

# The Paris Biota decapod (Arthropoda) fauna and the diversity of Triassic decapods

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Christopher Smith, Sylvain Charbonnier, James Jenks, Kevin Bylund, Gilles Escarguel, et al.. The Paris Biota decapod (Arthropoda) fauna and the diversity of Triassic decapods. Journal of Paleontology, 2022, pp.1-29. 10.1017/jpa.2022.34. mnhn-03812429

# HAL Id: mnhn-03812429 https://mnhn.hal.science/mnhn-03812429

Submitted on 30 Oct 2023

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

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

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

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#### 37 Introduction

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

2019; Leu et al., 2019). The Paris Biota offers a unique opportunity to study one of the most 50 51 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 52 is composed of a mixture of long-term survivors and newly-evolved taxa. It comprises almost 53 all the clades of the Modern evolutionary fauna. It yielded algae, sponges (Botting and Brayard, 54 2019), brachiopods, bivalves, echinoderms (Saucède et al., 2019; Thuy et al., 2019), 55 cephalopods (Doguzhaeva et al., 2018; Brayard et al., 2019), vertebrate remains and coprolites 56 (Romano et al., 2019), and arthropods (Lerner et al., 2017; Charbonnier and Brayard, 2019; 57 Laville et al., 2021). Among arthropods, many well-preserved decapods (an order of 58 crustaceans characterized, among others, by the presence of 5 pairs of walking appendages), 59 were uncovered. This is of major importance as they represent some of the earliest 60 representatives of their order. 61

62 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 63 southcentral Oklahoma, USA, and which is the only known Paleozoic Dendobranchiata 64 (Feldmann and Schweitzer, 2010); (ii) Palaeopalaemon newberryi (Whitfield, 1880), also from 65 the late Devonian of northeast Ohio, South New York state, central Kentucky and southeast 66 Iowa, USA and that corresponds to the oldest Pleocyemata documented (Schram et al., 1978); 67 and (iii) Eryma antiquum (Birshtein, 1958), from the Late Permian of Ukhta region, Siberia 68 (Schram, 1980), which is the oldest Erymidae reported, but whose systematic position above 69 the superfamily rank remains uncertain (Devillez and Charbonnier, 2017). The Early Triassic 70 71 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 72 Litogaster turnbullensis, and the poorly age-constrained Dienerian-Smithian decapod-rich 73 fossil sites from the Ambilobé region, NW Madagascar (Besairie, 1932; Marramà et al., 2017; 74

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

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

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### 95 Geological setting

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

(Paris Canyon, Stewart Canyon and Georgetown) are located in southeastern Idaho. At each 100 101 site, fossils were collected from exposures of the Lower Triassic Thaynes Group (sensu Lucas et al., 2007) that is mainly characterized by alternating limestones and shales of Smithian-102 103 Spathian age which corresponds to relatively shallow, epicontinental marine depositional environments (e.g., Caravaca et al., 2018). During the Early Triassic, the western USA Basin 104 was located at a near-equatorial latitude on the western margin of the Pangea *i.e.*, the eastern 105 106 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 southeastern Idaho by Guex et al. (2010), Jenks et al. (2013) and Brayard et al. (2019). With 108 109 the exception of those of the Immigrant Canyon site (Smith et al., 2021), all decapod specimens were collected from early Spathian beds, corresponding to the Bajarunia-Tirolites-Albanites 110 111 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 (Smith et al., 2021). 113

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#### 115 Material and methods

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

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

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

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

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141 Systematic paleontology

143	Phylum ARTHROPODA Latreille, 1829
144	Subphylum CRUSTACEA Brünnich, 1772
145	<b>Class</b> MALACOSTRACA Latreille, 1802
146	Subclass EUMALACOSTRACA Grobben, 1892
147	Superorder EUCARIDA Calman, 1904
148	Order DECAPODA Latreille, 1802

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#### Suborder DENDROBRANCHIATA Spence Bate, 1888 150 **Superfamily** PENAEOIDEA Rafinesque, 1815 Family AEGERIDAE Burkenroad, 1963 151

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

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

Remarks.—The Aegeridae family was erected by Burkenroad (1963) and initially only included 167 Aeger and Acanthochirana. Nonetheless, until Schweigert (2001) revised Aeger tipularius 168 (Schlotheim, 1822), the type species of Aeger, and assigned it to Aegeridae, most authors 169 continued to assign Acanthochirana and Aeger to Penaeidae (e.g., Förster, 1967; Glaessner, 170 1969; Förster and Crane, 1984; Garassino and Teruzzi, 1990). A few years later, Feldmann et 171 172 al. (2007) also confirmed the placement of *Acanthochirana* within Aegeridae as previously suggested by Etter (2004). Finally, Schweitzer et al. (2014) added the genera *Anisaeger* and *Distaeger* to Aegeridae.

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

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

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#### Genus ACANTHOCHIRANA Strand, 1928

195 1862 Acanthochirus Oppel, p. 97-98.

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

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

Other species.—Triassic: Acanthochirana norica (Pinna, 1974) n. comb; Acanthochirana
spinifera (Schweitzer et al., 2014) n. comb.; Acanthochirana triassica Garassino, 2013. PostTriassic : Acanthochirana angulata Oppel, 1862; Acanthochirana cordata (Münster, 1839)
(junior synonym: Acanthochirus longipes Oppel, 1862); Acanthochirana krausei (Förster,
1967b); Acanthochirana liburiaensis Garassino, Audo, Charbonnier & Schweigert in Bravi et
al., 2014; Acanthochirana smithwoodwardi (Van Straelen, 1940) (junior synonym:
Acanthochirus cenomanicus Glaessner, 1945).

*Emended diagnosis by Charbonnier et al. (2017).*—Rostral carina with spines pointing forward; smooth rostrum, spineless; one epigastric spine in the third anterior of dorsal margin; weak cervical groove, not joined to dorsal margin; oblique branchiocardiac groove joined to hepatic groove at level of strong hepatic spine; short hepatic groove backward directed; cephalic region with postorbital spine; hypertrophied Mxp3 with rows of movable spines; branch-like Mxp3 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, a hypertrophied Mxp3 with rows of movable spines, and chelate P1-P3. Additionally, 214 215 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. Acanthochirana can be distinguished from other Aegeridae based on its characteristic rostrum, 217 usually moderately long, that presents multiple basal dorsal teeth. This genus also exhibits a 218 distinctive spinose Mxp3 that is hypertrophied, but just moderately longer than the pereiopods, 219 and with a branch-like dactylus, unlike that of Aeger that is considerably longer than the 220 221 pereiopods, or that of Anisaeger that has an acuminate (brush tip shaped) dactylus and that is not (or only very thinly) setose. When identifiable, *Acanthochirana* carapace grooves are alsodiscriminant.

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- 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.

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Holotype.—Almost complete individual (n° 3380) from the Zambelli Rocco collection
reposited at the Museo civico di Scienze Naturali di Bergamo, Italy. The specimen was collected
near the village of Cene (Val Seriana, Bergamo, Italy) in the Norian Zorzino Limestone
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 suprarostral teeth and no infrarostral teeth; an antennal angle rather acute bearing an antennal spine; the presence of 238 supraorbital and hepatic spines; a gastro-frontal groove from which a gastro-orbital groove 239 departs dorsoventrally towards the hepatic spine; and an hepatic groove under the hepatic spine 240 and that bends forward and downwards towards the pterygostomial angle; antennae very robust; 241 antennal flagella very long; scaphocerite well developed; Mxp3 well developed with propodus, 242 carpus and merus carrying two rows of dense and robust spines along their anterior and 243 posterior margin; P1-P3 chelate; P4-P5 achelate; s1-s3 increasing in length with rounded pleura; 244 245 s4-s5 axially keeled; s6 elongated, longer than high; pl1-pl5 of considerable size; pl1 often transformed in petasma; pl2-pl5 composed of subrectangular basipodite which bear two very 246

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

# *Emended diagnosis by Pinna (1976; translated from Italian; partial modification of his original diagnosis following the discovery of additional better preserved specimens).*—The posterior margin of the carapace is slightly more sinuous than previously reconstructed as the lower part projects backwards in a more markedly way; the rostrum also possesses a series of suprarostral teeth arranged along the entire central portion of the rostrum, and a well-developed infrarostral tooth in the apical position, additionally to the two proximal suprarostral teeth previously 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 from the Norian (Upper Triassic) of Cene (Lombardy, Italy). The author provided a thorough 257 study including a full description of the holotype, a reconstruction of the species, and a 258 259 discussion on its ontogenetic variations and its exuvia. Later, Pinna (1976) described 34 specimens from the Norian (Upper Triassic) of Valvestino, a neighbouring locality in 260 261 Lombardy. Despite the presence of new characters (i.e., posterior margin of the carapace 262 slightly more sinuous; additional suprarostral teeth and a well-developed infrarostal teeth; uropodal exopod much longer than endopod; uropodal exopod with diaeresis), he ascribed these 263 specimens to Antrimpos noricus, considering that observed differences between the Cene and 264 265 the Valvestino specimens were of taphonomic origin, the Valvestino specimens being better preserved. Garassino et al. (1996) later described nine specimens from Rio Seazza (Preone, 266 Italy), one specimen from Caprizzi (Socchieve, Italy), and one specimen from Forni di Sopra 267 (Udine, Italy), all Norian in age. Based on the similarities between these specimens and the 268 specimens from Valvestino, they ascribed them to Antrimpos noricus. However, they raised the 269 270 hypothesis of the existence of two distinct taxa. Unfortunately, the illustrations provided by Pinna (1974, 1976) and Garassino et al. (1996) are not sufficient to clarify this matter. However, 271

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

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

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

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

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

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

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

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

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

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#### Genus AEGER Münster, 1839

317 1839 Aeger Münster, p. 64-65.

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

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

330 Emended diagnosis by Charbonnier et al. (2017).-Rostrum with one infrarostral spine; cervical groove steeply inclined, not joined to the dorsal margin, joined to antennal groove; 331 oblique and sinuous branchiocardiac groove, crossing all the carapace from the posterior margin 332 333 to the hepatic region; convex hepatic groove joined anteriorly to cervical groove and posteriorly to branchiocardiac groove; short inferior groove backward directed, not joined to ventral 334 335 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 exopod with diaeresis. 337

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

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344

Aeger sp.

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Figures 2-3

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

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

348

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

361 Pleon.—s1-s6 smooth. s1-s3 roughly the same height although gradually longer posteriorly. s1s2 with sinuous posterior margins and s2 also with a sinuous anterior margin. Tergopleuron of 362 363 s2 slightly front-turned. s3 is the highest and longest somite and is subtriangular with a rounded termination. s4-s5 suboval with a rounded termination, higher than long, and of the same length 364 although s4 is higher than s5. s4-s5 anterior margin slightly convex with posterior margin 365 366 slightly concave and presenting an axial notch. s6 elongated, longer than high, subrectancular and axially keeled. s6 ventral margin thinly rimed. Telson badly preserved in all studied 367 specimens. 368

369 Cephalic appendages.—Antennular peduncle barely perceptible and only a small piece of thin370 antennular flagellum identified. Antenna with rather long peduncle composed of three segments

371 increasingly thinner and longer distally. Antennal flagellum multi-articulated, incomplete but

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

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)

exhibit remains of the digestive track throughout the pleon. The intestine extends parallel to the

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

Paris Canyon, Idaho, USA (early Spathian, Early Triassic); UBGD33011BIS [not
"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.

*Remarks.*—The large majority of the sampled specimens are small (2-3 cm), rather stocky and occur in mass (over 30 specimens on a 35cm x 35 cm slab). They present cephalic structures diagnostic of *Aeger* (*e.g.*, cervical groove steeply inclined, not joined to the dorsal margin, joined to antennal groove that in our specimens is most probably mingled with the anterior section of the branchiocardiac groove; oblique and sinuous branchiocardiac groove; hepatic groove; postorbital spine). Unfortunately, the lack of complete rostrum and cephalothoracic appendages prevents identification at the species level.

One specimen (UBGD294002), much larger but poorly preserved, is also ascribed to *Aeger* sp. It consists of an isolated and incomplete carapace. Based on the preservation state of the posterior part of the carapace, this specimen probably corresponds to an exuvia. Nonetheless, the rostrum is partially preserved and appears to be elongated, granular and with only oneisolated infrarostral spine, which is reminiscent of the rostrum of *Aeger*.

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

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

Remarks.—The placement of Anisaeger within Aegeridae is based on the presence of a hepatic 430 spine, a long scaphocerite, a long antennal flagellum, well-developed third maxillipeds and 431 pereiopods, chelate pereiopods 1 to 3, and pleopods composed of two multi-articulated flagella 432 433 each. As mentioned previously, Anisaeger was erected based on An. brevirostrus (type species) and An. spiniferus. These two taxa are significantly different (e.g., respectively a short smooth 434 435 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 the same genus. An. spiniferus is assigned to Acanthochirana (see section on this genus), and 437 438 based on observations made on An. longirostrus nov. sp, and on An. brevirostrus, we provide herein a new diagnosis for Anisaeger. 439

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

446

447

448

Anisaeger atavus (Bill, 1914) new combination

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

Neotype.—Holotype destroyed. Neotype designated by Gall (1971): almost complete specimen 453 (PEN 1) from the Anisian Grès à meules Formation, France, and reposited in the Grauvogel-454 455 Gall collection at the Ecole et Observatoire des Sciences de la Terre, Strasbourg, France. Emended diagnosis by Gall (1971; translated from French).—Crustacean with a narrow and 456 elongated body, laterally compressed, generally fossilized in the dorso-ventral position. Thin 457 458 and smooth cephalothoracic carapace, bearing 3 pairs of short grooves (cervical, hepatic and branchiocardiac) and two pairs of spines in the anterior region. It is extended in front by a long 459 and pointed rostrum, adorned with a few dorsal teeth in the large specimens. Abdomen longer 460 than the cephalothorax, formed of 6 segments, the last of which is about twice as long as it is 461 height. Triangular telson, finished in a point. Short antennae formed by two unequal rami. 462 463 Antennae with a long multi-jointed whip and a broad scale with the outer edge differentiated into a thorn. Third maxilliped with stiff bristles. Slender and smooth thoracic legs, the first three 464 ending in a claw. Abdominal appendages unknown. Strongly chitinized uropods; the exopodite 465 is articulated. 466

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 pereiopods 1 to 3, and

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

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

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- 492

Anisaeger longirostrus new species

#### Figures 4-6

- 493 2017 Penaeoid shrimp Brayard et al., p. 4, fig. 6.C; fig. S20.A,E.
- 494

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

Type locality.—Paris Biota of Paris Canyon, southeastern Idaho and NoName, northeasternNevada, USA.

501 Type age.—Early Spathian, Early Triassic.

*Diagnosis.*—Carapace with a very long spineless rostrum; postorbital spine present; cervical groove inclined and terminated by an hepatic spine; long oblique branchiocardiac groove; well pronounced orbital notch; third maxilliped smooth and slightly longer than pereiopods; acuminate dactylus of third maxilliped; pereiopods 1–3 with moderate sized chelae; s1 narrower and shorter than s2, with a strong anteriorly incurved ventral termination; s3 higher than others 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 straight, and a rounded termination. s3 is higher and longer than the others, triangular, and overlapping s2. s4 is ovoid with a rounded end, about the same dimension as s2 with an anterior margin slightly convex and a posterior margin slightly concave with an axial notch. s5 is the smallest, slightly higher than long, with a convex anterior margin, a concave posterior margin also presenting an axial notch, and a rounded termination. s6 is elongated, longer than high, subrectancular. s5 and s6 show traces of an axial keel. Straight, triangular and elongated telson, 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.

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

Pleonal appendages.—Protopodite of pleopods moderately long, ovoid to slightly triangular, preserved in pairs. No remains of pleopod flagella. First pair of pleopods distinctively bigger than others in some specimens, potentially petasma. Rounded to subtriangular uropodal basipodite. Uropodal exopod and endopod ovoid with smooth lateral margins, and rounded 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 of545 longitudinal streaks. Uropodal exopod with diaeresis.

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

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

Sampled specimens are flattened but abundant, allowing to distinguish recurrent anatomical features from simple compression artefacts. These features are the inclined cervical groove, the long and oblique branchiocardiac groove, and the hepatic and postorbital spines. Hepatic and postorbital spines as well as a shallow cervical groove were also identified in *An*. *brevirostrus*, but no branchiocardiac carina were reported so far from the latter. However, this difference should be taken with caution as it may result from a taphonomic bias *i.e.*, the compression of the carapace may have erased some cephalic features. There are, however, other features differentiating the two species. The rostrum of *An. longirostrus* n. sp. is very long (table 2) whereas it is never much longer than the eyestalks in *An. brevirostrus*. *An brevirostrus* also exhibits setal pits on the third maxilliped whereas *An. longirostrus* n. sp. does not present any setose or spinose thoracic appendages, implying that if setose or spinose were present, they were very thin. Finally, the third maxilliped of *An. longirostrus* n. sp. is much slenderer than 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.

*Emended diagnosis by Glaessner (1930; translated in modern terms).*—Carapace and rostrum
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
- scaphocerite; third maxilliped with foliole-shaped dactylus; P1–P3 with elongate chelae; P3

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

Remarks.—Aeger crassipes was described based on four specimens from the Carnian Raibl 595 596 Formation, Italy (De Zanche et al., 2000). As specified by Bronn (1858), the specimens are poorly preserved, complicating their identification. None the less, he identified five pairs of 597 pereiopods and long antennae. Additionally, he also noticed a long third maxilliped that he 598 599 identified as a 6th pair of pereiopods. Based on the similarities of its overall shape, the antennae, 600 the thoracic appendages, and the uropods, Bronn (1858) assigned these specimens to Aeger. Finally, based on the rather robust P4 and P5 differing from those of other Aeger species that 601 602 are usually filiform, he erected Aeger crassipes. Later, Glaessner (1930) revised this species based on 23 specimens, also from the Raibl Formation, and among which six exhibited the 603 carapace and pleon, and three also presented pereiopods. He described a triangular foliole-604 605 shaped dactylus for the third maxillipeds that are long, and three anterior pairs of pereiopods that are chelate, the third pair of pereiopods being the longest. The apparent absence of traces 606 607 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 this species presents the general characteristics of Penaeoidea but not those of Aeger, and 609 finding more shared features with Antrimpos than with Aeger, Glaessner (1930) proposed the 610 new combination Antrimpos crassipes (Bronn, 1858). Schweitzer (2010) followed this opinion. 611 Nowadays however, Antrimpos is considered as a "wastebasket" taxon (e.g., Garassino and 612 Teruzzi, 1995; Garassino et al., 2013; Robalino et al., 2016). Finally, Hyžný and Garassino (in 613 press) restudied the original material of Bronn (1858) and Glaessner (1930). After not being 614 able to identify any important diagnostic character that would support an attribution to one of 615 616 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 other618 genera.

After examination of the illustrations in Bronn (1858) and Glaessner (1930), we identified the 619 620 presence of well-developed third maxillipeds, at least as long as the pereiopods, P1-P3 chelate with the third pair longer than the others, very long antennal flagellum, and pleopods with two 621 multi-articulated flagella each. These characters suggest that Antrimpos crassipes should be 622 reassigned to Aegeridae. Additionally, given the presence of a spineless rostrum, Mxp3 about 623 624 as long as the pereiopods that themselves are moderately long, the absence of traces of setose or spinose on the Mxp3 that are terminated by an acuminate dactylus, and the s1 narrower and 625 626 shorter than s2 with a strong anteriorly incurved ventral termination, we argue for an assignment to Anisaeger. Anisaeger crassipes (Bronn, 1858) n. comb. differs from Anisaeger brevispinus 627 by its long rostrum, and the seemingly smooth Mxp3. Anisaeger crassipes also shows relatively 628 629 robust thoracic appendages among which the P1-P3 are terminated by relatively big chelae, contrary to Anisaeger longirostrus n. sp. in which the thoracic appendages are rather slender 630 631 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:
641	ornata Meyer, 1851).

Litogaster

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

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

- 657
- Litogaster turnbullensis Schram, 1971 658 Figures 7-8 659 660 Litogaster turnbullensis Schram, p. 534-537, figs. 1-3. 1971 Litogaster turnbullensis Amati et al., p. 150, 155, fig. 2.2. 661 2004 662 2010 Schweitzer et al., p. 19. 663 2013 Karasawa et al., p. 79. Charbonnier et al., p. 229-230, figs. 495-496. 664 2013

*Type material.*—Holotype by monotypy (FMNH PE 16215) from the Early Triassic, Upper
Siltstone Member of the Thaynes Formation of locality NW1/4, NW1/4, S 19, T. 15 S., R 45
E, on the top of a ridge about <sup>3</sup>/<sub>4</sub> miles east of Hot Springs, Bear Lake, Idaho, United States of
America.

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

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

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

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

695 Cephalic appendages.—Poorly preserved, only a fragment of probable antennal flagellum is696 visible.

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

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

Pleonal appendages.—Uropodal endopod and exopod as long as telson, with strong median
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

between the carapace, the pleon, the endophragmal skeleton and the pereiopods, which suggests

a probable exuvia origin; UBGD30560 is a subcomplete specimen preserved in dorso-ventral

position; UBGD30548 is an isolated pleon preserved in dorsal view.

712 *Measurements.*—Available in Table 3.

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

716	subchelate P1-P3 are also very typical of <i>Litogaster</i> . 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 pereiopods 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 Vìa, 1971; Pemphix silesiacus Assmann, 1927;
740	Pemphix sueurii (Desmarest, 1817).

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

Emended diagnosis (present work).-Carapace tuberculate with strongly inflated 749 cephalothoracic regions; gastric, hepatic, meso- gastric, metagastric, and epibranchial regions 750 well defined; spatulate rostrum, broadly rimmed; long antennae with leaf-shaped scaphocerite; 751 752 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 branchiocardiac directed toward the dorsal margin with angle ca 30° and converging dorsally 754 755 but without dorsal connection; biconvex hepatic groove; subchelate pereiopods 1 to 3; 756 pereiopod 1 strongly developed; pereiopods 4-5 achelate; subrectangular pleonal somites; tergopleura blunt-triangular, directed posteriorly; uropodal exopodite with straight diaeresis; 757 subrectangular telson with rounded extremity. 758

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- 760

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#### Pemphix krumenackeri new species

#### Figure 9

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

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

767 Type age.—Early Spathian, Early Triassic.

Diagnosis.—Carapace tuberculate with strongly inflated cephalothoracic regions; rostrum large 768 769 and dorsoventrally flattened; very deep cervical groove; branchiocardiac grooves directed dorsally and converging close to postero-dorsal extremity; moderately biconvex hepatic 770 771 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 process rimmed by one triangular groove at the fold separating tergopleuron from tergum on 774 775 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 dorsal connection; moderately biconvex hepatic groove; deep cardiac groove joined ventrally 782 and slightly anteriorly to postcervical groove; cardiac groove cutting dorsal midline 783 perpendicularly; ornamentation of carapace poorly preserved but remains of small tubercles are 784 present on cephalic and branchial regions. 785

Pleon.—Pleon as wide as carapace; subrectangular s1, smaller than the others; s1 tergum with short transversal groove; s2-s5 of similar size and shape; s2-s5 terga with one transversal groove interrupted by a short median carina, s2-s5 tergopleura with one strong nodulose process rimmed by one triangular groove at the fold separating tergopleuron from tergum; s2-s5 tergopleura acuminate; s6 tergum with median carina; s6 tergopleuron with one strong nodulose process rimmed by incurved groove, at the fold separating tergopleuron from tergum;
subrectangular telson with rounded extremity; telson with one pair of broad proximal tubercles.
Pleonal appendages.—Pleopods not preserved; uropods as long as telson, with one longitudinal
carina; uropodal exopod with straight diaeresis.

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

797 *Measurements.*—Available in Table 4.

798 Remarks.—This new taxon shows diagnostic characters of Pemphix Meyer, 1835 such as the carapace groove pattern (very deep cervical groove, parallel postcervical and branchiocardiac 799 800 grooves, very deep cardiac groove cutting dorsal midline perpendicularly) and the originally strongly inflated regions of carapace (flattened on the fossil). Schweitzer et al. (2010) listed 801 three species in Pemphix: Pemphix sueurii (Desmarest, 1817) from the Middle Triassic of 802 803 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 P. sueurii but much smaller and with a gastric region without strong sculpture. A potential 807 808 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). The poor preservation of *Pemphix malladai* Via, 1971 precludes any comparison with other 810 Pemphicidae species and even raises the question of its placement within Pemphix. Pemphix 811 812 krumenackeri n. sp. represent the oldest known Pemphix species, enlarging the temporal extent of the genus back to the Early Triassic, and extending its spatial range to the American 813 814 continent.

- 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

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

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

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

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

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#### 852 **Diversification trends data**

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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 from all continents but Oceania and Antarctica. When taxa were reported from two closely-857 858 located sites and from the same age, they were grouped under the same locality name. For each listed taxon, the taxonomic and systematic validity was verified. Several taxonomic and 859 860 systematic issues were raised, especially regarding Aegeridae. Therefore, when illustrations were sufficient to have solid arguments to reattribute the species, we did so, despite not having 861 seen the type material, either because it has gone missing (e.g., type specimens of *Penaeus* 862 atavus, Bill, 1914 destroyed by fire) or it was not easily accessible. A first graphic 863 representation of the decapod taxonomic richness is presented by epoch in Fig.10. 1 and by 864 stage in Fig.10. 2. However, there is a strong correlation between the raw taxonomical richness 865
and the number of sites from which the taxa were reported (Fig.10. 3-4). In order to minimize 866 867 a possible co-variance between the two latter, we also studied the mean of the observed alpha diversity of each site  $[\alpha_s]$  per studied interval (Fig.10. 5-6). This mean  $[\alpha_m]$  was calculated for 868 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 869 (Whittaker, 1960). This approach presents the advantage of being easily applicable to any 870 dataset in which the sampling sites are reported. It is favored to other model-based approaches 871 (e.g., subsampling models, coverage-based models, rarefaction models) due to the limited size 872 of the dataset. Such approach is all more important when the fossil record is highly 873 heterogeneous (Fig. 10. 3-4), as is the case for the Triassic (Muscente et al., 2017). 874

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### 876 **Discussion**

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

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

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

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 representatives of Aegeridae. They thus extend the temporal range of these genera and this 904 905 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 group within Penaeoidea (Burkenroad, 1963, 1983; Tavares and Martin, 2010). With the 907 isolated Famennian (Devonian) specimen of Aciculopoda mapesi Feldmann & Schweitzer, 908 2010 and the previously mentioned Malagasy Penaeidae for which the dating is rather poorly 909 constrained (Marramà et al., 2017; Laville et al., 2021), the Paris Biota specimens represent 910 some of the oldest occurrences of Dendobranchiata (Schram, 1977, 1980; Schram et al., 1978; 911 912 Feldmann and Schweitzer, 2010). They therefore fill-in an important gap in the history of this group, from which present-day representatives are well studied for their economic interest 913 914 (Farfante, 1988; Cervantes-Hernández et al., 2010; Robalino et al., 2016; Fernández de Alaiza García Madrigal et al., 2018), but whose origin remains elusive. 915

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

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

A first comparison can be made between our dataset and other available Triassic 929 930 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 datasets are rather similar in terms of decapod taxonomic richness (PBDB: 63 species and 20 932 higher rank taxa; Supplementary file 5; our dataset: 74 species including the 3 new ones from 933 the Paris Biota). However, 29 taxa reported in our dataset (over 40% of the total, the newly 934 described taxa excluded) do not occur in the PBDB dataset (Supplementary file 6), implying 935 936 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 of taxa, as Jurassic, Cretaceous, and even Paleocene occurrences are registered as being Triassic 938 (Supplementary file 5). Some other issues such as synonymy mistakes, invalid taxa, and even 939 some microcoprolites registered as valid decapod species, have also been noticed 940

941 (Supplementary file 5). It thus appears that the PBDB Triassic decapod dataset is inappropriate942 to analyze the Decapoda diversity trends throughout the Triassic.

Based on our dataset at the epoch-scale, decapods apparently underwent an important 943 diversification throughout the Triassic (Fig.10.1). However, at the stage-scale (Fig.10.2), this 944 trend is more contrasted, with the Anisian and Norian being the most diverse stages. This 945 differential pattern likely results from the heterogeneity of the decapod fossil record and 946 947 sampling effort. Indeed, a very few sites have been intensively sampled comparatively to the majority of them (e.g., in the south-west of Germany and the Guizhou province of China for 948 the Anisian, and in the Italian Lombardy region for the Norian). Additionally, certain time 949 950 intervals are much better represented than others, with more known fossiliferous localities.

Based on  $\alpha_m$ , the Triassic decapod diversification trend significantly differs from that 951 952 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 rather constant throughout the Triassic (Fig.10. 6). At the stage-scale, whereas the Olenekian 954 955 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 (Fig. 10. 6). These differences illustrate how the heterogeneity of the fossil record can strongly 957 958 bias observed diversity trends. The evolution of the apparent decapod mean alpha diversity ( $\alpha_m$ ) throughout the Triassic (Fig.10. 5-6) can be interpreted in two ways: 959

(i) If considered that the taxonomy and systematics of Triassic decapods remain too amiss: then
any apparent diversity trend should be considered hardly interpretable. The Triassic decapod
taxonomy and systematic inaccuracy likely originate from the scarce occurrences of Triassic
decapods that led to important knowledge gaps. Such poor fossil record is not specific to
decapods (Twitchett, 2001; Muscente et al., 2017), implying that similar hiatus likely exist for
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 scenario974 for decapods.

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## 976 **Conclusion**

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

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

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

997 The co-occurrence of these decapods in the Paris Biota provides evidence for an early diversification of this group, as soon as the early Spathian. This is congruent with available 998 999 decapod phylogenies and diversification models that argue for a Triassic diversification of these groups (Gherardi et al., 2010; Lavalli and Spanier, 2010; Schweitzer and Feldmann, 2014; 1000 Robalino et al., 2016; Wolfe et al., 2019). Besides, all the Paris Biota taxa extend the Triassic 1001 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), marine vertebrates (Tintori et al., 2014). Another interpretation could lie in the incomplete 1006 1007 knowledge of an otherwise cosmopolitan decapod distribution during the Triassic.

The description of the Paris Biota specimens also led to a taxonomic and systematic revision of Triassic decapods, highlighting the significance of this biota in the debates on the Early Triassic recovery and on the rise of the modern ecosystems. Using a refined dataset of known Triassic decapod taxa that strongly differs from that of the PBDB, we showed that: (*i*) the apparent increase in decapod taxonomic richness throughout the Triassic mainly results from the heterogeneity of the fossil record and/or the sampling intensity; (*ii*) the Decapoda 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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# 1041 Acknowledgments

We thank N. Goudemand, E. Vennin, P. Guenser, D. Stephen and L.J. Krumenacker for their 1043 1044 help during fieldwork. We also acknowledge D. Audo and M. Hyžný for their constructive 1045 comments on earlier version of the manuscript. This work was supported by the ANR project 1046 AFTER (ANR-13-JS06-0001-01) and the French "Investissements d'Avenir" program, project ISITE-BFC (ANR-15-IDEX-03). We acknowledge the Bear Lake County road department and 1047 1048 D. M. Clow (Ogden) for allowing access to the studied exposures at Paris Canyon. We thank 1049 the BLM (Permit N-094706) and US Forest Service (Caribou National Forest, Special Use 1050 Permit CT5.01) for allowing access and collection at NoName and Stewart Canyon sites. The Winecup Gamble Ranch is thanked for allowing access to Immigrant Canyon site. Sample 1051 1052 management and valorization benefited from ANR-11-INBS-0004-RECOLNAT. 1053 1054 Accessibility of supplemental data 1055 1056 1057 Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hmgqnk9jp [Supplementary data awaiting for acceptance on DRYAD. Therefore, the DOI link is not active 1058 1059 yet. Pending acceptance of Supplementary data, it is available at: https://datadryad.org/stash/share/OClQZ98IIV-L59Rh48Y3vdyyJAERJS1M1PZlCc6nffE 1060 1061 1062 1063 1064 1065

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### 1539 **Figure caption**

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Figure 1: Location of the sites from which the Paris Biota has been reported. (1) Present-day 1541 1542 map; (2) Early Triassic paleogeographic map; (3) Simplified map of northeastern Nevada; (4) Simplified map of southeastern Idaho. Yellow rectangle indicates the location of the western 1543 USA basin. Small red rectangles in (1) indicate the location of map (3) and (4). Stars indicate 1544 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 Paris Biota. Maps, following Romano et al. (2012). 1547 1548 Figure 2: Aeger sp. (1-3) Right lateral view of specimen UBGD30555a; (4-6) Right lateral 1549 view of specimen UBGD30558; (7-8) Left lateral view of specimen UBGD30553a. (1, 4, 7) 1550 Line drawings; (2, 5, 8) Under UV illumination; (3, 6, 9) Under natural illumination. 1551 1552 Abbreviations: a - branchiocardiac groove; b1 - hepatic groove; e1e - cervical groove; eskt -1553 endophragmal skeleton; hs - hepatic spine; on - optical notch; P - pereiopod; pl - pleopod; prs postrostral spine; ps - postorbital spine; r - rostrum; s - pleonal somite; t - telson. The beige 1554

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

colour corresponds to digestive track traces. Scale is 1 cm.

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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

paratype, specimen UBGD294001. (1, 4, 7) Line drawings ;(2, 5, 10) Under UV illumination;
(3, 6, 8, 9) Under natural illumination. Abbreviations: a - branchiocardiac groove; a2 - antenna;
as - antennal spine; bp - basipodite; di - diaeresis; e1e - cervical groove; en - endopodite; eskt endophragmal skeleton; ex - exopodite; hs - hepatic spine; mxp3 - third maxilliped; P pereiopod; pl - pleopod; ps - postorbital spine; r - rostrum; s - pleonal somite; sc - scaphocerite;
t - telson. Scale is 1 cm.

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Figure 5: Anisaeger longirostrus n. sp. (1-3) Dorso-right lateral view of paratype, specimen 1571 UBGD294004; (4-6) Left lateral view of specimen UBGD30553b; (7, 8) Left lateral view of 1572 specimen UBGD294005c; (9-11) Right lateral view of paratype, specimen UBGD33022BIS. 1573 (1, 4, 8, 9) Line drawings; (2, 5, 7, 10) Under UV illumination; (3, 6, 11) Under natural 1574 illumination. Abbreviations: a - branchiocardiac groove; a1 - antennula; a2 - antenna; as -1575 1576 antennal spine; crp - carpocerite; bas - basicerite; bp - basipodite; di - diaeresis; e1e - cervical groove; eskt - endophragmal skeleton; hs - hepatic spine; mxp3 - third maxilliped; P -1577 1578 pereiopod; pl - pleopod; ps - postorbital spine; r - rostrum; s - pleonal somite; sc - scaphocerite; 1579 t - telson. Scale is 1 cm.

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Figure 6: Anisaeger longirostrus n. sp. (1-3) Left lateral view of specimen UBGD294005a; (46) Left lateral view of specimen UBGD294005b. (7-9) left lateral view of specimen
UBGD30555b; (10) Mirrored counter-impression of UBGD30555b. (1, 4, 7) Line drawings;
(2, 5, 9, 10) Under UV illumination; (3, 6, 8) Under natural illumination. Abbreviations: a branchiocardiac groove; as - antennal spine; bp - basipodite; di - diaeresis; en - endopodite; ex
exopodite; P - pereiopod; pl - pleopod; r - rostrum; s - pleonal somite; sto - stomach traces; t
telson. The beige colour corresponds to digestive track traces. Scale is 1 cm.

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

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

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

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

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

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

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1619 Table 2: Measurements (in mm) of specimens of *Anisaeger longirostrus* n. sp. When both left1620 and right appendages were measurable, both measures are given.

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**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 left1626 and right appendages were measurable, both measures are given.

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

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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.

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

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

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

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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Per epoch











