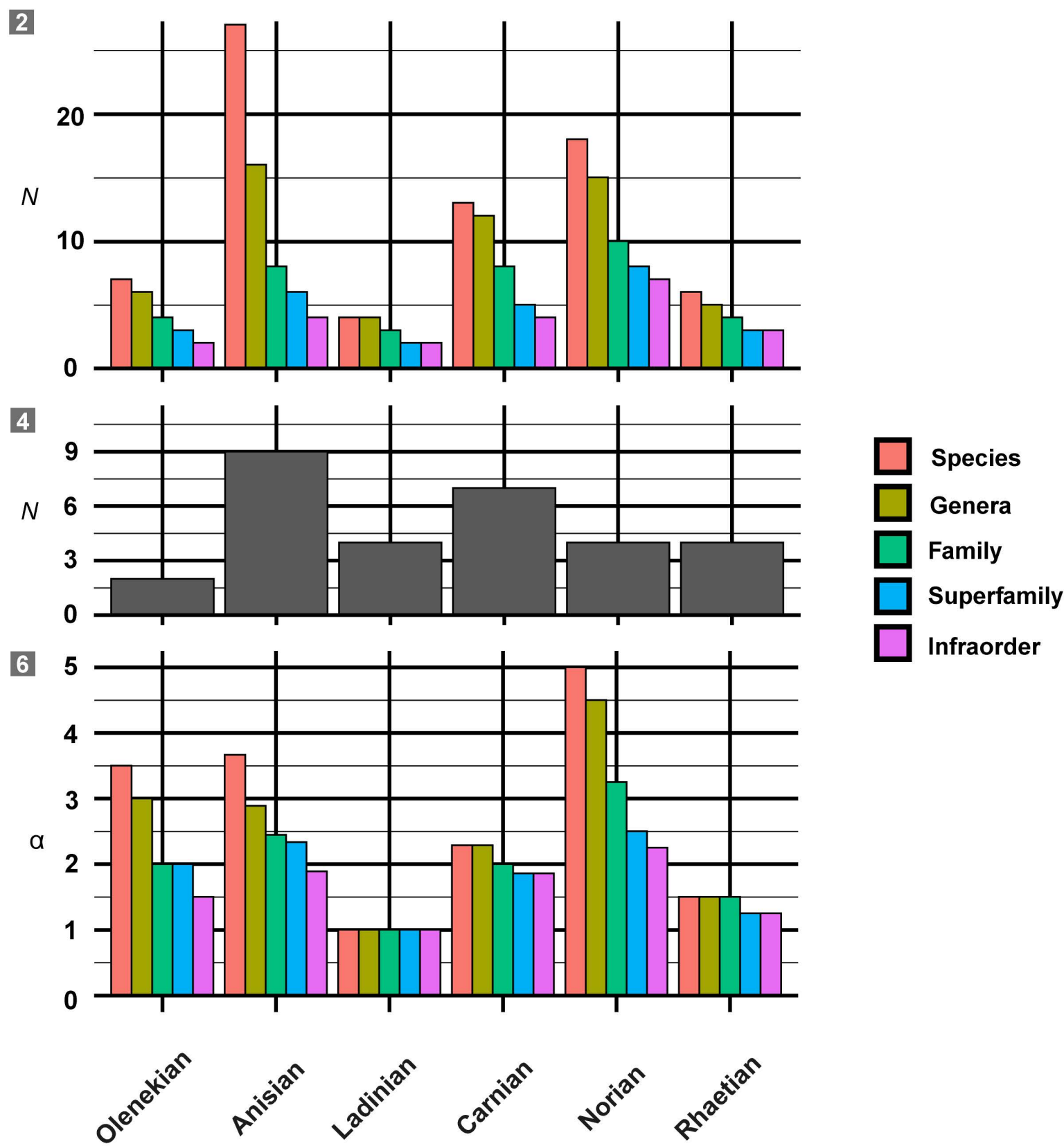
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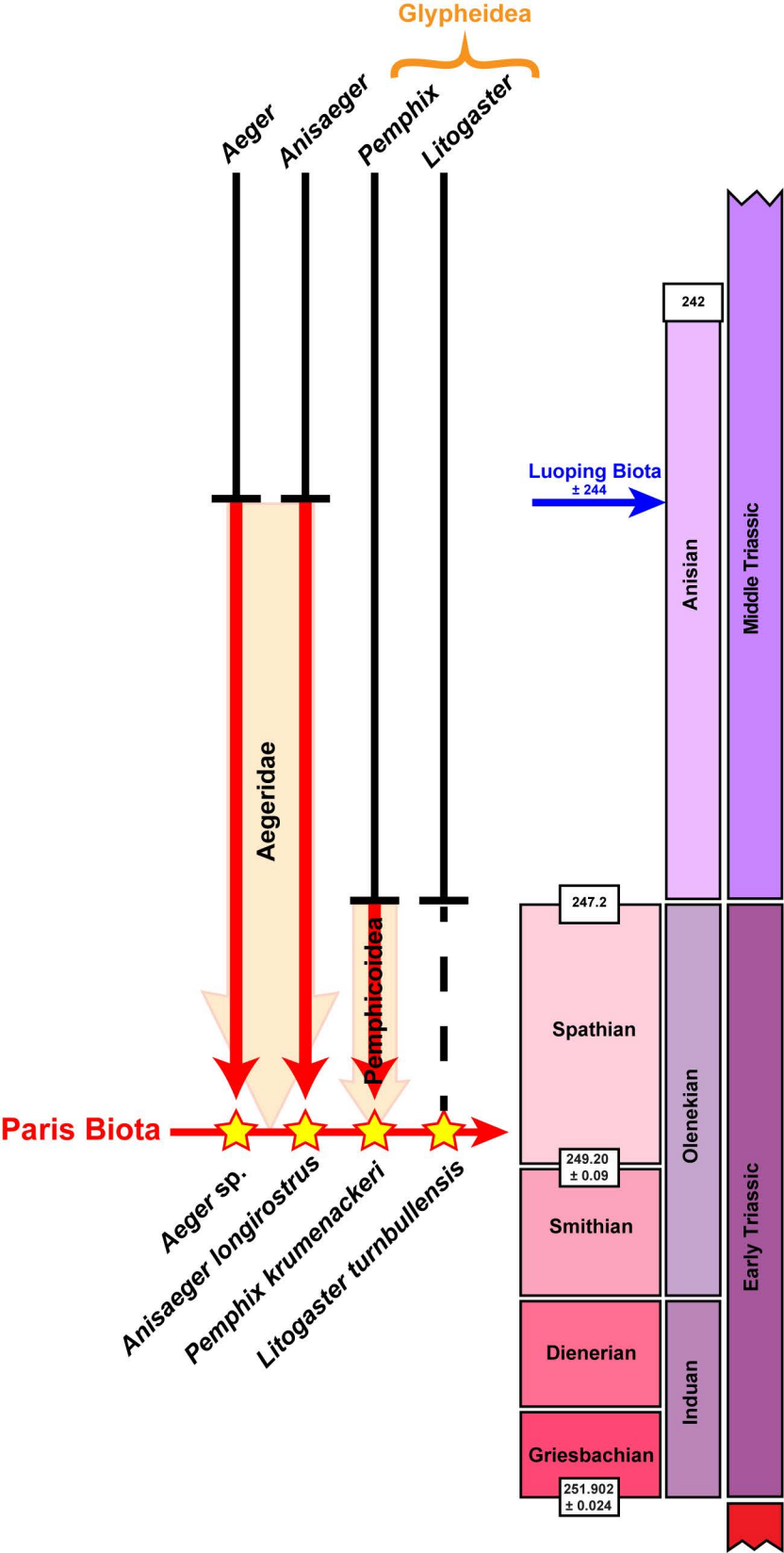


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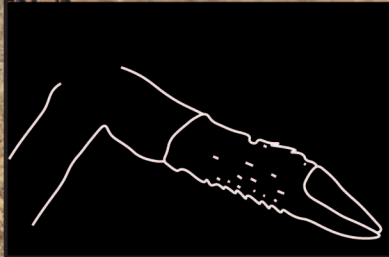
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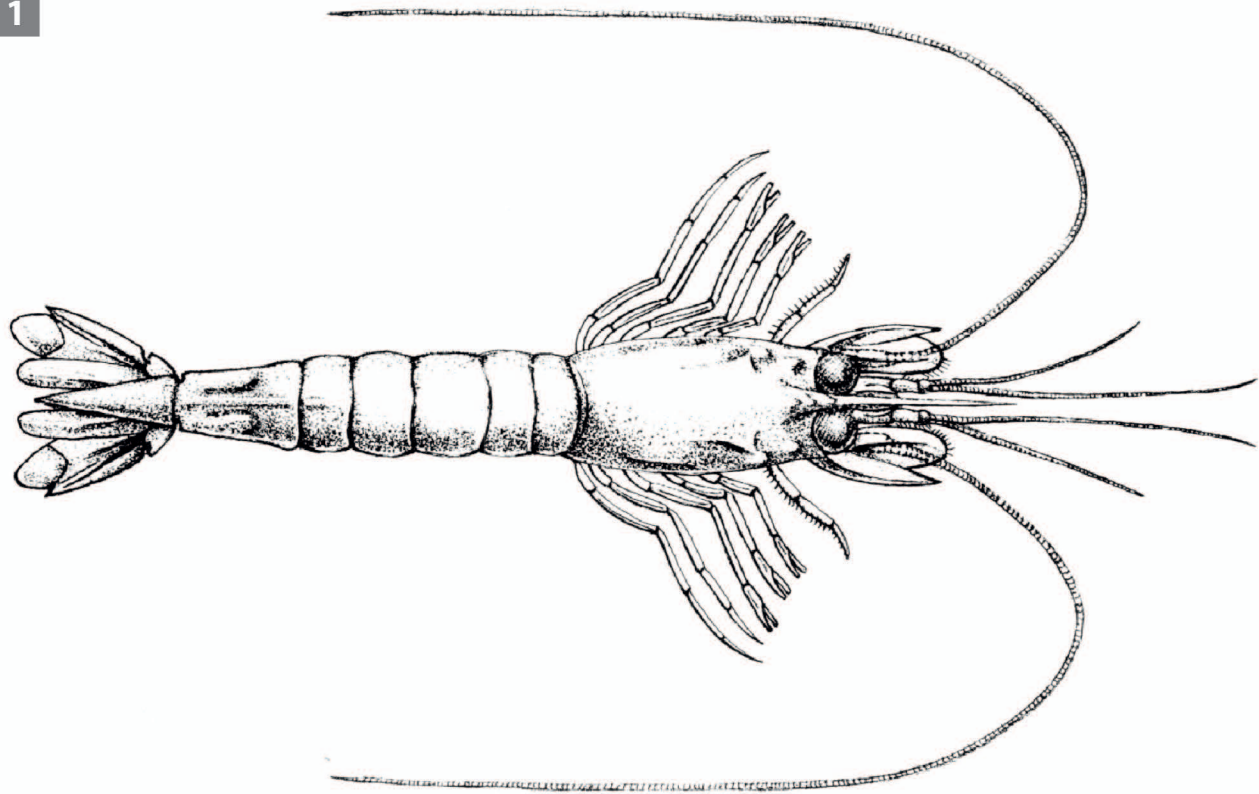




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