

FOSSIL CALIBRATIONS FOR THE ARTHROPOD TREE OF LIFE

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ABSTRACT

Fossil age data and molecular sequences are increasingly combined to establish a timescale for the Tree of Life. Arthropods, as the most species-rich and morphologically disparate animal phylum, have received substantial attention, particularly with regard to questions such as the timing of habitat shifts (e.g. terrestrialisation), genome evolution (e.g. gene family duplication and functional evolution), origins of novel characters and behaviours (e.g. wings and flight, venom, silk), biogeography, rate of diversification (e.g. Cambrian explosion, insect coevolution with angiosperms, evolution of crab body plans), and the evolution of arthropod microbiomes. We present herein a series of rigorously vetted calibration fossils for arthropod evolutionary history, taking into account recently published guidelines for best practice in fossil calibration. These are restricted to Palaeozoic and Mesozoic fossils, no deeper than ordinal taxonomic level, nonetheless resulting in 80 fossil calibrations for 102 clades. This work is especially timely owing to the rapid growth of molecular sequence data and the fact that many included fossils have been described within the last five years. This contribution provides a resource

27 for systematists and other biologists interested in deep-time questions in arthropod evolution.

28

29 **KEYWORDS**

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31 Arthropods; Fossils; Phylogeny; Divergence times

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33 **ABBREVIATIONS**

34

35 AMNH, American Museum of Natural History; AMS, Australian Museum, Sydney; AUGD, University of
36 Aberdeen; BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin; BMNH, The Natural
37 History Museum, London; CNU, Key Laboratory of Insect Evolutionary & Environmental Change,
38 Capital Normal University, Beijing; DE, Ulster Museum, Belfast; ED, Ibaraki University, Mito, Japan;
39 FMNH, Field Museum of Natural History; GMCB, Geological Museum of China, Beijing; GSC,
40 Geological Survey of Canada; IRNSB, Institut Royal des Sciences Naturelles de Belgique, Brussels;
41 KSU, Kent State University; Ld, Musée Fleury, Lodève, France; LWL, Landschaftsverband Westfalen-
42 Lippe-Museum für Naturkunde, Münster; MACN, Museo Argentino de Ciencias Naturales, Buenos
43 Aires; MBA, Museum für Naturkunde, Berlin; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-
44 Gasteiz, Álava, Spain; MCZ, Museum of Comparative Zoology, Harvard University; MGSB, Museo
45 Geologico del Seminario de Barcelona; MN, Museu Nacional, Rio de Janeiro; MNHN, Muséum
46 national d'Histoire naturelle, Paris; NHMUK, The Natural History Museum, London; NIGP, Nanjing
47 Institute of Geology and Palaeontology; NMS, National Museum of Scotland; OUM, Oxford University
48 Museum of Natural History; PBM, Palaöbotanik Münster; PIN, Paleontological Institute, Moscow; PRI,
49 Paleontological Research Institution, Ithaca; ROM, Royal Ontario Museum; SAM, South Australian
50 Museum, Adelaide; SM, Sedgwick Museum, University of Cambridge; SMNK, Staatliches Museum für
51 Naturkunde, Karlsruhe; SMNS, Staatliches Museum für Naturkunde, Stuttgart; TsGM, F.N. Chernyshev
52 Central Geologic Prospecting Research Museum, St. Petersburg; UB, University of Bonn; USNM, US

- 53 National Museum of Natural History, Smithsonian Institution; UWGM, University of Wisconsin Geology
54 Museum; YKLP, Yunnan Key Laboratory for Palaeobiology, Yunnan University; YPM, Yale Peabody
55 Museum; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.
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57 1. Introduction

58

59 Accurate and precise systematic placement and dating of fossils underpins most efforts to infer
60 a chronology for the Tree of Life. Arthropods, as a whole or in part, have received considerable focus
61 owing to their incredible morphological disparity, species richness, and (relative to much of the Tree of
62 Life) excellent fossil record. A growing number of recent studies have constructed timetrees for
63 arthropods as a whole or for major groups therein (e.g. Bellec and Rabet, 2016; Bond et al., 2014;
64 Bracken-Grissom et al., 2014, 2013; Djernæs et al., 2015; Fernández et al., 2016, 2014; Fernández
65 and Giribet, 2015; Garrison et al., 2016; Garwood et al., 2014; Giribet and Edgecombe, 2013; Herrera
66 et al., 2015; Klopstein et al., 2015; Legendre et al., 2015; Malm et al., 2013; McKenna et al., 2015;
67 Misof et al., 2014; Oakley et al., 2013; Rehm et al., 2011; Schwentner et al., 2013; Song et al., 2015;
68 Sun et al., 2015; Thomas et al., 2013; Tsang et al., 2014; Wahlberg et al., 2013; Wiegmann et al.,
69 2011; Wood et al., 2013; Xu et al., 2015; Zhu et al., 2015). These studies vary in how well they have
70 adhered to best practices for selecting calibration fossils, as many previous calibrations assume that
71 fossil taxonomy accurately reflects phylogeny. Compounding the issue is the expansion of divergence
72 time studies for a variety of comparative questions far beyond systematics and biogeography,
73 including habitat shifts (Letsch et al., 2016; Lins et al., 2012; Rota-Stabelli et al., 2013a; Yang et al.,
74 2013), genome evolution (Cao et al., 2013; Schwarz et al., 2014; Starrett et al., 2013; Wissler et al.,
75 2013; Yuan et al., 2016), origins of novel characters and behaviours (Rainford et al., 2014; Sanggaard
76 et al., 2014; Wheat and Wahlberg, 2013), evolution of parasites and disease (Ibarra-Cerdeña et al.,
77 2014; Palopoli et al., 2014; Rees et al., 2014; Zhou et al., 2014), rate of diversification and its
78 relationship to morphology and ecology (Lee et al., 2013; Wiens et al., 2015), coevolution (Kaltenpoth
79 et al., 2014; Shelomi et al., 2016; Wilson et al., 2013), conservation (Owen et al., 2015), and the use
80 of arthropods as a model for methodological development (O'Reilly et al., 2015; Ronquist et al., 2012;
81 Warnock et al., 2012; Zhang et al., 2016).

82 Recent consensus on best practices for selecting calibration fossils comes with several

83 requirements. There must be references to specific fossil specimen(s), phylogenetic or morphological
84 evidence justifying placement of the fossil, and stratigraphic and/or radiometric dating information for
85 the fossil (Parham et al., 2012). The importance of accurate phylogenetic knowledge of calibration
86 fossils is underscored by recent controversies in dating the evolution of insects, where arguments
87 hinge on the classification of particular 'roachoid' fossils on the stem lineage of Dictyoptera, with
88 resulting differences on the order of 100 Myr (Kjer et al., 2015; Tong et al., 2015). With the explosion of
89 taxonomic sampling in molecular phylogenies due to improvements in sequencing technology,
90 improving the coverage of fossil calibrations is equally important. Recommendations include, for
91 example, including as many as one fossil per ten extant taxa for precise ages, with a varied
92 distribution across lineages and clade depth (Bracken-Grissom et al., 2014). As a response, we have
93 compiled an atlas of 80 rigorously scrutinized calibration fossils for 102 key nodes in arthropod
94 phylogeny. These represent four basal ecdysozoan and arthropod clades, 17 chelicerates, 12
95 myriapods, 30 non-hexapod pancrustaceans, and 39 hexapod clades.

96 Where possible, we favour clade topologies resulting from a phylogenetic analysis of the
97 largest total dataset. If phylogenomic analysis of genomes or transcriptomes has been performed but
98 conflicts with morphology, a strongly supported molecular result is presented (e.g. putative clades
99 such as Oligostraca that do not yet have identified morphological autapomorphies). If, however,
100 molecular phylogenies have been constructed with few genes (e.g. clades such as Peracarida) or with
101 highly conflicting results (e.g. Arachnida), morphological results are given greater weight. Where
102 relevant, we discuss clade names with respect to NCBI's GenBank taxonomy (as recommended by
103 the Fossil Calibrations Database: Polly et al., 2015), as this review is intended to be used by molecular
104 biologists who are interested in dating the evolution of arthropod groups.

105 As there are >1.2 million species of arthropods, our calibrations are limited to fossils from the
106 Palaeozoic and Mesozoic. Many extant clades have their oldest fossils in Cenozoic ambers such as
107 the Eocene Baltic amber but are predicted to be vastly older based on fossils of allied taxa (e.g.
108 Symphyla and Pauropoda relative to Chilopoda and Diplopoda).

109 While acknowledging the complexity of estimating an age prior for a fossil species known from
110 multiple deposits, we use the oldest (e.g. section 28.3) and/or best known (e.g. section 51.3) horizons
111 to provide minimum age constraints with the narrowest and most accurate age interval. Where there is
112 substantial variation in age estimates for a fossil species, this issue is noted in the text. To
113 accommodate the possibility of older fossils not yet discovered, we provide generous soft maxima (Ho
114 and Phillips, 2009). Accordingly, when conducting divergence time analyses, prior distributions
115 accounting for the large probability tail (e.g. gamma or lognormal) of an older undiscovered fossil may
116 be appropriate. All fossil calibrations described herein are listed with their age information in Table A.1,
117 formatted for adding age constraints in BEAST or PhyloBayes.

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119 **2. Crown Ecdysozoa**

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121 This clade comprises Euarthropoda, Onychophora (velvet worms), Tardigrada (water bears),
122 Nematoida (itself comprising Nematoda and Nematomorpha), and Scalidophora (itself comprising
123 Kinorhyncha, Loricifera, and Priapulida), their last common ancestor and all of its descendants (**Fig.**
124 **1**). Monophyly has been demonstrated on the basis of coding and non-coding molecular data
125 (Campbell et al., 2011).

126

127 *2.1. Fossil specimens*

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129 *Rusophycus* trace fossils in Member 2 of the Chapel Island Formation of the southwestern
130 Burin Peninsula of southeastern Newfoundland, defining the base of the *R. avalonensis* Biozone.
131 Arbitrarily, we fix this calibration on a specimen (**Fig. 2a**) from this unit figured by Narbonne et al.
132 (1987: Fig. 6l; GSC 85983), as in Benton et al. (2015).

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134 *2.2. Phylogenetic justification*

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Rusophycus trace fossils are widely accepted to have been produced by arthropod-grade organisms, showing bilateral symmetry and evidence of segmented limbs used in their construction, the latter an apomorphy of Euarthropoda (Budd and Jensen, 2000).

2.3. Age justification

Rusophycus occurs well below the first animal body fossils in Cambrian sections around the world (Crimes, 1987; Crimes and Jiang, 1986; Goldring and Jensen, 1996; MacNaughton and Narbonne, 1999; Weber and Zhu, 2003). In many of these regions, records of *Rusophycus* begin with proximity to the base of the Cambrian. However, their ages are only well constrained in sections in Newfoundland, Canada, and Yunnan, China. Of these, records of *Rusophycus* begin low in Member 2 of the Chapel Island Formation of the southwestern Burin Peninsula of southeastern Newfoundland, defining the base of the *R. avalonensis* Biozone (Narbonne et al., 1987). The Biozone is itself dated through correlations to a section in New Brunswick where the younger ash bed has been dated by U-Pb series to 530.02 Ma \pm 1.2 Myr (Isachsen et al., 1994; Peng et al., 2012), thus providing for a minimum constraint of 528.82 Ma.

A soft maximum constraint is based on that used by Benton et al. (2015), the maximum age interpretation of the Lantian Biota (Yuan et al., 2011). This, together with the Doushantuo Biota (Yuan et al., 2002), provides a series of Konservat-Lagerstätten preserving the biota in Orsten- and Burgess Shale-like modes of fossilization. None of these Lagerstätten, least of all the Lantian, preserves anything that could possibly be interpreted as even a total group eumetazoan and on this basis we define our soft maximum constraint at 635.5 Ma \pm 0.6 Myr (Condon et al., 2005) and, thus, 636.1 Ma.

3. Crown Arthropoda

161 This clade comprises Euarthropoda and Onychophora (*sensu* Ortega-Hernández, 2016), their
162 last common ancestor and all of its descendants (**Fig. 1**). This clade has traditionally been called
163 Panarthropoda (Nielsen, 1995), however, this latter name is most often used to refer to a group
164 encompassing Arthropoda and Tardigrada, but we exclude tardigrades from our current grouping.
165 Monophyly of this clade has been established through phylogenetic analysis of both non-coding and
166 protein-coding gene datasets (Campbell et al., 2011), and morphological data sets (Legg et al., 2013),
167 although it has been challenged by other recent morphological analyses that endorsed a rival sister
168 group relationship between Euarthropoda and Tardigrada (e.g. Smith and Ortega-Hernández, 2014).
169 Note the name Arthropoda in GenBank refers to what we consider Euarthropoda; there is no GenBank
170 taxonomy ID for the clade comprising Euarthropoda and Onychophora.

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172 3.1. *Fossil specimens*

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174 As for 2.1.

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176 3.2. *Phylogenetic justification*

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178 As for 2.2.

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180 3.3. *Age justification*

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182 As for 2.3.

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184 4. **Crown Euarthropoda**

185

186 This clade comprises Chelicerata, Myriapoda and Pancrustacea, their last common ancestor

187 and all of its descendants (**Fig. 1**). The monophyly of Euarthropoda, comprising the sister clades
188 Chelicerata and Mandibulata (itself comprising Myriapoda and Pancrustacea) has been established on
189 the basis of protein-coding and noncoding molecular data, as well as morphological data (Rota-Stabelli
190 et al., 2011). Note that in Benton et al. (2015) this node was named Arthropoda (likely with reference
191 to GenBank taxonomy). Here we follow the naming conventions outlined by Ortega-Hernández (2016).

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193 4.1. Fossil specimens

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195 *Yicaris dianensis* Zhang et al., 2007. YKLP 10840, holotype (**Fig. 2b,c**), consisting of an almost
196 complete articulated specimen (Zhang et al., 2007).

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198 4.2. Phylogenetic justification

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200 Several phylogenetic analyses of morphology (Edgecombe, 2010; Legg et al., 2013; Wolfe and
201 Hegna, 2014) and morphology plus molecules (Oakley et al., 2013) place *Y. dianensis* within the
202 crown group of Pancrustacea. Key characters include the presence of epipodites on the thoracic
203 limbs; paddle-shaped mandibular and maxillary exopods; and the protopodite of post-mandibular limbs
204 elongated as soft, setiferous endites. Any position supported within the crown group of Pancrustacea
205 is within crown Euarthropoda.

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207 4.3. Age justification

208

209 *Y. dianensis* was recovered from the Yu'anshan Formation at Xiaotan section, Yongshan,
210 Yunnan Province, attributed to the *Eoredlichia*–*Wutingaspis* Biozone (Zhang et al., 2007). Chinese
211 Cambrian stratigraphy has been revised substantially and the *Eoredlichia* – *Wutingaspis* Biozone is no
212 longer recognized (Peng, 2009, 2003). However, *Eoredlichia* is known to co-occur with *Hupeidiscus*,

213 which is diagnostic of the *Hupeidiscus-Sinodiscus* Biozone, which is formally recognised as the
214 second biozone of the Nangaoan Stage of the Qiandongian Series of the Cambrian of China (Peng
215 and Babcock, 2008). The Nangaoan is the proposed third stage of the Cambrian System for the
216 International Geologic Timescale (Peng et al., 2012). Thus, a minimum constraint can be established
217 on the age of the top of the Nangaoan, which has been dated to 514 Ma (Peng et al., 2012; Peng and
218 Babcock, 2008).

219 Soft maximum as for 2.3.

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221 4.4. Discussion

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223 There are older records of euarthropods than *Y. dianensis*, notably trilobites, but their
224 phylogenetic position within Arthropoda is contested (it is unclear whether trilobites are stem-
225 Euarthropoda, stem-Chelicerata or stem-Mandibulata). *Wujicaris muelleri* Zhang et al., 2010 has an
226 equal claim to being the earliest record of Arthropoda, but it is of equal age to the holotype of *Y.*
227 *dianensis*.

228

229 5. Crown Chelicerata

230

231 This clade comprises Pantopoda (sea spiders) and Euchelicerata, their last common ancestor
232 and all of its descendants (**Figs. 1, 3 and 4**). Monophyly of this clade has been established by
233 phylogenetic analysis of nuclear protein-coding genes (Regier et al., 2010), transcriptomes
234 (Meusemann et al., 2010; Rota-Stabelli et al., 2011), and morphology (Legg et al., 2013).

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236 5.1. Fossil specimens

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238 *Wisangocaris barbarahardyae* Jago, García-Bellido and Gehling, 2016. SAM P45427,

239 holotype, almost complete specimen (**Fig. 2d**).

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241 5.2. *Phylogenetic justification*

242

243 Few recent phylogenetic studies have addressed the stem-lineage of Euchelicerata (notable
244 exceptions being Lamsdell, 2013; Legg, 2014; Legg et al., 2013). Including *W. barbarahardyae* in the
245 dataset of Legg (2014), this species was resolved in most shortest cladograms as sister taxon to the
246 middle Cambrian *Sanctacaris* and *Sidneyia*, and in all shortest cladograms as more closely related to
247 Euchelicerata than Pantopoda, i.e. as crown group Chelicerata (Jago et al., 2016). This relationship is
248 supported by the shared presence of pediform cephalic exites, multi-partite trunk exites, and a trunk
249 composed of a posterior limb-less abdomen in both crown euchelicerates and the Cambrian taxa.

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251 5.3. *Age justification*

252

253 *W. barbarahardyae* was collected from the Emu Bay Shale on Kangaroo Island, South Australia.
254 Trilobite biostratigraphy correlates this unit with the upper part of the *Pararaia janeae* Zone in
255 mainland South Australia (Jell in Bengtson et al., 1990; Fig. 2 in Jago et al., 2012), equivalent to the
256 Canglangpuan Stage in South China and the late Botoman in Siberia (Gehling et al., 2011, Fig. 9).
257 This dates the Emu Bay Shale to Cambrian Series 2, Stage 4, providing a minimum constraint of 509
258 Ma.

259 Soft maximum as for 2.3.

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261 5.4. *Discussion*

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263

264 Until recently the oldest evidence of chelicerates in the fossil record were thought to be

265 represented by *Chasmataspis*-like trace fossils from the Furongian of Texas (Dunlop et al., 2004), and
266 a putative pycnogonid larva from the Furongian of Sweden (Waloszek and Dunlop, 2002). However, in
267 a number of recent phylogenetic analyses (e.g. Legg, 2014; Legg et al., 2013), a number of taxa from
268 the middle Cambrian Burgess Shale Formation, namely *Sanctacaris uncata* Briggs and Collins, 1988,
269 *Sarotrocercus oblita* Whittington, 1981, and *Sidneyia inexpectans* Walcott, 1911, have been resolved
270 as stem-lineage representatives of Euchelicerata. These relationships are preserved with the addition
271 of the older *W. barbarahardyae* to the dataset (Jago et al., 2016). Although another purported species
272 of *Sidneyia* (*S. sinica* Zhang et al., 2002) is known from the older Chengjiang biota, it lacks many
273 diagnostic features of this genus, and could therefore not be reliably used for calibration purposes. It
274 should also be noted that *Sidneyia* only resolved as a stem representative of Euchelicerata under
275 some iterations of the analysed data set of Legg (2014), specifically only when all characters were
276 weighted equally, and therefore its exact phylogenetic position is equivocal.

277

278 6. Crown Pantopoda

279

280 This clade comprises Ammotheidae, Austrodecidae, Callipallenidae, Colossendeidae,
281 Endeididae, Nymphonidae, Pallenopsidae, Phoxichilidiidae, Pycnogonidae and Rhynchothoracidae,
282 their last common ancestor and all of its descendants (**Fig. 3**). Phylogenetic analyses of protein-
283 coding genes (Arabi et al., 2010) or protein-coding genes combined with morphology (Arango and
284 Wheeler, 2007) indicate monophyly.

285

286 6.1. Fossil specimens

287

288 *Haliestes dasos* Siveter et al., 2004. OUM C.29571, holotype (**Fig. 5a**). As the reconstruction of
289 Herefordshire fossils requires serial grinding and photography of 20 µm sections (Sutton et al., 2002),
290 the holotype figured in Siveter et al. (2004) and herein was thus destroyed in preparation.

291 Morphological data for Herefordshire fossils are published as 3D models of the thin section
292 photographs.

293

294 6.2. *Phylogenetic justification*

295

296 Arango and Wheeler (2007) resolved *H. dasos* as sister to part of Ammonotheidae (nested within
297 clade of Ammonotheidae, Callipallenidae, Nymphonidae, Pallenopsidae, Phoxichilidiidae,
298 Rhynchothoracidae), i.e. as crown-group Pantopoda. *H. dasos* was classified separately from extant
299 pycnogonids (Pantopoda) as an Order Nectopantopoda by Bamber (2007), although without explicit
300 phylogenetic justification. It should be noted that *H. dasos* was included in the phylogenetic analysis of
301 Legg et al. (2013), and resolved as sister-taxon to *Palaeopantopus*, which in turn resolved as sister-
302 taxon to extant pycnogonids, however, just three extant exemplars were included in this study and as
303 this was not extensive enough to determine the exact position of these fossil taxa with respect to
304 crown-group exemplars, we continue to follow Arango and Wheeler (2007) in their placement.

305

306 6.3. *Age justification*

307

308 This fossil is preserved as a carbonate concretion from the volcanoclastic Herefordshire
309 Lagerstätte of Herefordshire, England, at the Sheinwoodian-Homerian stage boundary, within the
310 Early Silurian Wenlock Series (Siveter, 2008). As the Homerian begins at 430.5 Ma \pm 0.7 Myr, a
311 minimum age constraint for the Herefordshire can thus be placed at 429.8 Ma.

312 Soft maximum as for 2.3.

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314 6.4. *Discussion*

315

316 Although *H. dasos* is the oldest assignable crown group pycnogonid, there is an older fossil,

317 *Cambropycnogon klausmuelleri* Waloszek and Dunlop, 2002, from the Cambrian Orsten biota
318 (minimally 497 Ma). *C. klausmuelleri*, however, is known only from larval stages, and does not share
319 specific apomorphies with any extant larva. Without such characters, it is not possible to adequately
320 confirm crown group affinity. Another fossil species, *Palaeomarachne granulata* Rudkin et al., 2013
321 from the Late Ordovician of Manitoba, is specifically noted as a stem pantopod due to its likely
322 plesiomorphic head tagmosis.

323

324 **7. Crown Euchelicerata**

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326 This clade comprises Xiphosurida (horseshoe crabs) and Arachnida, their last common
327 ancestor and all of its descendants (**Fig. 3**). Monophyly is established on the basis of phylogenetic
328 analysis of transcriptomes (Rota-Stabelli et al., 2011; Sharma et al., 2014) and morphology (Legg et
329 al., 2013). Note that monophyly of Euchelicerata is challenged by a recent morphological phylogeny, a
330 result attributed to outgroup sampling (Garwood and Dunlop, 2014). Euchelicerata is not recognized in
331 GenBank taxonomy.

332

333 *7.1. Fossil specimens*

334

335 *Chasmataspis*-like resting trace fossils (MBA 1084), **Fig 5b**. Described and illustrated in
336 Dunlop et al. (2004, Figs. 9 and 10).

337

338 *7.2. Phylogenetic justification*

339

340 The assignment of the traces to Chasmataspida is based on impressions of plate-like
341 opisthosomal opercula, one of the characters used to define Euchelicerata (Dunlop et al., 2004)
342 Furthermore, recent phylogenetic analyses of morphology place chasmataspid body fossil species

343 within Euchelicerata, as sister group to eurypterids (Garwood and Dunlop, 2014; Legg et al., 2013) or
344 sister group to a clade composed of eurypterids and arachnids (Lamsdell, 2013; Lamsdell et al., 2015;
345 Selden et al., 2015).

346

347 7.3. Age justification

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349 The *Chasmataspis*-like resting traces were found in the Cambrian Hickory Sandstone Member
350 of the Riley Formation, Texas (Dunlop et al., 2004). The top of the Hickory Sandstone preserves
351 trilobite representatives of the *Bolaspidella* Zone and the *Cedarina* Zone (Miller et al., 2012; Palmer,
352 1954). These trilobite biozones are assigned to the lowermost Marjumiid Biome in the Marjuman
353 Stage of the Lincolnian Series (Miller et al., 2012). The early Marjuman itself is correlated to the
354 Drumian Stage of Cambrian Series 3 (Taylor et al., 2012). The end of the Drumian is dated to 500.5
355 Ma, providing a minimum age for *Chasmataspis*-like trace fossils.

356 Soft maximum as for 2.3.

357

358 8. Crown Xiphosurida

359

360 This clade comprises four extant species, all members of the family Limulidae: *Carcinoscorpius*
361 *rotundicauda*, *Limulus polyphemus*, *Tachypleus gigas* and *Tachypleus tridentatus*, their last common
362 ancestor and all of its descendants (**Fig. 3**). Monophyly is established by phylogenetic analyses of
363 housekeeping genes (Obst et al., 2012) and morphology (Lamsdell and McKenzie, 2015).

364

365 8.1. Fossil specimens

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367 *Tachypleus gadeai* Vía Boada and de Villalta, 1966. MGSB 19195, holotype.

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369 8.2. Phylogenetic justification

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371 *Heterolimulus gadeai* Vía Boada and de Villalta, 1966 was reassigned to the extant genus
372 *Tachypleus* by Diedrich (2011), who cited the presence of lateral immobile opisthosomal spines as
373 evidence. This was validated by the phylogenetic analysis of Lamsdell and McKenzie (2015), who
374 resolved *T. gadeai* as sister-taxon to a clade composed of all other members of *Tachypleus*. This more
375 inclusive clade in turn resolved as sister-taxon to the extant genus *Carcinoscorpius*.

376

377 8.3. Age justification

378

379 *T. gadeai* was discovered in the Alcover unit of the Montral site, Tarragona province, Catalonia,
380 Spain (Vía Boada and de Villalta, 1966). Based on sequence stratigraphy, the Alcover dolomite unit is
381 dated to the late Muschelkalk, a European regional stage of the Triassic (Calvet and Tucker, 1995; Vía
382 Boada and de Villalta, 1966). The middle and late Muschelkalk correspond to the global Ladinian
383 stage (Calvet and Tucker, 1995). The upper boundary of the Ladinian is 237.0 Ma \pm 1 Myr (Ogg,
384 2012), thus, a minimum age of 236.0 Ma.

385 Soft maximum as for 2.3.

386

387 8.4. Discussion

388

389 We note that morphological phylogenetic analysis has suggested paraphyly of Xiphosura
390 (crown Xiphosurida plus several fossil genera), and resolved synziphosurines as basal euchelicerates
391 (Lamsdell, 2013). A subsequent morphological phylogeny resolved synziphosurines as polyphyletic
392 (Garwood and Dunlop, 2014). Some other morphological phylogenies resolve the traditional
393 monophyletic Xiphosura (Briggs et al., 2012; Legg et al., 2013).

394 Crown xiphosurid affinities of older fossils cannot be confirmed. For example, an undescribed

395 Early Ordovician fossil from Morocco (Van Roy et al., 2010) exhibits fused opisthosomal tergites, a
396 synapomorphy of Xiphosurida *sensu* Lamsdell (2013), but its position with respect to the crown has
397 not been tested in a phylogeny. The Late Ordovician *Lunataspis aurora* Rudkin et al., 2008 and the
398 Pennsylvanian genus *Euproops* are resolved on the stem group of Xiphosurida in a morphological
399 phylogeny (Lamsdell, 2013).

400 Morphological conservatism in the evolution of Xiphosura (as illustrated by a Jurassic member
401 assigned to a living genus) has led to use of the misnomer 'living fossil' for the clade, despite
402 continued molecular evolution throughout its history (Avisé et al., 1994; Obst et al., 2012). The more
403 appropriate term of 'stabilomorph' was proposed with the discovery of *Limulus darwini* (Kin and
404 Błażejowski, 2014); it refers to morphological stability over evolutionary history, at the genus level.
405 However, long branches unbroken by unsampled extinct species may have significantly
406 underestimated divergence times among crown Xiphosurida (Lamsdell and McKenzie, 2015), though
407 this assertion has not yet been tested with a divergence time analysis.

408

409 **9. Crown Arachnida**

410

411 This clade comprises Acariformes (acariform mites), Opiliones (harvestmen), Palpigradi
412 (microwhip scorpions), Parasitiformes (parasitiform mites, ticks), Pseudoscorpiones, Ricinulei (hooded
413 tickspiders), Schizomida, Scorpiones, Solifugae (camel spiders), and Tetrapulmonata, their last
414 common ancestor and all of its descendants (**Fig. 4**). Monophyly is established on the basis of
415 phylogenetic analysis of transcriptomes (Rota-Stabelli et al., 2013a), nuclear protein-coding genes
416 (Regier et al., 2010), strong support from morphology (Garwood and Dunlop, 2014; Legg et al., 2013;
417 Rota-Stabelli et al., 2011; Shultz, 2007), and combined morphological and molecular data (Giribet et
418 al., 2002; Lee et al., 2013). Some recent phylogenetic analyses of transcriptomes have failed to
419 resolve a monophyletic Arachnida; instead Xiphosurida is variably placed within the traditional
420 arachnids (Sharma et al., 2014; von Reumont et al., 2012).

421

422 9.1. Fossil specimens

423

424 *Palaeophonus loudonensis* Laurie, 1899. NMS 1897.122.196 (holotype), a dorsally preserved
425 specimen lacking walking legs and telson (**Fig. 5h**). For additional anatomical detail, we refer to
426 *Eramoscorpius brucensis* Waddington et al., 2015. ROM 53247, holotype (**Fig. 5g**).

427

428 9.2. Phylogenetic justification

429

430 The genus *Dolichophonus* Petrunkevitch, 1949, was erected for *P. loudonensis*, based on the
431 increased length of the prosoma compared to other palaeophonids, namely *P. nuncius* Thorell and
432 Lindström, 1885, and *P. caledonicus* Hunter, 1886. An examination (by D.A.L.) of the single known
433 specimen of *P. loudonensis* could not confirm this character because the specimen is very poorly
434 preserved, and the junction between the prosoma and mesosoma is not easily distinguished. We
435 retain the holotype within *Palaeophonus*. It is even possible that this specimen may belong to one of
436 the other currently recognised species of *Palaeophonus*, although more material would be required. *P.*
437 *loudonensis* was included in a phylogenetic analysis by Legg et al. (2013), in which it resolved
438 amongst total-group Scorpiones. Other Siluro-Devonian fossil scorpions such as *Proscorpius osborni*
439 Whitfield, 1885 and *Palaeoscorpius devonicus* Lehmann, 1944 have been placed in the stem group of
440 Orthosterni (crown-group Scorpiones) (e.g. Legg et al., 2013; Garwood and Dunlop, 2014), which are
441 therefore crown group members of Arachnida.

442

443 9.3. Age justification

444

445 *P. loudonensis* was recovered from the Gutterford Burn section of the “Eurypterid Bed”
446 (Reservoir Formation) in the Pentland Hills, Midlothian, Scotland (Kjellesvig-Waering, 1986), which

447 has been dated as Late Llandovery. The associated graptolite fauna suggests a late Llandovery
448 (Telychian) age for this formation, within the *Oktavites spiralis* Biozone (Bull and Loydell, 1995). A
449 spline-fit age for the upper boundary of the *O. spiralis* Biozone provides a minimum age constraint of
450 435.15 Ma (Melchin et al., 2012).

451 Soft maximum as for 2.3.

452

453 **10. Crown Opiliones**

454

455 This clade comprises Cyphophthalmi and Phalangida (itself comprising Laniatores, Dyspnoi
456 and Eupnoi), their last common ancestor and all of its descendants (**Fig. 4**). Monophyly has been
457 demonstrated by phylogenetic analysis of transcriptomes (Sharma et al., 2014), morphology (Garwood
458 et al., 2011), and combined morphology and molecules (Garwood et al., 2014; Giribet et al., 2002).

459

460 *10.1. Fossil specimens*

461

462 *Eophalangium sheari* Dunlop et al., 2003. PBM slide no. 3503, holotype (**Fig. 5d**), consisting of
463 a lateral thin section outlining nearly the entire female body (Dunlop et al., 2003).

464

465 *10.2. Phylogenetic justification*

466

467 In a phylogenetic analysis of morphology, *E. sheari* was placed in a polytomy with members of
468 Phalangida, to the exclusion of Cyphophthalmi (Garwood and Dunlop, 2014). In combined analysis of
469 molecules and morphology, *E. sheari* was resolved as a stem group Cyphophthalmi (Garwood et al.,
470 2014). Both positions, however, fall within the crown group of Opiliones.

471

472 *10.3. Age justification*

473

474 This fossil is known from the Early Devonian (Pragian) Rhynie Chert of Aberdeenshire,
475 Scotland. Spore assemblages of the Windyfield and stratigraphically underlying Rhynie Chert are
476 dated to the early but not earliest Pragian to early (earliest?) Emsian (polygonalis-emsian Spore
477 Assemblage Biozone) (Parry et al., 2011). Radiometric dating of the underlying Milton of Noth
478 Andesite at ca. 411 Ma (Parry et al., 2013, 2011) has been subject to a dispute over its temporal
479 relationship to hot spring activity associated with the cherts (Mark et al., 2013, 2011) and predates the
480 biostratigraphic dating of the Rhynie Chert relative to the global dating of the base of the Pragian
481 Stage. Therefore, a minimum age constraint may be defined at 405.0 Ma for the Rhynie Chert, using
482 the Pragian-Emsian boundary (407.6 Ma \pm 2.6 Myr) as a reference.

483 A soft maximum constraint comes from the oldest chelicerate *W. barbarhardyae* from the Emu
484 Bay Shale on Kangaroo Island, South Australia, which has been correlated based on trilobite
485 biostratigraphy to the upper part of the *Pararaia janeae* Zone in mainland South Australia (Jell in
486 Bengtson et al., 1990; Fig. 2 in Jago et al., 2012). As this is equivalent to the Canglangpuan Stage in
487 South China and the late Botoman in Siberia (Gehling et al., 2011, Fig. 9), the Emu Bay Shale can be
488 dated to Cambrian Series 2, Stage 4, providing a maximum age of ~514 Ma.

489

490 **11. Crown Acariformes**

491

492 This clade comprises Sarcoptiformes, Trombidiformes and 'Endeostigmata', their last common
493 ancestor and all of its descendants (**Fig. 4**). Monophyly is established by phylogenetic analysis of
494 nuclear ribosomal genes (Pepato and Klimov, 2015), morphology (Garwood and Dunlop, 2014), and
495 combined molecular and morphological data (Pepato et al., 2010).

496

497 *11.1. Fossil specimens*

498

499 *Protacarus crani* Hirst, 1923. BMNH In. 24665, holotype, preserving a nearly complete
500 individual in chert (**Fig. 5k**).

501

502 11.2. *Phylogenetic justification*

503

504 Originally described as a single species (Hirst, 1923), *P. crani* from the Rhynie Chert was
505 subsequently treated as five species belonging to five different genera (Dubinin, 1962). *P. crani* itself,
506 as exemplified by the holotype, was described as a member of Eupodidae, within Trombidiformes
507 (Hirst, 1923), or potentially more basal within the Acariformes (Bernini, 1986). While the specifics of its
508 classification may be debatable due to the lack of preserved diagnostic characters, the fan-like setae
509 observed dorsally in *P. crani* support a relationship with endeostigmatids within crown group
510 Acariformes (Bernini, 1986; Dunlop and Selden, 2009).

511

512 11.3. *Age justification*

513

514 As for 10.3.

515

516 11.4. *Discussion*

517

518 Bernini et al. (2002) figured a putative oribatid mite from terrestrial sediments dated to the Early
519 Ordovician of Sweden. However, its age and systematic placement were queried by Dunlop (2010, p.
520 134) and this species is not used for calibration herein.

521 Arguments that *P. crani* is a Recent contaminant (Crowson, 1985) have been countered by
522 Kühne and Schlüter (1985) and Greenslade (1988). Other species of fossil Acariformes have also
523 been described from the Rhynie Chert (all originally *P. crani*), including *Protospeleorchestes*
524 *pseudoprotacarus*, *Pseudoprotacarus scoticus*, *Palaeotydeus devonicus*, and *Paraprotocarus hirsti* (all

525 Dubinin, 1962).

526

527 **12. Crown Parasitiformes**

528

529 This clade comprises Opilioacariformes, Ixodida (hard and soft ticks), Holothyrida and
530 Mesostigmata, their last common ancestor and all of its descendants (**Fig. 4**). Monophyly is
531 established by phylogenetic analysis of nuclear ribosomal genes (Pepato and Klimov, 2015) and
532 morphology (Garwood and Dunlop, 2014).

533

534 *12.1. Fossil specimens*

535

536 *Cornupalpatum burmanicum* Poinar and Brown, 2003. Holotype larva (accession number A-10-
537 260; **Fig. 5i**) and paratype (accession number A-10-261; **Fig. 5j**) deposited in the Poinar amber
538 collection maintained at Oregon State University, later to be deposited at the California Academy of
539 Sciences (Poinar, 2015; Poinar and Brown, 2003).

540

541 *12.2. Phylogenetic justification*

542

543 Morphological characters such as the subcircular body with a marginal groove, free coxae,
544 ventral anal opening, the presence of a capitulum and Haller's organ, absence of an anal groove, and
545 elongate four-segmented palpi are all suggestive of Parasitiformes affinity for *C. burmanicum* (Poinar
546 and Brown, 2003). A particularly diagnostic character, suggesting placement within at least total-group
547 Ixodida (and thus crown Parasitiformes), is the presence of claws on palpal segment 3 in the larva
548 (Poinar and Brown, 2003). Putative morphologies similar to bacterial pathogens exclusive to modern
549 Ixodida were recently described from the paratype (Poinar, 2015).

550

551 12.3. Age justification

552

553 This fossil is sourced from amber mines in the Hukawng Valley of Kachin State, northern
554 Myanmar (formerly Burma). The depositional age of Burmese amber was estimated from U-Pb dating
555 of zircons from the volcanoclastic matrix surrounding the amber (Shi et al., 2012). Shi et al. (2012)
556 argue the amber is not older than its associated sediments, as burial and preservation would have to
557 be rapid for survival of organic material, so the amber was probably formed at, but not earlier than the
558 U-Pb date: at 98.79 Ma \pm 0.62 Myr. Therefore, a minimum age for any fossil from Burmese amber
559 deposits is 98.17 Ma.

560 Soft maximum as for 10.3.

561

562 13. Crown Pseudoscorpiones

563

564 This clade comprises Feaelloidea, Chthonioidea, Neobisiodea, Garypoidea, Sternophoroidea
565 and Cheliferoidea, their last common ancestor and all of its descendants (**Fig. 4**). While relationships
566 between superfamilies remain unclear, monophyly of Pseudoscorpiones was demonstrated with wide
567 taxon sampling and three genes (Muriene et al., 2008). More limited taxon sampling supports
568 monophyly with morphology (Garwood and Dunlop, 2014) and morphology combined with ribosomal
569 genes (Pepato et al., 2010).

570

571 13.1. Fossil specimens

572

573 *Protofeaella peetersae* Henderickx in Henderickx and Boone, 2016. NHM II 3115, holotype,
574 near complete specimen preserved in amber (**Fig. 5c**).

575

576 13.2. Phylogenetic justification

577

578 Although *P. peetersae* has not been included in a formal phylogenetic analysis, it was assigned
579 to the extant family Feaellidae by Henderickx and Boone (2016:8), based on its narrow cephalothorax,
580 granulated abdomen, and presence of small pedipalps with narrow coxa and small hands. Whilst
581 these features are certainly found in both *P. peetersae* and feaellids, other features, such as slender
582 pedipalp fingers, and the overall shape of the cephalic shield are more like those of pseudogarypids
583 (Harvey, 1992). Both the feaellid and pseudogarypids belong to the superfamily Feaelloidea (*sensu*
584 Harvey, 1992), and thus it is still likely *P. peetersae* belongs within the pseudoscorpion crown-group.

585

586 13.3. Age justification

587

588 As for 12.3.

589

590

591 13.4. Discussion

592

593 *Dracochela deprehendor* Schawaller et al., 1991 from the Middle Devonian of Gilboa, New
594 York State, was originally interpreted as a crown-group pseudoscorpion but was reassigned to the
595 pseudoscorpion stem group (Judson, 2012). Preliminary morphological phylogenetic analyses by one
596 of us (D.A.L.), however, suggest that *D. deprehendor* may be within the crown group. If so, this would
597 drastically extend the range of crown Pseudoscorpiones by over 280 Myr (to a minimum age of 382.7
598 Ma; Richardson et al., 1993).

599 Note that other Cretaceous pseudoscorpions have been preserved in amber (older from
600 Lebanon and Spain; younger from France, New Jersey and Alberta), but these have yet to be fully
601 described or examined for their systematic positions (Judson, 2009). If the Lebanese or Spanish
602 fossils were found to be members of the crown group, they could extend the range of

603 Pseudoscorpiones by up to 27 Myr.

604

605 **14. Crown Palpigradi**

606

607 This clade comprises the families Eukoeneniidae and Prokoeneniidae, their last common
608 ancestor and all of its descendants (**Fig. 4**). Monophyly has been supported by a phylogenetic
609 analysis of two nuclear ribosomal and one mitochondrial gene (Giribet et al., 2014).

610

611 *14.1. Fossil specimens*

612

613 *Electrokoenenia yaksha* Engel et al., 2016b. NIGP 163253, holotype in amber (**Fig. 5e**).

614

615 *14.2. Phylogenetic justification*

616

617 *E. yaksha* was classified within the extant family Eukoeneniidae (Engel et al., 2016b). This was
618 justified with morphological characters, in particular the rounded lateral “arms” to the frontal organ of
619 the propeltidium, as seen in the extant genus *Leptokoenenia* (Engel et al., 2016b). Thus *E. yaksha* is
620 within the crown group of Palpigradi.

621

622 *14.3. Age justification*

623

624 As for 12.3.

625

626 **15. Crown Solifugae**

627

628 This clade comprises Ammotrechidae, Ceromidae, Daesiidae, Eremobatidae, Galeodidae,

629 Gylippidae, Hexisopodidae, Karschiidae, Melanoblossidae, Mummuciidae, Rhagodidae and
630 Solpugidae, their last common ancestor and all of its descendants (**Fig. 4**). No phylogenetic analysis
631 has yet included all families, but limited taxon sampling has shown monophyly with morphology
632 (Garwood and Dunlop, 2014; Shultz, 2007) and morphology combined with nuclear genes (Giribet et
633 al., 2002; Pepato et al., 2010). Extensive morphological work on the homology of cheliceral characters
634 was recently published by Bird et al. (2015).

635

636 15.1. Fossil specimens

637

638 *Cratosolpuga wunderlichi* Selden and Shear, 1996 (Sol. 1 in the private Wunderlich collection,
639 Straubenhardt, Germany), holotype. An additional specimen (SMNK 1268 PAL; **Fig. 5f**), not a
640 paratype, is also deposited.

641

642 15.2. Phylogenetic justification

643

644 *C. wunderlichi* was assigned to the extant family Ceromidae on the basis of shape of the
645 cheliceral flagellum, shape of the propeltidium, eye tubercle, and leg spination (Selden and Shear,
646 1996). Only a single tarsal segment is present on the legs (Selden and Shear, 1996). A position in
647 total-group Ceromidae would therefore be within crown-group Solifugae.

648

649 15.3. Age justification

650

651 This fossil was recovered from the Nova Olinda Member of the Crato Formation in the Araripe
652 Basin, northeastern Brazil. This unit is generally agreed to be around the Aptian/Albian border (Martill
653 et al., 2007). Batten (2007) suggests that if assemblages in the upper layers are consistent across the
654 lower layers, a late Aptian date should be considered. The Crato formation has been dated using

655 palynomorphs (Pons et al., 1990) to the Aptian, though an accurate date for the Nova Olinda Member
656 is not available. The upper boundary of the Aptian, at 113.0 Ma \pm 0.4 Myr, gives a minimum date of
657 112.6 Ma.

658 Soft maximum as for 10.3.

659

660 15.4. Discussion

661

662 The Pennsylvanian *Protosolpuga carbonaria* Petrunkevitch, 1913, the only older possible fossil
663 solifuge, was discounted from the crown group of Solifugae in the same paper as described *C.*
664 *wunderlichi* (Selden and Shear, 1996). It is too poorly preserved to assign to the crown group without
665 additional phylogenetic justification.

666

667 16. Crown Scorpiones

668

669 This clade comprises Buthida and Iurida, their last common ancestor and all of its descendants
670 (**Fig. 4**). The composition of Buthida and Iurida are as detailed in Sharma et al. (2015). Monophyly has
671 been supported by phylogenetic analysis of transcriptomes (Sharma et al., 2015, 2014), morphology
672 (Garwood and Dunlop, 2014; Shultz, 2007), and combined ribosomal sequences and morphology
673 (Pepato et al., 2010).

674

675 16.1. Fossil specimens

676

677 *Protoischnurus axelrodurum* Carvalho and Lourenço, 2001. MN-7601-I, holotype, a male. We
678 also refer to the specimen SMNS 65534, which preserves phylogenetically relevant details of the
679 pedipalps (Fig. 3c in Menon, 2007).

680

681 16.2. *Phylogenetic justification*

682

683 Menon (2007) placed *P. axelrodurum* in the extant family Hemiscorpiidae, based on, amongst
684 other things, an inverse Y-shape on sulcus on the cephalic shield, the placement of Est trichobothria
685 on the pedipalp chela, and the placement of carinae V2 and V3 in the pedipalp chela, all of which are
686 diagnostic of the hemiscorpidid subfamily Hormurinae (Soleglad et al., 2005). Hemiscorpiidae is
687 classified within Iurida (Sharma et al., 2015), and is thus crown group Scorpiones.

688

689 16.3. *Age justification*

690

691 As for 15.3.

692

693 16.4. *Discussion*

694

695 A number of fossil taxa have been placed within crown group scorpion families, including
696 *Protobuthus elegans* Lourenço and Gall, 2004, from the Early Triassic Buntsanstein of France. It was
697 assigned to the superfamily Buthoidea, however, a subsequent study (Baptista et al., 2006),
698 considered this taxon and *Archaeobuthus* from the Early Cretaceous of Lebanon, outside the crown-
699 group based on trichobothrial arrangement.

700 *Araripescorpius ligabuei* Campos, 1986 is coeval to *P. axelrodurum*, and from the same locality.
701 Menon (2007) placed *A. ligabuei* in the extant family Chactidae based on general habitus and
702 trichobothrial pattern. Therefore it is also a member of the crown group of Scorpiones, albeit a less
703 well-preserved species.

704

705 17. **Crown Tetrapulmonata**

706

707 This clade comprises Pedipalpi and Araneae (spiders), their last common ancestor and all of its
708 descendants (**Fig. 6**). Monophyly is supported by phylogenetic analysis of transcriptomes (Sharma et
709 al., 2014), nuclear protein-coding genes (Regier et al., 2010), and morphology (Garwood and Dunlop,
710 2014; Legg et al., 2013; Shultz, 2007). This clade is not recognized in GenBank taxonomy.

711

712 17.1. Fossil specimens

713

714 *Parageralinura naufraga* (Tetlie and Dunlop, 2008), LWL Ar.K.1 (**Fig. 7a**). Counterpart in the
715 private collection of W. Elze, Ennepetal, Germany.

716

717 17.2. Phylogenetic justification

718

719 Tetlie and Dunlop (2008) interpreted Coal Measures uropygids to comprise a plesion on the
720 stem of the extant Thelyphonidae, the sole extant family of Thelyphonida. A subchelate pedipalp is
721 considered apomorphic of the crown group but is lacking in *Geralinura* and *P. naufraga*. This identifies
722 them as crown Uropygi, and thus, Tetrapulmonata.

723

724 17.3. Age justification

725

726 Of the uropygid fossils, the oldest are *P. naufraga* (formerly *Prothelyphonus naufragus*) from
727 deposits of "Ziegelei-Grube," Hagen-Vorhalle, Nordrhein-Westphalia, Germany (Brauckmann and
728 Koch, 1983; Tetlie and Dunlop, 2008). The fossil-bearing deposits are assigned to the Namurian B
729 (Marsdenian) based on the *Bilinguites metabilinguis* R2c1 subzone of ammonoid stratigraphy
730 (Brauckmann et al., 1994; Tetlie and Dunlop, 2008). The (late) Namurian-(early) Westphalian
731 boundary is defined by the earliest occurrence of the goniatite *Gastrioceras subcrenatum* (Waters and
732 Davies, 2006), but lacks a precise isotopic date. Pointon et al. (2012) estimated an age of c. 319.9 Ma

733 for the base of the Westphalian (top of the Namurian, only slightly younger than the Marsdenian)
734 based on Milankovitch cycles of sedimentation, giving a minimum age for *P. naufraga*.

735 Soft maximum as for 10.3.

736

737 **18. Crown Pedipalpi**

738

739 This clade comprises Amblypygi (tailless whip scorpions) and Uropygi, their last common
740 ancestor and all of its descendants (**Fig. 6**). Monophyly is supported by phylogenetic analysis of
741 transcriptomes (Sharma et al., 2014), nuclear protein-coding genes (Regier et al., 2010), and
742 morphology (Garwood and Dunlop, 2014; Legg et al., 2013; Shultz, 2007). This clade is not
743 recognized in GenBank taxonomy.

744

745 *18.1. Fossil specimens*

746

747 As for 17.1.

748

749 *18.2. Phylogenetic justification*

750

751 As for 17.2.

752

753 *18.3. Age justification*

754

755 As for 17.3.

756

757 **19. Crown Uropygi**

758

759 This clade comprises Thelyphonida (whip scorpions) and Schizomida, their last common
760 ancestor and all of its descendants (**Fig. 6**). Monophyly is supported by phylogenetic analysis of
761 nuclear protein-coding genes (Regier et al., 2010), and morphology (Garwood and Dunlop, 2014;
762 Legg et al., 2013; Shultz, 2007).

763

764 *19.1. Fossil specimens*

765

766 As for 17.1.

767

768 *19.2. Phylogenetic justification*

769

770 As for 17.2.

771

772 *19.3. Age justification*

773

774 As for 17.3.

775

776 **20. Crown Amblypygi**

777

778 This clade comprises Paracharontidae, Charinidae, Charontidae, Phrynichidae and Phrynidae,
779 their last common ancestor and all of its descendants (**Fig. 6**). Monophyly of Amblypygi has not been
780 fully investigated with phylogenetic analysis; however, monophyly has been shown for at least some
781 families with morphological data (Garwood and Dunlop, 2014; Shultz, 2007) and morphology
782 combined with nuclear genes (Pepato et al., 2010).

783

784 *20.1. Fossil specimens*

785

786 *Graeophonus anglicus* Pocock, 2011. BMNH In. 31233, holotype (**Fig. 7b**). Figured in Dunlop
787 et al. (2007: Fig. 1 a,b).

788

789 20.2. Phylogenetic justification

790

791 *G. anglicus* was redescribed by Dunlop et al. (2007) as a member of the Amblypygi crown
792 group. This was based on several morphological character comparisons to living members, such as
793 the pedipalp femur with dorsal spination similar to *Paracharon* (the monotypic extant species of the
794 family Paracharontidae). *G. anglicus*, unlike *Paracharon*, has a pear-shaped ocular tubercle,
795 suggesting it was not blind. *G. anglicus* is inferred to be on the stem lineage of Paracharontidae, and
796 thus, crown group Amblypygi (Dunlop et al., 2007).

797

798 20.3. Age justification

799

800 The genus *Graeophonus* was originally described from the Sydney Basin, Cape Breton
801 Carboniferous Coal Measures, Nova Scotia, Canada, which corresponds to Westphalian in age
802 (Dunlop et al., 2007; Giles et al., 2002; Scudder, 1890a). Further studies are needed on the Canadian
803 material, so the minimum age was taken from the oldest European specimen (which is roughly the
804 same age as the Cape Breton specimen) from the British Middle Coal Measures (Coseley,
805 Staffordshire), which is Westphalian B (or Duckmantian) at the youngest (Waters et al., 1994; Waters
806 and Davies, 2006). U-Pb dating of zircons constrains the upper boundary of the Duckmantian to
807 313.78 Ma \pm 0.08 Myr (Pointon et al., 2012), so a minimum age for *G. anglicus* is 313.70 Ma.

808 Soft maximum as for 10.3.

809

810 21. Crown Araneae

811

812 This clade comprises Mesothelae, Mygalomorphae (tarantulas, funnel-web spiders) and
813 Araneomorphae (most spiders), their last common ancestor and all of its descendants (**Fig. 6**).
814 Monophyly is established by phylogenetic analysis of transcriptomes (Fernández et al., 2014a;
815 Garrison et al., 2016) and morphology (Garwood and Dunlop, 2014; Legg et al., 2013; Shultz, 2007).

816

817 21.1. Fossil specimens

818

819 *Palaeothele montceauensis* Selden, 2000. Muséum d'Histoire naturelle, Autun: 51961
820 (holotype; **Fig. 7c**), and BMNH 62050, second specimen (not a paratype, **Fig. 7d**; Selden, 1996). We
821 also compare to *Arthrolycosa* sp. B Selden et al. 2014. PIN 5431/9 (**Fig. 7e**).

822

823 21.2. Phylogenetic justification

824

825 The deep, narrow sternum of *P. montceauensis* (formerly *Eothele montceauensis* Selden,
826 1996) is shared by extant members of Mesothelae (Selden, 1996). Several other characters that are
827 symplesiomorphic within Araneae, such as spinnerets, suggest a position within crown Araneae, and
828 perhaps on the stem lineage of Mesothelae (Selden, 1996).

829

830 21.3. Age justification

831

832 *P. montceauensis* was found in the Montceau Lagerstätte, Montceau-les-Mines, Massif
833 Central, France. The nodule-rich layer is just above the first seam in the Great Seams Formation (late
834 Stephanian) (Perrier and Charbonnier, 2014). The age within the Stephanian has been assigned to
835 Stephanian B, with some biostratigraphic evidence for Stephanian C (Racheboeuf et al., 2002). The
836 Stephanian B/C is a European stage of the Pennsylvanian, straddling the boundary of the globally

837 used Kasimovian and Gzhelian (Richards, 2013). The upper boundary of the Gzhelian is 298.9 Ma \pm
838 0.15 Myr, hence the minimum age of the Montceau Lagerstätte is 298.75 Ma.

839 Soft maximum as for 10.3.

840

841 21.4 Discussion

842

843 A possible older spider, *Arthrolycosa* sp. B Selden et al., 2014, is known from the
844 Krasnodonsky Horizon of Rostov Province, Russia (Duckmantian, ~313 Ma). It shares characters with
845 extant Mesothelae, such as the position and morphology of the eye tubercles, but lacks spinnerets, so
846 the inference is largely based on better-known *Arthrolycosa* from other localities (Selden et al., 2014).
847 Because phylogenetic evidence for crown group membership is largely indirect, we maintain *P.*
848 *montceauensis* as the oldest well-supported Araneae.

849

850 22. Crown Mandibulata

851

852 This clade comprises Myriapoda and Pancrustacea, their last common ancestor and all of its
853 descendants (**Fig. 1**). Monophyly has been independently demonstrated based on protein-coding
854 genes and microRNAs, as well as morphological data (Rota-Stabelli et al., 2011).

855

856 22.1. Fossil specimens

857

858 As for 4.1.

859

860 22.2. Phylogenetic justification

861

862 As for 4.2.

863

864 22.3. *Age justification*

865

866 As for 4.3.

867

868 22.4. *Discussion*

869

870 *Wujicaris muelleri* Zhang et al., 2010 has an equal claim to being the earliest record of
871 Mandibulata, but it is of equal age to the holotype of *Y. dianensis*.

872

873 **23. Crown Myriapoda**

874

875 This is the clade comprising Chilopoda (centipedes) and Progoneata, their last common
876 ancestor and all of its descendants (**Fig. 1**). Monophyly has been demonstrated by morphology
877 (Edgecombe, 2004; Legg et al., 2013; Rota-Stabelli et al., 2011), nuclear protein-coding genes (Regier
878 et al., 2010; Zwick et al., 2012), transcriptomes (Rehm et al., 2014), and combined analysis of
879 molecules and morphology (Lee et al., 2013).

880

881 23.1. *Fossil specimens*

882

883 *Cowiedesmus eroticopodus* Wilson and Anderson, 2004. AMS F.64845, holotype (**Fig. 2e**).

884

885 23.2. *Phylogenetic justification*

886

887 Membership of *C. eroticopodus* in Diplopoda is indicated by its strict diplosegmentation,
888 whereas its cuticular mineralization supports membership in the subgroup Chilognatha, and its

889 modified legs on trunk segment 8 support membership in Helminthomorpha. *C. eroticopodus* is
890 resolved as total-group Helminthomorpha in the morphological cladistic analysis of Fernández et al.
891 (2016) and is accordingly a member of the crown-groups of Chilognatha, Diplopoda, Progoneata and
892 Myriapoda.

893

894 23.3. Age justification

895

896 The earliest myriapods in the body fossil record are three species of Diplopoda from the
897 *Dictyocaris* Member of the Cowie Formation at Cowie Harbour, near Stonehaven, Aberdeenshire,
898 Scotland, one of which is *C. eroticopodus* (Wilson and Anderson, 2004). Based on associated spores,
899 the Cowie Formation taxa are late Wenlock to early Ludlow in age (Marshall, 1991; Wellman, 1993)
900 and the Early Ludlow upper boundary (Gorstian-Ludfordian boundary) is 425.6 Ma \pm 0.9 Myr, so the
901 minimum age for Myriapoda is 424.7 Ma.

902 Soft maximum as for 2.3.

903

904 23.4. Discussion

905

906 *Albadesmus almondi* and *Pneumodesmus newmani* (both described by Wilson and Anderson,
907 2004) have an equal claim to being the oldest myriapod, sourced from the same locality and unit as *C.*
908 *eroticopodus*. The latter was selected because it has been explicitly coded in a morphological cladistic
909 analysis (Fernández et al., 2016). We have not used trace fossil evidence suggestive of Ordovician
910 diplopods (Wilson, 2006) for dating.

911

912 24. Crown Progoneata

913

914 This clade comprises Diplopoda (millipedes), Pauropoda and Symphyla, their last common

915 ancestor and all of its descendants (**Fig. 8**). Monophyly is supported by phylogenetic analysis of
916 nuclear protein-coding genes (Regier et al., 2010; Zwick et al., 2012), whole mitochondrial genomes
917 (Brewer et al., 2013), and morphology (Edgecombe, 2004; Legg et al., 2013). Two recent molecular
918 phylogenies reject monophyly of Progoneata in favour of a putative clade of Chilopoda and Diplopoda:
919 one based on three protein-coding genes (Miyazawa et al., 2014) and one on transcriptomes (Rehm
920 et al., 2014). This clade is not recognized in GenBank taxonomy.

921

922 *24.1. Fossil specimens*

923

924 As for 23.1.

925

926 *24.2. Phylogenetic justification*

927

928 As for 23.2.

929

930 *24.3. Age justification*

931

932 As for 23.3.

933

934 *24.4. Discussion*

935

936 As for 23.4.

937

938 **25. Crown Diplopoda**

939

940 This clade comprises Penicillata (bristly millipedes) and Chilognatha, their last common

941 ancestor and all of its descendants (**Fig. 8**). Monophyly is supported by morphological analyses
942 (Blanke and Wesener, 2014), nuclear protein-encoding genes (Regier et al., 2010), and
943 transcriptomes (Fernández et al., 2016; Rehm et al., 2014).

944

945 *25.1. Fossil specimens*

946

947 As for 23.1.

948

949 *25.2. Phylogenetic justification*

950

951 As for 23.2.

952

953 *25.3. Age justification*

954

955 As for 23.3.

956

957 *25.4. Discussion*

958

959 As for 23.4.

960

961 **26. Crown Penicillata**

962

963 This clade comprises Polyxenoidea and Synxenoidea, their last common ancestor and all of its
964 descendants (**Fig. 8**). Monophyly has been defended based on the shared presence of serrate setae
965 arranged in lateral and caudal tufts (Enghoff, 1984).

966

967 26.1. *Fossil specimens*

968

969 *Electroxenus jezzinensis* Nguyen Duy-Jacquemin and Azar, 2004 (Acra collection, provisionally
970 deposited at MNHN: JS 231/1), holotype (**Fig. 9a,b**), adult in amber (Nguyen Duy-Jacquemin and
971 Azar, 2004, Fig. 1A, B).

972

973 26.2. *Phylogenetic justification*

974

975 Cretaceous amber penicillates are readily assigned to two of the three extant families,
976 Polyxenidae and Synxenidae (Nguyen Duy-Jacquemin and Azar, 2004; classification of Penicillata
977 following Short in Enghoff et al., 2015). *E. jezzinensis* preserves diagnostic characters of Polyxenidae
978 such as lateral extensions of the gnathochilarial palps. Membership in an extant family indicates status
979 as crown Penicillata.

980

981 26.3. *Age justification*

982

983 *E. jezzinensis* was discovered in amber from the Jouar Ess-Souss locality, in the Jezzine area,
984 South Lebanon (Azar et al., 2010). Previous work suggested a Neocomian (Valanginian-Hauterivian)
985 age for the Jezzine area (Azar et al., 2010). However, Lebanese stratigraphy has recently been
986 revised; the Jouar Ess-Souss locality is now recognized as part of the lowermost interval of the Grès
987 du Liban (Maksoud et al., 2016). The lower interval lies below a shale layer bearing the echinoid fossil
988 *Heteraster oblongus*, and below a pisolitic interval bearing charyophyte fossils (Maksoud et al., 2016).
989 The charyophyte layer is associated to the *Cruciata-Paucibracteatus* Zone of Martín-Closas et al.
990 (2009) in the late Barremian-early Aptian, but this layer is also older than the Banc de Mrejatt subunit
991 within Lebanon, thus Jezzine amber is older than the Ba2 layer in Fig. 6 of Maksoud et al. (2016).
992 Jezzine amber is therefore no younger than early Barremian. The upper boundary of the early

993 Barremian is proposed to be the first appearance of the ammonite *Ancyloceras vandenheckii* (Ogg et
994 al., 2012). Cyclostratigraphy dates the *A. vandenheckii* Zone beginning at 129.41 Ma (Ogg et al.,
995 2012), providing a minimum age for Jezzine Lebanese amber fossils.

996 A soft maximum age is obtained from the oldest mandibulate, *Y. dianensis*, which was
997 recovered from the Yu'anshan Formation at Xiaotan section, Yongshan, Yunnan Province, attributed to
998 the *Eoredlichia*–*Wutingaspis* Biozone (Zhang et al., 2007). Chinese Cambrian stratigraphy has been
999 revised substantially and the *Eoredlichia* – *Wutingaspis* Biozone is no longer recognized (Peng, 2009,
1000 2003). However, *Eoredlichia* is known to co-occur with *Hupeidiscus*, which is diagnostic of the
1001 *Hupeidiscus*-*Sinodiscus* Biozone, which is formally recognised as the second biozone of the
1002 Nangaoan Stage of the Qiandongian Series of the Cambrian of China (Peng and Babcock, 2008). The
1003 Nangaoan is the proposed third stage of the Cambrian System for the International Geologic
1004 Timescale (Peng et al., 2012). Thus, a soft maximum constraint can be established on the age of the
1005 lower boundary of the Nangaoan, which has been dated to 521 Ma (Peng et al., 2012; Peng and
1006 Babcock, 2008).

1007

1008 26.4. Discussion

1009

1010 Another species of Polyxenidae from Lebanese amber, *Libanoxenus hammanaensis* Nguyen
1011 Duy-Jacquemin and Azar, 2004, is likewise known from a single specimen, from the Mdeiriji/Hammana
1012 locality in Central Lebanon. Its age data are similar to those of the more completely known *E.*
1013 *jezzinensis*, so the latter is used for calibration.

1014

1015 27. Crown Chilognatha

1016

1017 This clade comprises Pentazonia (pill millipedes) and Helminthomorpha (long-bodied
1018 millipedes), their last common ancestor and all of its descendants (**Fig. 8**). Monophyly is supported by

1019 morphological analyses (Blanke and Wesener, 2014), nuclear coding genes (Miyazawa et al., 2014),
1020 and transcriptomes (Fernández et al., 2016). Chilognthan monophyly has rarely been opposed: some
1021 analyses of nuclear protein coding genes by Regier et al. (2005) found weak support for an
1022 unconventional grouping of Penicillata with Pentazonia, but others retrieved Chilognatha.

1023

1024 *27.1. Fossil specimens*

1025

1026 As for 23.1.

1027

1028 *27.2. Phylogenetic justification*

1029

1030 As for 23.2.

1031

1032 *27.3. Age justification*

1033

1034 Minimum as for 23.3. Soft maximum as for 26.3.

1035

1036 *27.4. Discussion*

1037

1038 As for 23.4.

1039

1040 **28. Crown Chilopoda**

1041

1042 This clade comprises Scutigermorpha (house centipedes) and Pleurostigmophora, their last
1043 common ancestor and all of its descendants (**Fig. 8**). Monophyly is robustly supported by
1044 morphological analyses (Edgecombe and Giribet, 2004; Muriene et al., 2010), nuclear protein-coding

1045 genes (Miyazawa et al., 2014; Regier et al., 2010; Zwick et al., 2012), and transcriptomics (Fernández
1046 et al., 2016; Rehm et al., 2014).

1047

1048 28.1. Fossil specimens

1049

1050 *Crussolum* sp. Jeram et al., 1990. DE 1.3.2/50 (Fig. 1N) and DE 3.1.1/88 (Fig. 1P; Jeram et al.,
1051 1990). As mentioned below, we also refer to material from the Windyfield Chert (AUGD 12307-12308;
1052 Anderson and Trewin, 2003) for morphological details (**Fig. 9c-e**).

1053

1054 28.2. Phylogenetic justification

1055

1056 *Crussolum* was resolved as stem-group Scutigeromorpha in the morphological cladistic
1057 analysis of Fernández et al. (2016). Codings were a composite of material described as *Crussolum* sp.
1058 from the Windyfield Chert (Pragian) of the Dryden Flags Formation, Aberdeenshire, Scotland (figured
1059 by Anderson and Trewin, 2003), and the one formally named species of the genus, *C. crusseratum*
1060 (Shear et al., 1998), known from isolated and fragmentary legs from the Middle Devonian Gilboa
1061 locality, Schoharie County, New York State (Givetian).

1062

1063 28.3. Age justification

1064

1065 The oldest examples of *Crussolum* are isolated legs from Ludford Lane in England (Shear et
1066 al., 1998), which come from a horizon 0.15-0.20 m above the base of the Ludlow Bone Bed Member,
1067 in the Downtown Castle Sandstone Formation. The Ludlow Bone Bed Member is early Pridoli in age
1068 (Jeram et al., 1990), that stage having an upper boundary of 419.2 Ma \pm 3.2 Myr, providing a minimum
1069 age of 416.0 Ma. *Crussolum* as currently delimited crosses the Silurian-Devonian boundary.

1070 Soft maximum as for 2.3.

1071

1072 **29. Crown Scutigeromorpha**

1073

1074 This clade comprises Scutigeridae, Scutigerinidae and Psellioididae, their last common
1075 ancestor and all of its descendants (**Fig. 8**). Monophyly is robustly supported by morphological
1076 analyses (Edgecombe and Giribet, 2004), targeted gene sequencing (Murienne et al., 2010), and
1077 transcriptomics (Fernández et al., 2016).

1078

1079 *29.1. Fossil specimens*

1080

1081 *Fulmenocursor tenax* Wilson, 2001. SMNS 64275, holotype (**Fig. 9f**), nearly complete
1082 specimen (Wilson, 2001, Pl. 1, Fig. 2).

1083

1084 *29.2. Phylogenetic justification*

1085

1086 Wilson (2001) assigned *F. tenax* to the extant family Scutigeridae based on the proportions of
1087 its antennal articles and its styliiform male gonopods. Paired spine-bristles on the tibia of the second
1088 maxilla (synapomorphy of Psellioididae + Scutigeridae) are consistent with this interpretation
1089 (Edgecombe, 2011). These affinities place the genus in crown-group Scutigeromorpha.

1090

1091 *29.3. Age justification*

1092

1093 Minimum as for 15.3. Soft maximum as for 26.3.

1094

1095 *29.5 Discussion*

1096

1097 A total-group scutigeromorph from the Carboniferous Mazon Creek deposits, *Latzelia*
1098 *primordialis* Scudder, 1890b, cannot be reliably assigned to the scutigeromorph crown group
1099 (Edgecombe, 2011; J. T. Haug et al., 2014) and is accordingly not used for dating that clade.

1100

1101 **30. Crown Pleurostigmophora**

1102

1103 This clade comprises Craterostigmomorpha and Amalpighiata, their last common ancestor and
1104 all of its descendants (**Fig. 8**); membership is identical if the internal relationships of the clade are
1105 resolved as Lithobiomorpha + Phylactometria. Monophyly is supported by morphological analyses
1106 (Edgecombe and Giribet, 2004), nuclear ribosomal and mitochondrial genes, and their combination
1107 with morphology (Giribet and Edgecombe, 2006; Murienne et al., 2010), nuclear protein coding genes
1108 (Regier et al., 2010), and transcriptomics (Fernández et al., 2016, 2014b).

1109

1110 *30.1. Fossil specimens*

1111

1112 *Devonobius delta* Shear and Bonamo, 1988. AMNH slide 411-15-AR18, holotype (**Fig. 9g**),
1113 complete head with 15 or 16 trunk segments. We also refer to AMNH slide 4329-AR4 (**Fig. 9h**).

1114

1115 *30.2. Phylogenetic justification*

1116

1117 *D. delta* was resolved in a trichotomy with *Craterostigmus* and Epimorpha in the morphological
1118 cladistic analysis of (Edgecombe and Giribet, 2004, Fig. 9), and as sister group to extant
1119 Phylactometria when those data were combined with sequence data from four genes (Edgecombe
1120 and Giribet, 2004, Fig. 14). Published analyses agree on it being more closely related to Epimorpha
1121 than to Lithobiomorpha (Shear and Bonamo, 1988, Fig. 1; Murienne et al., 2010, Fig. 2; Fernández et
1122 al., 2016) and it is accordingly crown Pleurostigmophora.

1123

1124 30.3. *Age justification*

1125

1126 *D. delta* occurs in the Middle Devonian Gilboa locality, Schoharie County, New York State,
1127 USA. Fossils come from the upper part of the Panther Mountain Formation, dated to the Tioughniogan
1128 regional Stage, Givetian in the global time scale. Palynomorphs are consistent with a Givetian age
1129 (Richardson et al., 1993). Accordingly, minimum date for the end of the Givetian/base of the Frasnian
1130 is applied (382.7 Ma).

1131 Soft maximum as for 26.3.

1132

1133 31. Crown Amalpighiata

1134

1135 This clade comprises Lithobiomorpha (stone centipedes) and Epimorpha, their last common
1136 ancestor and all of its descendants (**Fig. 8**). Monophyly is supported by targeted gene sequencing
1137 (Regier et al., 2010) and transcriptomics (Fernández et al., 2016, 2014b).

1138

1139 31.1. *Fossil specimens*

1140

1141 *Mazoscolopendra richardsoni* Mundel, 1979. FMNH PE 22936, holotype, nearly complete
1142 specimen in siderite concretion (J. T. Haug et al., 2014; Mundel, 1979). We also refer to FMNH PE
1143 29002 (**Fig. 9i**).

1144

1145 31.2. *Phylogenetic justification*

1146

1147 *M. richardsoni* was coded by Fernández et al. (2016) for its morphological data based on
1148 descriptions and figures of Mundel (1979) and Haug et al. (J. T. Haug et al., 2014), and personal

1149 observation by G.D.E. of type and other material in the Field Museum. It was resolved as total-group
1150 Scolopendromorpha based on possession of autapomorphies of that order (e.g. single tergite on the
1151 forcipular/first leg-bearing segments, 21 pairs of trunk legs) but cannot be placed more precisely with
1152 regards to whether it is a stem- or crown-group scolopendromorph. Nonetheless, its membership in
1153 Scolopendromorpha assigns it to crown Amalpighiata. The same calibration would apply were the
1154 putative clade Phylactometria endorsed in lieu of Amalpighiata.

1155

1156 31.3. *Age justification*

1157

1158 Specimens are derived from the Francis Creek Shale Member of the Carbondale Formation,
1159 Mazon Creek, Illinois, of Westphalian D age (Baird et al., 1985; Shabica and Hay, 1997). The
1160 Westphalian D is equivalent to the latest Moscovian stage of the Pennsylvanian (Richards, 2013). As
1161 the upper boundary of the Moscovian is $307.0 \text{ Ma} \pm 0.1 \text{ Myr}$, this provides a minimum age of 306.9
1162 Ma.

1163 Soft maximum as for 26.3.

1164

1165 32. Crown Epimorpha

1166

1167 This clade comprises Scolopendromorpha and Geophilomorpha, their last common ancestor
1168 and all of its descendants (**Fig. 8**). Monophyly is supported by morphological analyses (Fernández et
1169 al., 2016; Murienne et al., 2010) and transcriptomics (Fernández et al., 2016, 2014b).

1170

1171 32.1. *Fossil specimens*

1172

1173 As for 31.1.

1174

1175 32.2. *Phylogenetic justification*

1176

1177 As for 31.2.

1178

1179 32.3. *Age justification*

1180

1181 As for 31.3.

1182

1183 **33. Crown Geophilomorpha**

1184

1185 This clade comprises Placodesmata and Adesmata, their last common ancestor and all of its
1186 descendants (**Fig. 8**). Monophyly is supported by morphological analyses, targetted sequencing, and
1187 combination of molecular and morphological data (Bonato et al., 2014a; Fernández et al., 2014b;
1188 Murienne et al., 2010) and transcriptomics (Fernández et al., 2016).

1189

1190 33.1. *Fossil specimens*

1191

1192 *Kachinophilus pereirai* Bonato et al., 2014b. AMNH Bu-Ba41a, holotype (**Fig. 9j,k**), complete
1193 adult male in amber (Bonato et al., 2014b, Fig. 1A-B, 2).

1194

1195 33.2. *Phylogenetic justification*

1196

1197 *K. pereirai* was originally assigned to the extant family Geophilidae based on a combination of
1198 characters that is unique to that family. More precisely it compares most closely to a subgroup within
1199 Geophilidae that has been classified as subfamilies Chilenophilinae or Pachymeriinae. *K. pereirai* was
1200 coded by Fernández et al. (2016) for its morphological data based on original observations on the type

1201 material. It was resolved as more closely related to extant Geophilidae (*sensu* Bonato et al., 2014a)
1202 than to members of any of the other sampled geophilomorph family, as predicted by its original
1203 classification. Thus it is unambiguously a member of crown Adesmata and accordingly crown
1204 Geophilomorpha.

1205

1206 33.3. *Age justification*

1207

1208 Minimum as for 12.3. Soft maximum as for 26.3.

1209

1210 33.4. *Discussion*

1211

1212 A total-group geophilomorph from the Late Jurassic of Germany, *Eogeophilus jurassicus*
1213 Schweigert and Dietl, 1997 (refigured by J. T. Haug et al., 2014), is too inadequately known to
1214 establish whether or not it is a member of the geophilomorph crown-group.

1215

1216 34. **Crown Pancrustacea**

1217

1218 This clade comprises Oligostraca, Multicrustacea, and Allotriocarida, their last common
1219 ancestor and all of its descendants (**Fig. 1**). The inclusion of Hexapoda in a paraphyletic ‘Crustacea’
1220 (and hence, erection of the clade Pancrustacea; Zrzavý and Štys, 1997) has been supported by
1221 numerous phylogenetic analyses, including those based on nuclear protein-coding genes (Regier et
1222 al., 2010, 2005), transcriptomes (Andrew, 2011; Meusemann et al., 2010; Rota-Stabelli et al., 2011;
1223 von Reumont et al., 2012), morphology (Legg et al., 2013; Schram and Koenemann, 2004; Strausfeld
1224 and Andrew, 2011) and combined morphological and molecular data (Oakley et al., 2013).

1225 This clade has also been named Tetraconata (Dohle, 2001) referring to the shared apomorphy
1226 of four cone cells within the compound eye; however this character is absent in many members of the

1227 clade, with multiple possible reconstructions of homology (Oakley, 2003; T. Oakley, pers. comm.).
1228 Terminology that does not rely on the homology of cone cell arrangement is thus preferred. More
1229 recently, an amended version of 'Crustacea' has been proposed (Haug and Haug, 2015) to avoid a
1230 different application of the 'Pan-' prefix (Lauterbach, 1989). While this concept of Crustacea is in our
1231 view valid, for this purpose we favour the original use of Pancrustacea referring to the crown group
1232 members only (Zrzavý and Štys, 1997). Haug and Haug (2015) argue that fossils such as
1233 Phosphatocopina would need to be included within Pancrustacea, however recent phylogenetic
1234 analyses show the sister group to crown Pancrustacea is in fact crown Myriapoda, with all other fossils
1235 outside (Legg et al., 2013). Pancrustacea is the clade name implemented in GenBank, and is the most
1236 commonly used name among molecular workers.

1237

1238 *34.1. Fossil specimens*

1239

1240 As for 4.1.

1241

1242 *34.2. Phylogenetic justification*

1243

1244 As for 4.2.

1245

1246 *34.3. Age justification*

1247

1248 As for 4.3.

1249

1250 *34.4. Discussion*

1251

1252 As for 22.4.

1253

1254 **35. Crown Oligostraca**

1255

1256 This clade comprises Ostracoda (seed shrimp), Branchiura (fish lice), Pentastomida (tongue
1257 worms), and Mystacocarida, their last common ancestor and all of its descendants (**Fig. 10**).
1258 Monophyly of this clade has been demonstrated with nuclear protein-coding genes (Regier et al.,
1259 2010; Zwick et al., 2012) and combined phylogenetic analysis of molecules and morphology (Lee et
1260 al., 2013; Oakley et al., 2013; Zrzavý et al., 1998). GenBank taxonomy does not recognize this clade.
1261 Instead GenBank prefers the Maxillopoda hypothesis (Branchiura, Pentastomida, Mystacocarida,
1262 Thecostraca and Copepoda), which has not been recovered in molecular analyses (Abele et al., 1992;
1263 Regier et al., 2005) despite support from morphology (Legg et al., 2013).

1264

1265 *35.1. Fossil specimens*

1266

1267 *Boeckelericambria pelturae* Walossek and Müller, 1994. UB W116, holotype, consisting of a
1268 complete larva (**Fig. 11a**).

1269

1270 *35.2. Phylogenetic justification*

1271

1272 *B. pelturae* is likely a stem group pentastomid, based especially on the diagnostic
1273 synapomorphy of a head with two pairs of grasping hooks (similar to the extant *Reighardia* larva;
1274 Walossek and Müller, 1994, Fig. 25a). This species is a member of the round headed (as opposed to
1275 hammer headed) morphotype (Walossek and Müller, 1994). It was resolved in the pentastomid stem-
1276 group in a cladistic analysis that sampled the extant genera by Almeida and Christoffersen (Almeida
1277 and Christoffersen, 1999). Its pentastomid identity is not dependent on whether pentastomids are
1278 interpreted as Ichthyostraca (Møller et al., 2008; Regier et al., 2010; Sanders and Lee, 2010) or early

1279 diverging euarthropods (e.g. Castellani et al., 2011). Because we accept crown pentastomids as sister
1280 group to crown branchiurans on the basis of strong support from molecular data, *B. pelturae* must
1281 therefore be within crown Oligostraca.

1282

1283 35.3. Age justification

1284

1285 The Orsten fossils come from the lowest zone of the late Cambrian Alum Shale, formally called
1286 the *Agnostus pisiformis* Zone or Zone 1, previously corresponding to the Uppermost Zone of the
1287 Middle Cambrian (Babcock et al., 2005). The *Agnostus pisiformis* Zone was recently redefined as the
1288 uppermost zone of the Guzhangian, at the upper boundary of Cambrian Series 3 (Nielsen et al.,
1289 2014). This age of the uppermost stage of the Cambrian Series 3 is 499 Ma \pm 2 Myr. Thus the
1290 minimum age applied to Oligostraca is 497 Ma.

1291 Soft maximum as for 2.3.

1292

1293 36. Crown Ichthyostraca

1294

1295 This clade comprises Branchiura and Pentastomida, their last common ancestor and all of its
1296 descendants (**Fig. 10**). It was first proposed based on sperm ultrastructure (Wingstrand, 1972).
1297 Subsequent analyses of morphology combined with protein-coding genes (Zrzavý et al., 1998) or with
1298 transcriptomes (Oakley et al., 2013), as well as molecular data on their own (Møller et al., 2008;
1299 Regier et al., 2010) have supported monophyly of this clade.

1300

1301 36.1. Fossil specimens

1302

1303 As for 35.1.

1304

1305 36.2. *Phylogenetic justification*

1306

1307 As for 35.2.

1308

1309 36.3. *Age justification*

1310

1311 As for 35.3.

1312

1313 **37. Crown Ostracoda**

1314

1315 This clade comprises Myodocopa, Podocopa (including Palaeocopida), their last common
1316 ancestor and all its descendants (**Fig. 10**). Monophyly of this clade has been demonstrated by
1317 phylogenetic analysis of a dataset including nuclear protein-coding genes, transcriptomes, and
1318 morphology (Oakley et al., 2013). Additional phylogenetic analyses of morphology alone (Legg et al.,
1319 2013; Wolfe and Hegna, 2014) also support monophyly.

1320

1321 37.1. *Fossil specimens*

1322

1323 *Luprisca incuba* Siveter et al., 2014. YPM IP 307300, holotype, consisting of a complete
1324 pyritized specimen in ventral aspect (**Fig. 11b**).

1325

1326 37.2. *Phylogenetic justification*

1327

1328 To date, *L. incuba* is yet to be included in an extensive phylogenetic analysis, but a number of
1329 features confirm both its placement within Myodocopida, and therefore Myodocopa. Specifically, the
1330 arrangement of setae on the antennula of *L. incuba* is currently only observed amongst extant

1331 myodocopid ostracods (Kornicker, 1981).

1332

1333 37.3. Age justification

1334

1335 The holotype of *L. incuba* was collected from siltstone of the Original Trilobite Bed, Walcott
1336 Quarry of Beecher's Trilobite Bed, in the Frankfort Shale of upstate New York (Siveter et al., 2014).
1337 Beecher's site within the Frankfort Shale is within the Lorraine Group, part of the regional Maysvillian
1338 Stage of the Cincinnati Series (Farrell et al., 2011, 2009). Globally, the Maysvillian (*Amplexograptus*
1339 *manitoulinensis* Graptolite Zone) corresponds to the early Katian Stage, from the base of the
1340 *Diplacanthograptus caudatus* Graptolite Zone to the base of the *Pleurograptus linearis* Graptolite Zone
1341 (Bergström et al., 2009). The upper boundary of the Katian is 445.2 Ma \pm 1.4 Myr, providing a
1342 minimum age of 443.8 Ma.

1343 As in Oakley et al. (2013), we suggest the maximum age of ostracods must be 509 Ma, the
1344 age of the Burgess Shale. Myodocope ostracods possess bivalved, calcified carapaces, which are
1345 preserved from many other Burgess Shale arthropods. There is no taphonomic reason why they would
1346 not have been preserved from ostracods. The Burgess Shale type locality is from Unit 3 of the Collins
1347 Quarry on Mount Stephen in the Canadian Rocky Mountains, British Columbia, which falls within the
1348 Kicking Horse Shale Member of the "thick" Stephen Formation (Aitkin, 1997; Caron et al., 2010;
1349 Stewart, 1991), also referred to as the Burgess Shale Formation (Fletcher and Collins, 2003, 1998).
1350 This unit yields trilobites from the *Polypleuraspis insignis* Subzone of the *Glossopleura* Zone (Fletcher
1351 and Collins, 1998), and is the oldest soft-bodied fossil excavation of the Burgess Shale sites. The age
1352 of the *Glossopleura* Zone corresponds to the Cambrian Series 3 Stage 5, giving a maximum constraint
1353 of 509 Ma.

1354

1355 37.4. Discussion

1356

1357 Older fossils, from the Tremadocian (~40 Myr older) have been reported from numerous
1358 localities across the current and Ordovician world: Argentina, Australia, China, Iran, Norway, Sweden,
1359 and the UK (Williams et al., 2008). However, all of these fossils are known solely from carapaces,
1360 which are known to be highly homoplastic (Siveter et al., 2013). The affinities of Tremadocian
1361 ostracods are therefore ambiguous. Other bivalved crustacean-like taxa from the Cambrian, such as
1362 bradoriids and phosphatocopines, are demonstrably not closely related to ostracods, or even
1363 Oligostraca, based on phylogenetic analyses (Hou et al., 2010; Legg et al., 2013; Oakley et al., 2013;
1364 Wolfe and Hegna, 2014).

1365

1366 **38. Crown Podocopa**

1367

1368 This clade comprises Palaeocopida, Podocopida and Platycopida, their last common ancestor
1369 and all of its descendants (**Fig. 10**). Monophyly has been demonstrated by phylogenetic analysis of
1370 morphology (Horne et al., 2005), and morphology combined with nuclear protein-coding genes and
1371 transcriptomes (Oakley et al., 2013). Although the sole living representative of Palaeocopida, *Manawa*
1372 *staceyi*, has to date only been represented by a single ribosomal sequence and morphology, bootstrap
1373 support for its position as a sister to the remaining Podocopa is strong (Oakley et al., 2013).

1374

1375 *38.1. Fossil specimens*

1376

1377 *Cytherellina submagna* Krandijevsky, 1963. For phylogenetically relevant details, we refer to
1378 ZPAL O.60/001 (**Fig. 11c-e**), preserving soft anatomy, and ZPAL O.60/002, preserving adductor
1379 muscle scars (Olempska et al., 2012).

1380

1381 *38.2. Phylogenetic justification*

1382

1383 *C. submagna* is very similar to modern podocopes, particularly sigilloideans and
1384 darwinuloideans, with which it shares a particular adductor muscle scar pattern, long terminal seta on
1385 the seventh limb pair, and a furca with large distal setae (Olempska et al., 2012).

1386

1387 38.3. Age justification

1388

1389 Specimens of *C. submagna* were recovered from two localities in Podolia, Ukraine: Kasperovcy
1390 village, left border of the river Seret (type locality), and from the right escarpment of the River Dniester
1391 near the village Ivanye Zlote (Olempska et al., 2012). The type locality, part of the Chortkov/Chortkiv
1392 Horizon, underlies the second locality, which is part of the Ivanye Horizon (Filipiak et al., 2012;
1393 Olempska et al., 2012). Thus we must use the Chortkiv age as a minimum constraint on the age of *C.*
1394 *submagna*, to provide the narrowest interval of clade divergence. The Chortkiv Horizon comfortably
1395 lies within the middle Lochkovian stage of the Early Devonian (Filipiak et al., 2012; Małkowski et al.,
1396 2009; Plotnick, 1999). Conodont biostratigraphy places the upper boundary of the Chortkiv Horizon at
1397 the end of the *Caudicriodus postwoschmidtii* Biozone, the oldest conodont Biozone within the
1398 Devonian (Drygant and Szaniawski, 2012). Spline fits on radiometric ages for the Devonian place the
1399 *C. postwoschmidtii* Biozone at 417.27 Ma with a duration of 1.89 Myr (Becker et al., 2012). Thus the
1400 end of the *C. postwoschmidtii* Biozone, and a minimum age for the first appearance of *C. submagna*, is
1401 415.38 Ma.

1402 Soft maximum as for 37.3.

1403

1404 38.4. Discussion

1405

1406 Although isolated ostracod carapace valves are incredibly abundant in the fossil record, the
1407 morphology of carapaces has been shown to have little systematic value (Siveter et al., 2013). For this
1408 reason we have selected a taxon with soft-tissue preservation, of which *C. submagna* is the oldest

1409 recognized example, although other species of *Cytherellina* are known from older deposits including
1410 the later Silurian of Ludlow, England, with only the carapaces preserved (Olempska et al., 2012).
1411 These older species cannot be ruled out as myodocopes or stem members of any of Podocopa,
1412 Myodocopa, or even Ostracoda, as they lack diagnostic soft parts.

1413

1414 **39. Crown Myodocopa**

1415

1416 This clade comprises Myodocopida and Halocyprida, their last common ancestor and all of its
1417 descendants (**Fig. 10**). Monophyly has been demonstrated by phylogenetic analysis of morphology
1418 (Horne et al., 2005), and morphology combined with nuclear protein-coding genes and transcriptomes
1419 (Oakley et al., 2013).

1420

1421 *39.1. Fossil specimens*

1422

1423 As for 37.1.

1424

1425 *39.2. Phylogenetic justification*

1426

1427 As for 37.2.

1428

1429 *39.3. Age justification*

1430

1431 As for 37.3.

1432

1433 **40. Crown Myodocopida**

1434

1435 This clade comprises Cylindroleberidoidea, Cypridinoidea and Sarsielloidea, their last common
1436 ancestor and all of its descendants (**Fig. 10**). Monophyly has been demonstrated by phylogenetic
1437 analysis of morphology (Horne et al., 2005), and morphology combined with nuclear protein-coding
1438 genes and transcriptomes (Oakley et al., 2013).

1439

1440 *40.1. Fossil specimens*

1441

1442 As for 37.1.

1443

1444 *40.2. Phylogenetic justification*

1445

1446 As for 37.2.

1447

1448 *40.3. Age justification*

1449

1450 As for 37.3.

1451

1452 **41. Crown Altocrustacea**

1453

1454 This clade comprises Multicrustacea and Allotriocarida, their last common ancestor and all of
1455 its descendants (**Fig. 1**). Monophyly has been supported by phylogenetic analysis of nuclear protein-
1456 coding genes (Regier et al., 2010; Zwick et al., 2012), transcriptomes (von Reumont et al., 2012), and
1457 combined analysis of morphology and nuclear protein-coding genes (Lee et al., 2013) or morphology
1458 and transcriptomes (Oakley et al., 2013). However, this clade has been challenged as paraphyletic
1459 (containing Oligostraca) by Rota-Stabelli et al. (2013b), and has not been supported by morphological
1460 data alone. It is not recognized in GenBank taxonomy.

1461

1462 *41.1. Fossil specimens*

1463

1464 As for 4.1.

1465

1466 *41.2. Phylogenetic justification*

1467

1468 As for 4.2.

1469

1470 *41.3. Age justification*

1471

1472 As for 4.3.

1473

1474 *41.4. Discussion*

1475

1476 A series of disarticulated Small Carbonaceous Fossils (Harvey and Butterfield, 2008) from the
1477 early Cambrian Mount Cap Formation, Northwest Territories, Canada, have been cited as calibration
1478 fossils within Altocrustacea or even Allotriocarida (e.g. Rehm et al., 2011; Sun et al., 2015). These
1479 fossils were argued by Harvey (2008) to comprise part of the feeding apparatus of a single crustacean
1480 taxon. The Mount Cap arthropod fossils would have represented structures each specialized for
1481 precise feeding functions. The fossil species may have initially scraped food with saw-toothed and
1482 hooked setae, further processed particles with filter plates and other delicate setal associations, then
1483 macerated with mandibular molar surfaces and passed to the mouth with long fringing setae (Harvey
1484 and Butterfield, 2008). Estimates of the body size of the animal, based on regression of body length
1485 versus molar surface length (from extant crustaceans) suggest the Mount Cap arthropod was, in total,
1486 about the same size as an adult cladoceran or anostracan (Harvey and Butterfield, 2008). While direct

1487 synapomorphies linking the Mount Cap arthropod to crown group branchiopods are lacking, the
1488 evidence together suggests affinity along the stem lineage of Altocrustacea (Harvey, 2008, Fig. 5.6).

1489

1490 **42. Crown Multicrustacea**

1491

1492 This clade comprises Copepoda, Thecostraca (barnacles) and Malacostraca, their last
1493 common ancestor and all of its descendants (**Figs. 12 and 13**). Monophyly was first demonstrated by
1494 nuclear protein-coding genes (Regier et al., 2010) and supported by transcriptomes (von Reumont et
1495 al., 2012) and combined analysis of molecular and morphological data (Lee et al., 2013; Oakley et al.,
1496 2013). This clade has, however, not been recovered in any morphology-only phylogenetic analyses,
1497 presumably owing to widespread support for Malacostraca as sister to much of the rest of
1498 Pancrustacea (the Entomostraca hypothesis, e.g. Walossek and Müller, 1998). See Wolfe and Hegna
1499 (2014) for a morphological deconstruction of Entomostraca. Neither Multicrustacea nor Entomostraca
1500 is recognized in GenBank taxonomy.

1501

1502 *42.1. Fossil specimens*

1503

1504 *Arenosicaris inflata* Collette and Hagadorn, 2010a. PRI 10130), holotype from the Elk Mound
1505 Group (**Fig. 14a**), which is difficult to date (see 42.3). Therefore, we refer to a second specimen,
1506 UWGM 745.

1507

1508 *42.2. Phylogenetic justification*

1509

1510 *A. inflata* was identified within the Archaeostraca, the likely fossil sister group to extant
1511 Leptostraca (together comprising ‘Phyllocarida’) and included in the morphological cladistic analysis of
1512 Collette and Hagadorn (2010b). In that analysis, the exceptionally preserved fossils *Nahecaris stuerzi*

1513 Jaeckel, 1921 and *Cinerocaris magnifica* Briggs et al., 2004 were also included within Archaeostraca
1514 (Collette and Hagadorn, 2010b). A separate extensive combined molecular and morphological
1515 analysis placed *C. magnifica* within crown Malacostraca (as is traditionally assumed for members of
1516 Archaeostraca), while *N. stuarti* was equivocally stem Leptostraca or stem Malacostraca (Oakley et
1517 al., 2013), suggesting non-monophyly of Archaeostraca. *C. magnifica* was also crown Malacostraca in
1518 another morphological analysis that omitted *N. stuarti* (Legg et al., 2013). *A. inflata* is within the same
1519 archaeostracan clade as *N. stuarti* (Pephracaridina + Rhinocaridina) while *C. magnifica* is in a
1520 separate archaeostracan group (Echinocaridina; Collette and Hagadorn, 2010b). Given the uncertainty
1521 of crown affinities and potential monophyly of Archaeostraca, we conservatively assign *A. inflata* to
1522 crown-group Multicrustacea, but not Malacostraca.

1523

1524 42.3. Age justification

1525

1526 *A. inflata* is found in the Elk Mound Group (holotype) and in the Lodi Member of the St.
1527 Lawrence Formation, both in Wisconsin (Collette and Hagadorn, 2010a). Although the Elk Mound
1528 Group is the older of these, no biostratigraphically useful fossils co-occur with *A. inflata*, limiting the
1529 ability to determine the formation to which they belong (Collette and Hagadorn, 2010a). The St.
1530 Lawrence Formation is younger, containing *Saukia* Zone trilobites, which mark it as late Sunwaptan
1531 within the Furongian (Collette and Hagadorn, 2010a; Raasch, 1951). The Sunwaptan is the second
1532 latest stage of the Furongian, postdated by the Skullrockian (which extends into the Early Ordovician;
1533 Peng et al., 2012). The Sunwaptan-Skullrockian boundary is determined by the appearance of
1534 conodonts in the *Hirsutodontus hirsutus* Subzone of the *Cordylodus proavus* Zone (Peng et al., 2012).
1535 Based on the correlation diagram of Peng et al. (2012), the Sunwaptan-Skullrockian boundary is
1536 approximately 487 Ma, providing a minimum age estimate.

1537 Soft maximum as for 2.3.

1538

1539 43. Crown Copepoda

1540

1541 This clade comprises Calanoida, Cyclopoida, Gelyelloida, Harpacticoida (benthic copepods),
1542 Misophrioida, Mormonilloida, Platycopioida and Siphonostomatoida (fish parasites), their last common
1543 ancestor and all of its descendants (**Fig. 12**). Members of Calanoida, Cyclopoida, and
1544 Siphonostomatoida were included in a large combined analysis of transcriptomes and morphology,
1545 forming a monophyletic group (Oakley et al., 2013). Phylogenetic analysis of morphology (Huys and
1546 Boxshall, 1991; Ho, 1994), mitochondrial genes (Minxiao et al., 2011), and ribosomal genes combined
1547 with morphology (Huys et al., 2007) suggest this sampling covers distant lineages of Copepoda,
1548 although omitting Platycopioida, the presumed most basal order (Huys and Boxshall, 1991). Molecular
1549 data remain unavailable from Platycopioida, although comparative morphological investigations
1550 support copepod monophyly (Dahms, 2004).

1551

1552 43.1. Fossil specimens

1553

1554 *Kabatarina pattersoni* Cressey and Boxshall, 1989. BMNH IN. 63466, holotype, preserving the
1555 cephalothorax, mouthparts, oral cone, and first and second thoracic limbs (**Fig. 14b**). This specimen
1556 likely represents an adult female, recovered from the gills of a fossil teleost fish (Cressey and
1557 Boxshall, 1989).

1558

1559 43.2. Phylogenetic justification

1560

1561 *K. pattersoni* has not been included in a formal phylogenetic analysis. Cressey and Boxshall
1562 (1989) detail one apomorphy shared by the fossil and recent members of the family Dichelesthidae,
1563 which is a medial groove delimiting the distal part of the maxillary claw. A number of other characters
1564 are shared more generally with copepods, such as the shape of the oral cone (typical for fish parasitic

copepods), and biramous thoracic limbs with a 2-segmented protopod, joined by the intercoxal plate (Cressey and Boxshall, 1989). Dichelesthidae is a family belonging to the Siphonostomatoida. Even a position for *K. pattersoni* on the stem of Dichelesthidae or stem Siphonostomatoida would be within crown group Copepoda.

1569

1570 43.3. Age justification

1571

1572 *K. pattersoni* was found in the Cretaceous Santana Formation, Serra do Araripe, Ceará, Brazil
1573 (Cressey and Boxshall, 1989), which is mainly famous for concretions enclosing fossil fishes. The age
1574 of the Santana Formation is poorly constrained (as it lacks biostratigraphic index fossils and igneous
1575 rocks for radiometric dating); dates have been suggested that range from the Aptian to the Albian or
1576 Cenomanian (Martill, 2007). In order to ensure a minimum date, the upper boundary of the
1577 Cenomanian, which is 93.7 Ma (from 93.9 Ma \pm 0.2 Myr; Ogg et al., 2012), is used.

1578 Soft maximum as for 26.3.

1579

1580 43.4. Discussion

1581

1582 Despite their overwhelming abundance in modern aquatic ecosystems, copepods have a poor
1583 fossil record, likely due to their small size, unsclerotized cuticle, and planktonic ecology. Apart from *K.*
1584 *pattersoni*, putative copepod appendages have been reported from much older sediments in the
1585 Pennsylvanian (Selden et al., 2010) and even the Cambrian (Harvey et al., 2012; Harvey and Pedder,
1586 2013; These fossils each bear one to four characters found in crown copepods, from partial maxillae
1587 (Selden et al., 2010) and partial or complete mandibular gnathal edges (Harvey et al., 2012; Harvey
1588 and Pedder, 2013). Relationships between feeding habits and mandibular morphology have been
1589 observed in extant copepods (Michels and Schnack-Schiel, 2005), and variation may occur among
1590 closely related species (Sano et al., 2015). It is therefore extremely unlikely that mandibular characters

1591 have not experienced any homoplasy since the Cambrian.

1592 Nevertheless, divergence time analyses suggest Devonian-Carboniferous (calibrated with *K.*
1593 *pattersoni*; (Rota-Stabelli et al., 2013a), Carboniferous (calibrated with external fossils from other
1594 pancrustacean clades; Oakley et al., 2013), or Permian (external fossils; Wheat and Wahlberg, 2013)
1595 origins for crown Copepoda. These analyses do not conflict stratigraphically with a crown assignment
1596 for the Pennsylvanian fossils (Selden et al., 2010). Therefore we must caution that a Cretaceous age
1597 is likely a severe underestimate of crown copepod antiquity.

1598

1599 **44. Crown Thecostraca**

1600

1601 This clade comprises Facetotecta (y-larvae), Ascothoracida, and Cirripedia, their last common
1602 ancestor and all of its descendants (**Fig. 12**). Monophyly of Thecostraca has been demonstrated by
1603 separate analysis of nuclear housekeeping genes and morphology (Pérez-Losada et al., 2009a). All
1604 included clades have complex (sometimes only partially known) life histories, but particularly strong
1605 morphological support comes from a shared larval stage, the cyprid.

1606 More recently, the enigmatic parasitic Tantulocarida were added within Thecostraca based on
1607 analysis of a single ribosomal gene (Petrutina et al., 2014), however, other relationships within
1608 Pancrustacea differed significantly from those outlined herein. In light of the paucity of data other than
1609 ribosomal genes, we remain ambivalent about including Tantulocarida. As tantulocarids have no
1610 known fossil record, if further evidence supports their position within Thecostraca, this calibration may
1611 be modified to include them as well.

1612

1613 *44.1. Fossil specimens*

1614

1615 *Rhamphoverritor reduncus* Briggs et al., 2005. OUM C.29587, holotype (**Fig. 14c,d**),
1616 preserving a cyprid larva in a volcanoclastic concretion. As the reconstruction of Herefordshire fossils

1617 requires serial grinding and photography of 20 µm sections (Sutton et al., 2002), the holotype (figured
1618 in Briggs et al., 2005: Fig. 1) was thus destroyed in preparation. Morphological data for Herefordshire
1619 fossils are published as 3D models of the thin section photographs.

1620

1621 44.2. Phylogenetic justification

1622

1623 In a phylogenetic analysis of morphology, *R. reduncus* is the sister group of two species of
1624 Thoracica (both are members of Balanomorpha) (Legg et al., 2013). This is a position likely within the
1625 crown group of Thecostraca, however, no other thecostracans (such as Facetotecta and
1626 Ascothoracida) were included. Generally, the cyprid larval morphotype (with an elongated head shield,
1627 six swimming thoracopods, and robust modified antennules) is considered a synapomorphy of
1628 Thecostraca (Høeg et al., 2004). *R. reduncus* differs from cirripede cyprids as it lacks attachment
1629 discs, and its abdomen extends past the head shield; a differentiated abdomen is a condition of
1630 Ascothoracida (Briggs et al., 2005; Høeg et al., 2009a). Based on the presence of five shell plates in a
1631 juvenile specimen, Høeg et al. (2009b) suggested that *R. reduncus* may be placed on the cirripede
1632 stem lineage. In combination with the phylogenetic analysis of Legg et al. (2013), these apomorphies
1633 indicate that *R. reduncus* is very likely a member of crown group Thecostraca, and likely on the stem
1634 of Cirripedia.

1635

1636 44.3. Age justification

1637

1638 Minimum as for 6.3. Soft maximum as for 26.3.

1639

1640 45. Crown Cirripedia

1641

1642 This clade comprises Acrothoracica, Rhizocephala and Thoracica (barnacles), their last

1643 common ancestor and all of its descendants (**Fig. 12**). Monophyly has been demonstrated by separate
1644 phylogenetic analysis of nuclear housekeeping genes and morphology (Pérez-Losada et al., 2009a).

1645

1646 45.1. Fossil specimens

1647

1648 *Illilepas damrowi* Schram, 1986. FMNH P32055, holotype (**Fig. 14e**).

1649

1650 45.2. Phylogenetic justification

1651

1652 Schram (1975) described this fossil as *Praeilepas damrowi*, a congener of *P. jaworskii*
1653 Chernyshev, 1930. Restudy led to the transfer of this fossil to the new genus *Illilepas* under the
1654 combination *I. damrowi*, as the original description of a carina more closely resembled a tergum, and
1655 the original tergum was more likely an enlarged spine along the margin of the aperture, similar to that
1656 seen in Ibliformes (Thoracica) (Buckeridge and Newman, 2006; Schram, 1986). However, both
1657 molecular and morphological data place *Ibla* as the most basal clade of Thoracica (Pérez-Losada et
1658 al., 2009a, 2008), which, if *I. damrowi* is on the Ibliformes stem lineage, would still situate the fossil
1659 within the crown group of Cirripedia.

1660

1661 45.3. Age justification

1662

1663 As for 31.3.

1664

1665 45.4. Discussion

1666

1667 A possible Early Ordovician stalked barnacle (Pedunculata: Lepadomorpha?) was illustrated in
1668 Fig. 2c and S3h of Van Roy et al. (2010). It has not been formally described and its affinities are

1669 unclear.

1670 *P. jaworskii* is in some ways a more appropriate fossil calibration than *I. damrowi*. It is
1671 approximately coeval to *I. damrowi*, and was coded in a morphological phylogenetic analysis (Glenn
1672 et al., 1995), where it was placed within Thoracica (sister to all other Thoracica except *Ibla*). *P.*
1673 *jaworskii* has been used as a calibration fossil for Thoracica and Cirripedia (Pérez-Losada et al.,
1674 2009b, 2008; Rees et al., 2014). However, no specimen information was available in the original
1675 publication, nor was any significant stratigraphic data beyond Carboniferous of the Kusnetz Basin,
1676 Russia (Chernyshev, 1930). As the papers using *P. jaworskii* for calibration estimate its age at 306.5-
1677 311.7 Ma (e.g. Rees et al., 2014), substitution of the slightly younger *I. damrowi* will not significantly
1678 violate the minimum age.

1679

1680 **46. Crown Thoracica**

1681

1682 This clade comprises Ibliformes, 'Pedunculata' (goose barnacles) and Sessilia (acorn
1683 barnacles), their last common ancestor and all of its descendants (**Fig. 12**). Pedunculata is no longer
1684 supported as monophyletic (Buckeridge and Newman, 2006; Pérez-Losada et al., 2009a; Rees et al.,
1685 2014). Ibliformes is identified as the sister group of all other Thoracica (Pérez-Losada et al., 2009a).
1686 Monophyly has been established by phylogenetic analysis of nuclear housekeeping genes (Pérez-
1687 Losada et al., 2009a), although a morphological phylogenetic analysis in the same paper resolves all
1688 studied members of Rhizocephala and Thoracica together in a polytomy. This is because only larval
1689 characters can be scored for Rhizocephala, with missing data for all adult characters due to their
1690 parasitic lifestyle.

1691

1692 *46.1. Fossil specimens*

1693

1694 As for 45.1.

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46.2. Phylogenetic justification

As for 45.2.

46.3. Age justification

As for 31.3.

46.4. Discussion

As for 45.4.

47. Crown Sessilia

This clade comprises Verrucomorpha and Balanomorpha, their last common ancestor and all of its descendants (**Fig. 12**). Monophyly is supported by phylogenetic analysis of nuclear protein-coding and ribosomal genes (Pérez-Losada et al., 2008; Rees et al., 2014).

47.1. Fossil specimens

Brachylepas fallax Withers, 1935. For calibration, we refer to the stratigraphically oldest specimen (SM 704275), which is undescribed (A. Gale, pers. comm.).

47.2. Phylogenetic justification

1721 This species was originally described from disarticulated material by Darwin (1851) as
1722 *Pollicipes fallax*. Withers (1935, 1914) recognized it was a sessile, rather than pedunculate barnacle,
1723 and that it had similarities to the basal sessilian genus *Pycnolepas* in overall form and plate
1724 development. Synapomorphies shared by *B. fallax* and all crown Sessilia include: the absence of a
1725 peduncle, presence of an operculum, and absence of all lateral plates (Gale and Sørensen, 2015). *B.*
1726 *fallax* shares with crown Balanomorpha a low, hemiconical carina and rostrum (Gale and Sørensen,
1727 2015). On the basis of these characters, a recent cladogram depicts *B. fallax* as one of the most
1728 distant stem lineages of Balanomorpha, which is therefore a position within the crown group of
1729 Sessilia (Gale and Sørensen, 2015).

1730

1731 47.3. Age justification

1732

1733 The oldest known locality from which *B. fallax* has been recovered is Pit No. 125 (Brydone,
1734 1912), close to junction of Barnet Side Lande and King's Lane, Froxfield, Hampshire, England (A.
1735 Gale, pers. comm.). This locality bears fossils of *Holaster (Sternotaxis) planus*, and is thus part of the
1736 *S. planus* echinoid zone, which is the uppermost zone of the Turonian in English Chalk (Gale, 1996;
1737 Mortimore, 2011). The GSSP defining the global upper boundary of the Turonian remains debated
1738 (due to difficulty in identifying its index ammonite fossil, *Forresteria (Harleites) petrocoriensis* (Ogg et
1739 al., 2012). Currently, the upper boundary of the Turonian is dated to 89.8 Ma \pm 0.3 Myr, providing a
1740 minimum age of 89.5 Ma.

1741 Soft maximum as for 26.3.

1742

1743 47.4. Discussion

1744

1745 The Albian-Cenomanian *Verruca withersi* Schram and Newman, 1980 has been shown not to
1746 be a cirripede (Jagt and Buckeridge, 2005) and cannot be used as a minimum. *Proverruca* (coded at

the genus level) was included in a morphological phylogenetic analysis, where it was placed in a polytomy with the fossil *Eoverruca* and the crown family Verrucidae (Glenner et al., 1995), and subsequently used as a calibration fossil for divergence time analysis (Pérez-Losada et al., 2014, 2008). However, the placement of *Proverruca* was based on similarities to the extant genus *Neoverruca*, which was shown in molecular analyses to fall outside Sessilia entirely, instead within the Scalpelliformes (Pérez-Losada et al., 2008; Rees et al., 2014). More recent morphological phylogenetic analyses confirm the convergence between *Neoverruca* + *Proverruca* and crown Verrucomorpha (Gale, 2015; Gale and Sørensen, 2015).

The Albian *Pycnolepas rigida* Sowerby, 1836 was included in a morphological phylogenetic analysis, where it was placed on the stem lineage of Verrucomorpha (Gale, 2015). However, that analysis did not include members of Balanomorpha, so the topology did not explicitly exclude a position on the stem lineage of Sessilia. In fact, this species was referred to stem Sessilia (Gale, 2015, p. 770). Unlike crown group Sessilia, it retains the pedunculate character of a lateral plate, the tall upper latus (Gale, 2015).

Verruca tasmanica tasmanica (Buckeridge, 1983), a previously used calibration fossil at the base of Verrucomorpha (Herrera et al., 2015; Linse et al., 2013; Pérez-Losada et al., 2014, 2008; Rees et al., 2014), is known from the Santonian Gingin Chalk Formation of Dandaragan, Western Australia (as well as type material from younger Oligocene strata of Oamaru, New Zealand; Buckeridge, 1979). As it is both younger than *B. fallax* and has not been studied in a phylogenetic context, it is not used herein.

48. Crown Malacostraca

This clade comprises Leptostraca and Eumalacostraca, their last common ancestor and all of its descendants (**Fig. 13**). Its monophyly is one of the least contested matters in arthropod phylogeny; it has been demonstrated by phylogenetic analysis of morphology (Legg et al., 2013; Wills et al.,

1773 1998), nuclear ribosomal and protein-coding genes (Giribet et al., 2001; Regier et al., 2010, 2005),
1774 transcriptomes (von Reumont et al., 2012), and combined analysis of molecular and morphological
1775 data (Lee et al., 2013; Oakley et al., 2013).

1776

1777 48.1. Fossil specimens

1778

1779 *Cinerocaris magnifica* Briggs et al., 2004. OUM C.29565 (holotype; **Fig. 14g**), and OUM
1780 C.29566 (serially ground and reconstructed specimen; **Fig. 14f**). Morphological data for Herefordshire
1781 fossils are published as 3D models of thin section photographs.

1782

1783 48.2. Phylogenetic justification

1784

1785 *C. magnifica* was found to be a member of the stem group of Leptostraca (therefore crown
1786 group Malacostraca) in analyses of morphology (Legg et al., 2013) and morphology combined with
1787 molecules (Oakley et al., 2013).

1788

1789 48.3. Age justification

1790

1791 As for 44.3.

1792

1793 48.4. Discussion

1794

1795 The position of other fossil phyllocarids with respect to extant malacostracans (and the
1796 monophyly of phyllocarids themselves) have not been significantly investigated. The position of the
1797 Devonian phyllocarid *Nahecaris stuarti* in a phylogenetic analysis (Oakley et al., 2013) was
1798 equivocally stem Leptostraca or stem Malacostraca, casting doubt on the position of at least rhinocarid

1799 phyllocarids within crown Malacostraca. As *N. stuarti* has the same relationship to crown
1800 Malacostraca as *A. inflata* (at least in the analysis of Collette and Hagadorn, 2010b), neither fossil can
1801 be confidently placed within crown-group Malacostraca. Recent reinvestigation of *Ceratiocaris* cf.
1802 *macroura* (related to *A. inflata* and *N. stuarti* in the analysis of Collette and Hagadorn, 2010b)
1803 suggests this Silurian ‘phyllocarid’ may be a stem eumalacostracan due to possession of an antennal
1804 scale, casting further doubt on the monophyly of fossil phyllocarids (Jones et al., 2015). The *C.*
1805 *macroura* study, however, assumes malacostracan identity of phyllocarids (partly defined by biramous
1806 antennules), which, as discussed above (section 42.2), may not be robust to phylogenetic analysis. If,
1807 however, *Ceratiocaris* is within crown Malacostraca (either alone or with other archaeostracans), the
1808 oldest Malacostraca would be amended to *Ceratiocaris winneshiekensis* Briggs et al., 2015 from the
1809 Darriwilian Winneshiek Lagerstätte of Iowa (~14 Myr older than *C. magnifica*).

1810 Thylacocephalans are an enigmatic fossil arthropod clade ranging from the Silurian to the
1811 Cretaceous (C. Haug et al., 2014; Schram, 2014). Some Cambrian fossils have been proposed as
1812 thylacocephalans, but their membership is generally discounted (Schram, 2014; Vannier et al., 2006).
1813 Thylacocephalans have been compared to several extant arthropod clades, including the
1814 malacostracan stomatopods and decapods (Schram, 2014; Schram et al., 1999; Secrétan and Riou,
1815 1983; Vannier et al., 2016), which would extend the minimum age of Malacostraca slightly older within
1816 the Silurian (~433 Ma). The Jurassic thylacocephalan *Dollocaris ingens* Van Straelen, 1923 was coded
1817 in a morphological matrix, and found to be a stem eumalacostracan (therefore crown malacostracan)
1818 by phylogenetic analysis (Legg et al., 2013). However, their malacostracan affinities have been
1819 questioned, especially by C. Haug et al. (2014) studying a Silurian species, noting divergent trunk
1820 tagmosis and similarities to remipedes. Continued uncertainty over thylacocephalan affinities make
1821 them poor calibration fossils.

1822

1823 **49. Crown Eumalacostraca**

1824

1825 This clade comprises Verunipeltata (mantis shrimp, partial total group called Stomatopoda),
1826 Peracarida, 'Syncarida' (itself comprising Anaspidacea and Bathynellacea) and Eucarida, their last
1827 common ancestor and all of its descendants (**Fig. 13**). Monophyly is demonstrated by phylogenetic
1828 analysis of morphology (Legg et al., 2013; Richter and Scholtz, 2001), nuclear ribosomal and protein-
1829 coding genes (Regier et al., 2010), transcriptomes (von Reumont et al., 2012), and combined analysis
1830 of molecular and morphological data (Lee et al., 2013; Oakley et al., 2013; Wills et al., 2009). Although
1831 stomatopods and/or syncarids were not sampled in some of the above analyses, the best taxon
1832 sampling still resulted in eumalacostracan monophyly (Legg et al., 2013; Wills et al., 2009).

1833

1834 *49.1. Fossil specimens*

1835

1836 *Palaeopalaemon newberryi* Whitfield, 1880. The holotype at the AMNH, figured by Schram et
1837 al. (1978: Plate 3 #1-3), has been lost (B. Hussaini, pers. comm.), thus we refer to specimen KSU
1838 3484 (**Fig. 14h,i**).

1839

1840 *49.2. Phylogenetic justification*

1841

1842 Schram and Dixon (2004) coded *P. newberryi* into the morphological matrix of Dixon et al.
1843 (2003), finding it sister to a clade including Anomura, Brachyura, and Achelata to the exclusion of
1844 Astacidea, Axiidea, Gebiidea and Glypheidea. This position is within the crown group of Reptantia,
1845 hence within the crown groups of Decapoda and Eumalacostraca.

1846

1847 *49.3. Age justification*

1848

1849 The specimen of *P. newberryi* was found in gray shale near "Paine's Creek," LeRoy, Lake
1850 County, Chagrin (Erie) Shale, northeastern Ohio, USA (Feldmann et al., 1978; Schram et al., 1978).

1851 The Chagrin Shale is dated to the late Fammenian based on presence of the index alga *Foerstia*
1852 (Murphy, 1973), which in Ohio lies 40-70 m below surface outcrops (Feldmann et al., 1978). The upper
1853 boundary of the Fammenian is 358.9 Ma \pm 0.4 Myr, giving a minimum of 358.5 Ma.

1854 Soft maximum as for 26.3.

1855

1856 **50. Crown Anaspidacea**

1857

1858 This clade comprises the families Anaspididae, Koonungidae, Psammaspididae and
1859 Stygocarididae, their last common ancestor and all of its descendants (**Fig. 13**). Phylogenetic studies
1860 including Anaspidacea are extremely rare, but morphology (Schram, 1984) and mitochondrial 16S
1861 sequences (Camacho et al., 2002) indicated monophyly of the clade.

1862

1863 *50.1. Fossil specimens*

1864

1865 *Anaspidites antiquus* Chilton, 1929. AMS F64765, holotype, complete specimen (**Fig. 14k**).

1866

1867 *50.2. Phylogenetic justification*

1868

1869 Although not included in a formal phylogenetic analysis, Schram (1984) justified the
1870 membership of *A. antiquus* as essentially indistinguishable from living Anaspididae. Fusion of the
1871 first thoracomere into the cephalon, uniramous pleopods, and absence of an antennal scale are noted
1872 as diagnostic characters (Schram, 1984). As the fossil lacks preservation of diagnostic mouthparts,
1873 exact family affinities within total-group Anaspidacea are uncertain.

1874

1875 *50.3. Age justification*

1876

1877 *A. antiquus* was found in the Hawkesbury Sandstone at the former Brookvale Brick Quarry,
1878 New South Wales, Australia (Schram, 1984). The Hawkesbury Sandstone overlies the Narrabeen
1879 Group and underlies the Wianamatta Group (Herbert, 1997). Sequence stratigraphy places the
1880 Hawkesbury in Sequence F, including the appearance of *Aratrisporites parvispinosus* spores (Helby,
1881 1973; Herbert, 1997). The *A. parvispinosus* spore zone indicates an age during the Anisian (middle
1882 Triassic) (Herbert, 1997). The upper boundary of the Anisian is estimated at 241.5 ± 1 Ma (Ogg,
1883 2012), providing a minimum age at 240.5 Ma.

1884 Soft maximum as for 26.3.

1885

1886 50.4. Discussion

1887

1888 ‘Syncarida’, the traditional taxon containing Anaspidacea, is purposely excluded from this
1889 review, as its monophyly has been substantially challenged. In phylogenetic analyses, syncarid
1890 monophyly was only supported by the morphological dataset of Richter and Scholtz (2001),
1891 emphasizing the absence of a dorsal carapace in Anaspidacea and Bathynellacea (‘Syncarida’). Each
1892 of a partial mitochondrial gene (Camacho et al., 2002), two mitochondrial genes and morphology
1893 (Jenner et al., 2009) and morphology including putative syncarid fossils (Schram and Hof, 1998; Wills
1894 et al., 2009) failed to recover a sister group relationship between Anaspidacea and Bathynellacea.
1895 Wills et al. (2009) suggested that a paraphyletic grade of ‘Syncarida’, including fossils (*Acanthotelson*,
1896 *Palaeocaris*) represented the first divergences of Eumalacostraca.

1897

1898 51. Crown Verunipeltata

1899

1900 This is the clade comprising Bathysquilloidea, Erythrosquilloidea, Eurysquilloidea,
1901 Parasquilloidea, Gonodactyloidea, Lysiosquilloidea and Squilloidea, their last common ancestor and
1902 all of its descendants (**Fig. 13**). Although the extant members are often referred to Stomatopoda, that

1903 clade includes a number of extinct members forming a paraphyletic grade (Fig. 1 of Haug et al., 2010).
1904 As membership of fossil species within a crown group is only possible if they branch along the stem
1905 lineage of a living clade that is part of the crown itself, we agree with the assertion that crown
1906 ‘Stomatopoda’ is equivalent to the clade Verunipeltata *sensu* Haug et al. (2010). The stomatopod
1907 clade as a whole may be defined by several apomorphies, such as five pairs of maxillipeds, and
1908 modification of the first two pleopods as gonopods (Richter and Scholtz, 2001).

1909 All living members form a clade in analyses of morphology including both fossil and extant taxa
1910 (Ahyong, 1997; Ahyong and Harling, 2000). Analysis of combined molecular and morphological data,
1911 with limited sampling of verunipeltatan clades, strongly supports monophyly of those members (Jenner
1912 et al., 2009). As well, representatives of Gonodactyloidea, Lysiosquilloidea and Squilloidea were
1913 sequenced for six housekeeping genes; these were monophyletic in a diverse sample of
1914 Pancrustacea (Bybee et al., 2011).

1915

1916 51.1. Fossil specimens

1917

1918 *Ursquilla yehoachi* Remy and Avnimelech, 1955. For calibration, we refer to two specimens.
1919 Based on new phylogenetically relevant details, we use a new specimen (SMNS 67703) from Fig. 1
1920 and 2 of Haug et al. (2013). The SMNS specimen, however, lacks locality and stratigraphic information
1921 beyond “Late Cretaceous Negev Desert, Israel” as it was privately donated (Haug et al., 2013). We
1922 also therefore refer to the holotype (MNHN R. 62691).

1923

1924 51.2. Phylogenetic justification

1925

1926 The uropod morphology of *U. yehoachi* indicates its membership in the crown group of
1927 Verunipeltata. The uropodal exopod of *U. yehoachi* specimen SMNS 67703 is bipartite, a
1928 synapomorphy of Verunipeltata (Haug et al., 2013). Furthermore, *U. yehoachi* shares several

1929 characters with Squillidae (Squilloidea), such as prelateral lobes, submedian teeth with fixed apices
1930 and a subquadrate telson (Haug et al., 2013). As *U. yehoachi* has not been included in a phylogenetic
1931 analysis, it is uncertain whether it falls within crown Squilloidea (Haug et al., 2013) or on its stem;
1932 either position would remain within the crown group of Verunipeltata.

1933

1934 51.3. Age justification

1935

1936 The holotype of *U. yehoachi* was collected from a chert bank in the Chert Member of the
1937 Mishash Formation, near the city of Arad, Israel (Hof, 1998). The chert banks are within the
1938 *Hoplitoplacenticeras marroti* ammonite biozone (Reiss et al., 1986). *H. marroti* co-occurs with
1939 *Baculites* sp. (smooth) (Lehmann and Murphy, 2001), which is dated to the uppermost early
1940 Campanian. Based on a spline-fit of interbedded bentonites, the base of the Tethyan *Baculites* sp.
1941 (smooth) Zone is dated to 79.64 Ma, with a duration of 0.63 Myr (Ogg et al., 2012), thus the minimum
1942 age of *U. yehoachi* is 79.01 Ma.

1943 Soft maximum as for 26.3.

1944

1945 52. Crown Peracarida

1946

1947 This clade comprises Amphipoda (scuds/beach fleas), Isopoda (wood lice/pill bugs), Cumacea,
1948 Lophogastrida, Bochusacea, Mictacea, Mysida (opossum shrimp), Stygiomysida, Spelaeogriphacea,
1949 Tanaidacea and Thermosbaenacea, their last common ancestor and all of its descendants (**Fig. 13**).
1950 Monophyly has been demonstrated by phylogenetic analysis of morphology (Jones et al., 2016;
1951 Poore, 2005; Richter and Scholtz, 2001; Wills et al., 2009; Wirkner and Richter, 2010), and combined
1952 morphology and molecular data (Jenner et al., 2009). Molecular phylogenies based on ribosomal
1953 genes reject the inclusion of Mysida within Peracarida (Jenner et al., 2009; Meland and Willassen,
1954 2007; Spears et al., 2005), while Lophogastrida and Stygiomysida are removed from Mysidacea and

1955 found comfortably within Peracarida (Meland and Willassen, 2007; Meland et al., 2015). Note
1956 ribosomal genes alone are insufficient markers for deep divergences (Giribet and Ribera, 2000), so we
1957 cautiously include Mysida within Peracarida pending multilocus investigations.

1958

1959 *52.1. Fossil specimens*

1960

1961 *Hesslerella shermani* Schram, 1970. FMNH PE 16527, holotype, lateral view (illustrated in
1962 Wilson, 2012 and **Fig. 14j**).

1963

1964 *52.2. Phylogenetic justification*

1965

1966 *H. shermani* was included in a morphological cladistic analysis by Wilson (2012). It occurred at
1967 the base of Phreatoicidea (Wilson, 2012), a position within the crown group of Isopoda and thus,
1968 crown Peracarida. Note that the assignment of our calibration fossil to crown Isopoda means that
1969 exclusion of Mysida from Peracarida (Jenner et al., 2009; Meland and Willassen, 2007; Spears et al.,
1970 2005) will not change the date assessed for Peracarida.

1971

1972 *52.3. Age justification*

1973

1974 As for 31.3.

1975

1976 *52.4. Discussion*

1977

1978 Pygocephalomorpha is a eumalacostracan fossil clade with a number of symplesiomorphic
1979 characters. Pygocephalomorpha were proposed as members of Peracarida; however, a recent
1980 phylogeny depicted them in a polytomy in any of three positions: sister to Mysidacea (Mysida +

1981 Lophogastrida), sister to all non-Mysidacea peracarids, or on the peracarid stem lineage (Jones et al.,
1982 2016). Note also the molecular analyses discussed above that exclude Mysida from Peracarida (e.g.
1983 Jenner et al., 2009), which would mean two of three equally parsimonious positions for
1984 Pygocephalomorpha may be outside the peracarid crown group. If Pygocephalomorpha were shown
1985 to be more likely within the crown group of Peracarida (e.g. as sister to non-mysid peracarids), one
1986 species in this clade, *Tealliocaris walloniensis* Gueriau et al., 2014, would become the oldest peracarid
1987 (from the Fammenian stage of the Devonian ~50 Myr older; Gueriau et al., 2014).

1988 Within Peracarida, several orders have putative Mesozoic calibration fossils that do not fully
1989 meet our requirements. Putative Lophogastrida fossils were described from the middle Triassic Falang
1990 Formation of China (Taylor et al., 2001) and Grès à Voltzia, France (Bill, 1914). These were attributed
1991 to the extant family Eucopiidae (Taylor et al., 2001), although they resolved outside crown
1992 Lophogastrida in an older phylogeny including only the French species (Taylor et al., 1998). Putative
1993 Mysida were described from the Late Jurassic Solnhofen Plattenkalk of Germany, but are poorly
1994 preserved (Schram, 1986). Fossils separately attributed to each of Lophogastrida and Mysida have
1995 also been described from the Middle Jurassic La Voulte-sur-Rhône of France (Secrétan and Riou,
1996 1986). Other fossils noted as “mysidaceans” have been mentioned, but not yet described, from the
1997 middle Triassic Luoping Biota of China (Feldmann et al., 2015; Hu et al., 2010). None of these fossils
1998 have been evaluated in the context of molecular discoveries, i.e. they assume a sister relationship
1999 between Mysida and Lophogastrida. Therefore, none can be used as calibrations until their
2000 relationships with respect to potential polyphyletic Mysidacea have been assessed.

2001 Fossils allied to Spelaeogriphacea have been described from the Cretaceous Yixian Formation
2002 of China (Shen et al., 1998; section 60.3 for revised stratigraphy) and Las Hoyas of Spain (Jaume et
2003 al., 2013). However, poor preservation of diagnostic characters indicates these are stem
2004 spelaeogriphaceans (Jaume et al., 2013).

2005 Although several Mesozoic fossils have been assigned to Amphipoda, none have sufficient or
2006 accurate morphological placement (Starr et al., 2016; Vonk and Schram, 2007). Thus no known

2007 Mesozoic fossil qualifies as a crown group amphipod.

2008

2009 **53. Crown Isopoda**

2010

2011 This clade comprises Asellota, Phoratopodidea, Cymothoida, Microcereberidea, Limnoridea,
2012 Sphaeromatidea, Valvifera, Oniscidea (wood lice/pill bugs), Phreatoicidea, Calabozoidea and
2013 Tainisopidea, their last common ancestor and all of its descendants (**Fig. 13**). The list of isopod
2014 suborders is derived from Boyko et al. (2008). Isopod monophyly was recovered in phylogenetic
2015 analysis of four housekeeping genes (Lins et al., 2012) and of combined ribosomal genes and
2016 morphology (Wilson, 2009).

2017

2018 *53.1. Fossil specimens*

2019

2020 As for 52.1.

2021

2022 *53.2. Phylogenetic justification*

2023

2024 As for 52.2.

2025

2026 *53.3. Age justification*

2027

2028 As for 31.3.

2029

2030 **54. Crown Tanaidacea**

2031

2032 This clade comprises Apseudomorpha, Neotanaidomorpha and Tanaidomorpha, their last

2033 common ancestor and all of its descendants (**Fig. 13**). Phylogenetic analysis of three molecular loci
2034 demonstrated monophyly of Apseudomorpha and Tanaidomorpha; Neotanaidomorpha could not be
2035 included (Drumm, 2010). More expansive outgroup sampling (without Neotanaidomorpha) did not
2036 recover monophyletic Tanaidacea with ribosomal and morphological data (Wilson, 2009). However, a
2037 nuclear ribosomal analysis including Neotanaidomorpha supported monophyly (Kakui et al., 2011).

2038

2039 *54.1. Fossil specimens*

2040

2041 *Alavatanais carabe* Vonk and Schram, 2007. MCNA 9537, holotype in amber, male (**Fig. 14l**).
2042 For additional morphological details, we also refer to MCNA 9846a and MCNA 13888 (**Fig. 14m**), both
2043 males.

2044

2045 *54.2. Phylogenetic justification*

2046

2047 Spanish amber tanaids were originally misidentified as amphipods (Alonso et al., 2000). The
2048 fossils were placed in a new family, Alavatanaidae, part of the superfamily Paratanaoidea within
2049 Tanaidomorpha (Sánchez-García et al., 2015; Vonk and Schram, 2007). Characters supporting affinity
2050 within Tanaidomorpha include the presence of an articulated ischium, articulation of the last two
2051 pleopods (may be reduced in males), and seven or fewer antennal articles (Sánchez-García et al.,
2052 2015).

2053

2054 *54.3. Age justification*

2055

2056 Amber inclusions bearing arthropod fossils were discovered from the Peñacerrada I outcrop,
2057 Basque-Cantabrian Basin, Álava, Spain (Alonso et al., 2000; Peñalver and Delclòs, 2010). The
2058 Peñacerrada I outcrop itself is divided into three intervals, with the lowest bearing the amber (Barrón

et al., 2015). Earlier palynological study assigned Peñacerrada I to the Escucha Formation, in the late Aptian (Barrón et al., 2001). Recent restudy, however, amended this outcrop to the Utrillas Group (Barrón et al., 2015). The presence of marine palynomorphs characterized by *Chichaouadinium vestitum* and *Palaeohystrichophora infusorioides*, and the terrestrial *Distaltriangulisporites mutabilis* and *Senectotetradites varireticulatus* together constrain a late Albian age for the Peñacerrada I (Barrón et al., 2015). The upper boundary of the Albian stage is 100.5 Ma \pm 0.4 Myr (Ogg et al., 2012), providing a minimum estimate for Álava amber fossils at 100.1 Ma.

Soft maximum as for 26.3.

55. Crown Eucarida

This clade comprises Euphausiacea (krill) and Decapoda (crabs, shrimp, lobsters), their last common ancestor and all of its descendants (**Fig. 13**). Monophyly of Euphausiacea and Decapoda is supported by phylogenetic analysis of transcriptomes (von Reumont et al., 2012), ribosomal genes (Spears et al., 2005), and combined molecular and morphological data (Jenner et al., 2009; Wills et al., 2009). Amphionidacea was represented as its own order within Eucarida based on morphology (Jenner et al., 2009; Wills et al., 2009), but recently the first molecular sequence data have become available, indicating that Amphionidacea are larval stages of Caridea (i.e. within Decapoda) (De Grave et al., 2015).

55.1. Fossil specimens

As for 49.1.

55.2. Phylogenetic justification

2085 As for 49.2.

2086

2087 *55.3. Age justification*

2088

2089 As for 49.3.

2090

2091 **56. Crown Decapoda**

2092

2093 This clade comprises Dendrobranchiata (shrimp/prawns) and Pleocyemata (caridean shrimp,
2094 mud shrimp, true crabs, hermit and king crabs, lobsters, spiny lobsters, etc.), their last common
2095 ancestor and all of its descendants (**Fig. 13**). Decapod monophyly is established by phylogenetic
2096 analysis of protein-coding genes (Bracken et al., 2009; Bybee et al., 2011; Timm and Bracken-
2097 Grissom, 2015), morphology (Legg et al., 2013; Richter and Scholtz, 2001), and combined
2098 morphology and molecular data (Jenner et al., 2009). Analyses of whole mitochondrial genomes place
2099 Euphausiacea (krill) within Decapoda (Shen et al., 2015), a result congruent with acquisition of a
2100 nauplius larval stage (though this is accepted as convergent: (Jirikowski et al., 2013; Scholtz, 2000).
2101 We apply caution in interpreting deep splits inferred from mitochondrial DNA (Simon and Hadrys,
2102 2013); hence, we accept decapod monophyly to the exclusion of krill.

2103

2104 *56.1. Fossil specimens*

2105

2106 As for 49.1.

2107

2108 *56.2. Phylogenetic justification*

2109

2110 As for 49.2.

2111

2112 56.3. *Age justification*

2113

2114 As for 49.3.

2115

2116 **57. Crown Allotriocarida**

2117

2118 This clade comprises Branchiopoda, Cephalocarida, Remipedia, and Hexapoda, their last
2119 common ancestor and all of its descendants (**Fig. 15**). Monophyly of this clade was proposed by a
2120 combined phylogenetic analysis of transcriptomes, nuclear protein-coding genes, and morphology
2121 (Oakley et al., 2013). As of this writing, a transcriptome remains to be sequenced for Cephalocarida.
2122 This clade is not recognized in GenBank taxonomy.

2123

2124 57.1. *Fossil specimens*

2125

2126 *Rehbachella kinnekullensis* Müller, 1983. UB 644, holotype, consisting of a complete larva
2127 (**Fig. 16a**). This species has been extensively documented by Walossek (1993).

2128

2129 57.2. *Phylogenetic justification*

2130

2131 Recent phylogenetic analyses including *R. kinnekullensis* have strongly indicated a position on
2132 the branchiopod stem lineage (morphology: Legg et al., 2013; combined morphology and molecular:
2133 Oakley et al., 2013) or the cephalocarid stem lineage (morphology: Wolfe and Hegna, 2014). Either
2134 relationship (or a strict consensus position on the stem of Branchiopoda + Cephalocarida) would still
2135 be within the crown group of Allotriocarida.

2136

2137 57.3. *Age justification*

2138

2139 As for 35.3.

2140

2141 **58. Crown Branchiopoda**

2142

2143 This clade comprises Anostraca (fairy/brine shrimp), Notostraca (tadpole shrimp) and
2144 Diplostraca, their last common ancestor and all of its descendants (**Fig. 15**). Monophyly of this clade is
2145 established by phylogenetic analysis of protein-coding genes (Regier et al., 2010; Spears and Abele,
2146 2000), transcriptomes (von Reumont et al., 2012), morphology (Legg et al., 2013), and combined
2147 molecular and morphological data (Oakley et al., 2013).

2148

2149 58.1. *Fossil specimens*

2150

2151 *Lepidocaris rhyniensis* Scourfield, 1926. BMNH IN. 24493, holotype (**Fig. 16b**).

2152

2153 58.2. *Phylogenetic justification*

2154

2155 *L. rhyniensis* has been included in several phylogenetic analyses, coded from a composite of
2156 holotype and paratype material (Scourfield, 1926). With morphology only, *L. rhyniensis* is sister to
2157 extant Anostraca (Hegna, 2012; Legg et al., 2013); with morphology and molecular data, it is within
2158 Anostraca (Oakley et al., 2013). Therefore, it is unequivocally a crown group member of
2159 Branchiopoda.

2160

2161 58.3. *Age justification*

2162

2163 Minimum as for 10.3. Soft maximum as for 26.3.

2164

2165 *58.4. Discussion*

2166

2167 *R. kinnekullensis* has been frequently used to polarize the evolution of Branchiopoda. Its fossils
2168 are known only from larval stages, which may confound discussions of its morphology (Wolfe and
2169 Hegna, 2014). Recent phylogenetic analyses have indicated a position on the branchiopod stem
2170 lineage (Legg et al., 2013; Oakley et al., 2013) or the cephalocarid stem lineage (Wolfe and Hegna,
2171 2014), excluded from the branchiopod crown. Nevertheless, divergence time analyses suggest
2172 Cambrian origins for crown Branchiopoda (Oakley et al., 2013), such that molecular clock estimates
2173 do not conflict with branchiopod affinities for Cambrian filter plate fossils (Harvey and Butterfield, 2008)
2174 or *R. kinnekullensis*.

2175

2176 **59. Crown Anostraca**

2177

2178 This clade comprises Artemiidae, Branchinectidae, Branchipodidae, Chirocephalidae,
2179 Parartemiidae, Streptocephalidae, Tanymastigidae and Thamnocephalidae, their last common
2180 ancestor and all of its descendants (**Fig. 15**). Monophyly of five sampled families is established by
2181 phylogenetic analysis of six housekeeping genes and morphology (Richter et al., 2007). Full sampling
2182 of families produced monophyletic Anostraca in an analysis of one ribosomal gene (Weekers et al.,
2183 2002).

2184

2185 *59.1. Fossil specimens*

2186

2187 *Palaeochirocephalus rasnitsyni* Trussova, 1975. TsGM 7a/10303 and 9/10303, preserving male
2188 antennae, and TsGM 2/10303, preserving a female body. The holotype does not preserve any

2189 diagnostic characters for the Anostraca crown group.

2190

2191 59.2. *Phylogenetic justification*

2192

2193 *P. rasnitsyni* (formerly *Chirocephalus rasnitsyni* Trussova, 1971) has not been included in a
2194 phylogenetic analysis. Taxonomic placement of its family, Palaeochirocephalidae, implicitly relates
2195 them to the extant family Chirocephalidae, though this family is considered *incertae sedis* by Rogers
2196 (2013). Morphological characters (shared with Chirocephalidae) supporting this relationship include 11
2197 thoracic appendages bearing two pre-epipodites, the nine-segmented abdomen, and the basally
2198 separated two-segmented antennae in males (Trussova, 1971). A possible position on the stem
2199 lineage of Chirocephalidae would therefore place *P. rasnitsyni* within the crown group of Anostraca.

2200

2201 59.3. *Age justification*

2202

2203 The type locality of *P. rasnitsyni*, briefly described by Trussova (1971), is the left bank of Daya
2204 River, upstream from Shiviya Falls, in eastern Transbaikalia, Russia. This locality, within the Unda-Daya
2205 Basin, has been assigned to the Glushkovo Formation (Sinitshenkova, 2005). The age of the
2206 Glushkovo Formation is poorly constrained, suggested as Late Jurassic (Sinitsa and Starukhina,
2207 1986), Early Cretaceous (Sinitshenkova, 2005; Zherikhin et al., 1998), or perhaps at the
2208 Jurassic/Cretaceous boundary (Rasnitsyn and Quicke, 2002). However, *P. rasnitsyni* itself (along with
2209 palaeopteran insects such as *Proameletus caudatus* and *Equisetum undense*) correlates the
2210 Glushkovo Formation to the Baigul locality, also in Transbaikalia (Ignatov et al., 2011). The Baigul
2211 locality preserves fossil *Bryokhutuliinia jurassica*, one of only five known genera of Jurassic mosses
2212 (Ignatov et al., 2011). Thus Baigul can be correlated to the Ulugey Formation of Mongolia, which also
2213 preserves *Bryokhutuliinia* fossils (Ignatov, 1992). The Ulugey Formation, in turn, is correlated to the La
2214 Cabrúia (Sierra del Montsec, Pyrenees, Spain) locality based on the shared presence of the

2215 coleopteran genus *Gobicar* (Gratshev and Zherikhin, 2000; Legalov, 2010; Soriano et al., 2006). Fossil
2216 charophyte algae (*Atopochara trivolis triquetra*) indicate an age of late Hauterivian-early Barremian
2217 for the freshwater deposits of La Cabrúa (Gomez et al., 2002; Martín-Closas and López-Morón, 1995).
2218 Although it has been proposed that a minimum age of the Montsec limestone may be as young as the
2219 end Maastrichtian (O'Reilly et al., 2015), recent biostratigraphic work proposes the last appearance of
2220 *A. trivolis triquetra* is correlated to the *Deshayesites weissi* ammonite Zone at its youngest (Martín-
2221 Closas et al., 2009). Revision of Tethyan ammonite dates indicates the *D. weissi* Zone, now the *D.*
2222 *forbesi* Zone, had an upper boundary of 125.71 Ma (Ogg et al., 2012a). This age is early Aptian, and
2223 provides a minimum for the correlated Glushkovo Formation.

2224 Soft maximum as for 26.3.

2225

2226 59.4. Discussion

2227

2228 Oakley et al. (2013) placed the Early Devonian *L. rhyniensis* in the crown group of Anostraca,
2229 having sampled extant members of Artemiidae and Streptocephalidae. Earlier descriptions (Sanders,
2230 1963; Scourfield, 1940a, 1926; Walossek, 1993) support this position. However, the most extensively
2231 sampled morphological analyses of Hegna (2012) consistently place *L. rhyniensis* as sister to all
2232 extant Anostraca. The Late Devonian *Haltinnaias serrata* Gueriau et al., 2016, described from both
2233 sexes, likely also belongs to the total group of Anostraca.

2234 Other fossils from the Late Jurassic Daohugou Beds of China (Huang et al., 2006; Shen and
2235 Huang, 2008) and Early Cretaceous Koonwarra Formation of Australia are likely to belong to the
2236 crown group of Anostraca, as they have been included in a morphological phylogenetic analysis
2237 (Hegna, 2012), but these have not been described in detail.

2238

2239 60. Crown Notostraca

2240

2241 This clade comprises two extant genera, *Triops* and *Lepidurus*, their last common ancestor and
2242 all of its descendants (**Fig. 15**). Monophyly is established by phylogenetic analysis of housekeeping
2243 genes (Mathers et al., 2013), morphology (Lagebro et al., 2015), and combined morphological and
2244 molecular data (Richter et al., 2007).

2245

2246 60.1. Fossil specimens

2247

2248 *Chenops yixianensis* Hegna and Ren, 2010. CNU-CAL-HP-2009001 (part; **Fig. 16c**) and CNU-
2249 CAL-HP-2009002 (counterpart), holotype.

2250

2251 60.2. Phylogenetic justification

2252

2253 In the morphological phylogenetic analysis of Lagebro et al. (2015), *C. yixianensis* was in a
2254 polytomy with other crown Notostraca, including *Lepidurus batesoni*. The equal size of thoracic
2255 endopods and fourth and fifth endites may exclude *C. yixianensis* from crown Notostraca (Hegna and
2256 Ren, 2010). However, in previous morphological phylogenies (Hegna, 2012), *C. yixianensis* was sister
2257 taxon to the extant *L. batesoni*. This is because *L. batesoni* lacks elongated endites on the first
2258 thoracic appendage, suggesting a synapomorphy between *C. yixianensis* and the extant species, and
2259 perhaps membership in an entirely different genus (Hegna, 2012; Hegna and Ren, 2010). If indeed *C.*
2260 *yixianensis* is, based on phylogenies and endite morphology, a sister group of *L. batesoni*, it would
2261 remain within the crown Notostraca.

2262

2263 60.3. Age justification

2264

2265 This fossil was discovered in the Yixian Formation of northeastern China (Hegna and Ren,
2266 2010). The Yixian Formation lies between the overlying Jiufotang Formation and underlying Tuchengzi

2267 Formation; together they comprise the Jehol Group (e.g. Chang et al., 2009a; Zhou, 2006). Dating of
2268 the Jehol Group has been contentious, varying from Late Jurassic to Early Cretaceous based on
2269 biostratigraphic and radiometric techniques. Recent $^{40}\text{Ar}/^{39}\text{Ar}$ dates yielded ages of $129.7 \text{ Ma} \pm 0.5$
2270 Myr for basaltic lava from the bottom of the Yixian Formation and $122.1 \text{ Ma} \pm 0.3$ Myr for tuff layers at
2271 the bottom of the overlying Jiufotang Formation (Chang et al., 2009a). Other age estimates have fallen
2272 within this range (reviewed by Zhou, 2006). This debate underscores the point that reasonably precise
2273 radiometric dates may still be quite inaccurate. We conservatively use the younger of these estimates,
2274 so a minimum age for Yixian fossils is 121.8 Ma.

2275 Soft maximum as for 26.3.

2276

2277 60.4. Discussion

2278

2279 *Strudops goldenbergi* Lagebro et al., 2015 was recently described from the Late Devonian,
2280 which would be the oldest notostracan. In a morphological phylogenetic analysis, however, it could
2281 only be identified as a member of the total group (Lagebro et al., 2015), and thus cannot assign a
2282 minimum age to crown Notostraca.

2283 Morphological conservatism (i.e. Permian and Triassic fossils erroneously attributed to the
2284 extant species *Triops cancriformis*) has led to the misleading name 'living fossil' for Notostraca
2285 (Hegna, 2012; Mathers et al., 2013). Once touted as the 'oldest living species,' *T. cancriformis*
2286 *permiensis*, from the Permian of France, is more similar to the co-occurring *Lepidurus occitaniacus*
2287 than extant *Triops* (Lagebro et al., 2015). Decay experiments on living *T. cancriformis* confirm that
2288 carapace characters and elongated endites of the first thoracic limb are phylogenetically meaningful,
2289 thus rejecting a referral of any fossil to the extant species (Hegna, 2012).

2290

2291 61. Crown Diplostraca

2292

2293 This clade comprises Laevicaudata, Spinicaudata, Cyclestherida (these three collectively:
2294 'clam shrimp') and Cladocera (water fleas), their last common ancestor and all of its descendants (**Fig.**
2295 **15**). Monophyly is supported by phylogenetic analysis of transcriptomes (von Reumont et al., 2012)
2296 and 62 nuclear protein-coding genes (Regier et al., 2010), and combined molecules and morphology
2297 (Oakley et al., 2013) although Cyclestherida was not sampled in these analyses. Smaller molecular
2298 analyses (Richter et al., 2007 with indel costs) and morphological analyses (Hegna, 2012; Legg et al.,
2299 2013; Olesen, 2009, 1998; Richter et al., 2007) including data for Cyclestherida also support
2300 monophyly of Diplostraca.

2301

2302 *61.1. Fossil specimens*

2303

2304 *Leaia chinensis* Shen, 1983. NIGP 51786, holotype, preserving a left valve (**Fig. 16d**).

2305

2306 *61.2. Phylogenetic justification*

2307

2308 *L. chinensis* has not been treated in a phylogenetic context. It is placed within the fossil family
2309 Leaiidae primarily based on carapace shape, including the nearly straight ventral edge (Shen, 1978;
2310 Tasch, 1987). However, congeneric fossils, *L. gondwanella* Tasch, 1987 and *L. canadensis* Shen and
2311 Schram, 2014, may have preserved soft parts (Shen and Schram, 2014). These include biramous
2312 antennae, mandibles, as well as putative shell glands and digestive tubes, and radiating carinae (Shen
2313 and Schram, 2014). The short and delicate antennal flagella and radiating carinae of *L. chinensis*, in
2314 particular, are similar to extant Spinicaudata and Cyclestherida; the presence of growth lines is only
2315 known from Spinicaudata (Shen and Schram, 2014). However, the head shape of *L. chinensis* is more
2316 similar to Laevicaudata. This suggests phylogenetic positions either on the stem of Onychocaudata
2317 (Spinicaudata, Cyclestherida, and Cladocera) or on the stem of Laevicaudata. A position as stem
2318 Diplostraca would mean growth lines are ancestral for all diplostracans, and have been lost twice (in

2319 the ancestors of Laevicaudata and Cyclestherida + Cladocera), which is unparsimonious. Hence we
2320 support *L. chinensis* within crown Diplostraca.

2321

2322 61.3. Age justification

2323

2324 *L. chinensis* was found in sediments of the Guitou Group, near Chengma village, Hepu county,
2325 Guangxi Zhuang Autonomous Region, southern China (Shen, 1978). The upper subgroup of the
2326 Guitou Group, bearing conchostracan fossils, has purple-grey sandy shales within mudstone
2327 lamination, and is overlain by the Tungkangling Formation (Shen, 1978). The brachiopod
2328 *Stringocephalus*, the stromatoporoid corals *Endophyllum* and *Sunophyllum*, and the ostracods
2329 *Samarella crassa* and *Tuberokloedenia bituberculata* together indicate a Givetian age for the upper
2330 Tungkangling Formation (Liao and Ruan, 2003). The underlying Yingtang Formation (as well as the
2331 lower Tungkangling Formation) are correlated to the Eifelian Stage by the ostracods *Bairdocypris*
2332 *biesenbachi* and *Flatiella subtrapezoidalis* (Liao and Ruan, 2003), the brachiopod *Bornhardtina* and
2333 the conodonts *Polygnathus australis*, *P. costatus*, and *P. partitus* (Ma et al., 2009). As the
2334 conchostracan-bearing sediments underlie the Tungkangling Formation, they are no younger than
2335 Eifelian in age. The upper boundary of the Eifelian is 387.7 Ma \pm 0.8 Myr, providing a minimum age of
2336 386.9 Ma.

2337 Soft maximum as for 26.3.

2338

2339 62. Crown Spinicaudata

2340

2341 This clade comprises Leptestheriidae, Cyzicidae and Limnadiidae, their last common ancestor
2342 and all of its descendants (**Fig. 15**). Clade names are defined in Schwentner et al. (2009). Monophyly
2343 is established by phylogenetic analysis of morphology (Hegna, 2012; Olesen, 1998; Richter et al.,
2344 2007), three housekeeping genes (Schwentner et al., 2009), and six housekeeping genes plus

2345 morphology (Richter et al., 2007).

2346

2347 *62.1. Fossil specimens*

2348

2349 *Dundgobiestheria mandalgobiensis* Li et al., 2014. ED-A-14-1, holotype (**Fig. 16e**).

2350

2351 *62.2. Phylogenetic justification*

2352

2353 Phylogenetic analysis of spinicaudatan fossils is rare, owing to difficulty in character
2354 identification (Astrop and Hegna, 2015; see also 62.3). Members of Leptestheriidae appear to share
2355 emergence of dendritic reticulation and anastomizing ridge ornamentation with the fossil spinicaudatan
2356 family Loxomegaglyptidae (Astrop and Hegna, 2015; Shen, 1994). *D. mandalgobiensis* is perhaps the
2357 oldest definitive Loxomegaglyptidae, based on large-sized reticulate ornamentation and weakly
2358 defined growth lines, shared with other members of the family (Li et al., 2014). Due to the above
2359 ornamentation characters (Astrop and Hegna, 2015; T. Astrop, pers. comm.), it can be placed on the
2360 stem lineage of Leptestheriidae, and thus within crown Spinicaudata.

2361

2362 *62.3. Age justification*

2363

2364 *D. mandalgobiensis* is from the Eedemt Formation, Khootiin Khotgor coal mine region,
2365 Dundgobi Province, southeast Mongolia (Li et al., 2014). The spinicaudatan genus *Triglypta* (co-
2366 occurring with *D. mandalgobiensis*) provides a biostratigraphic constraint on the Eedemt Formation, as
2367 *Triglypta* species also occur in both the (older) *Euestheria ziliujingensis* fauna and (younger)
2368 *Sinokontikia* fauna in lacustrine sequences of northwestern China (Li et al., 2014; Li and Matsuoka,
2369 2012). First, the *E. ziliujingensis* fauna is distributed throughout east Asia, dated to a Bajocian-
2370 Bathonian (Jurassic) age by the occurrence of *Euestheria trotternishensis* (Chen et al., 2007). *E.*

2371 *trotternishensis* co-occurs in the *Skyestheria* spinicaudatan fauna of Skye, Scotland; the Bajocian-
2372 Bathonian date for this locality comes from ammonite and palynological index fossils (Chen and
2373 Hudson, 1991). Although the *Sinokontikia* fauna was once thought stratigraphically equal to the late *E.*
2374 *ziliujingensis* fauna (Chen et al., 2007; Li and Matsuoka, 2012), *Sinokontikia* has been determined to
2375 be younger based on occurrence in the Qiketai Formation of the Turpan Basin, northwest China. The
2376 Qiketai Formation is constrained only to the Callovian. As Chinese *Triglypta* (the index genus for the
2377 Eedemt Formation) is absent from any higher strata, a minimum age comes from the upper boundary
2378 of the *Sinokontikia* fauna (Li et al., 2014). The upper boundary of the Callovian is 163.5 Ma \pm 1.0 Myr,
2379 giving a minimum age for the Eedemt Formation of 162.5 Ma.

2380 Soft maximum as for 26.3.

2381

2382 62.4. Discussion

2383

2384 Preservation of the calcified spinicaudatan carapace is extremely common (some fossil species
2385 are used as biostratigraphic indices), but characters diagnostic for extant taxa (i.e. soft parts) are
2386 rarely preserved (Hegna, 2012; Orr and Briggs, 1999). Uniquely among ‘conchostracans’ (and indeed
2387 most arthropods), Spinicaudata do not moult their carapace, instead preserving growth lines. The
2388 number of growth lines necessarily increases through ontogeny, so it is a poor character to
2389 demonstrate phylogenetic relationships. Therefore relationships among fossil taxa have been
2390 determined based on ornamentation of the carapace (e.g. Gallego, 2010); however, these characters
2391 have not yet been integrated with morphological study of extant carapaces. Ongoing work seeks to
2392 demonstrate the utility of carapace ornamentation as valid phylogenetic characters (Astrop and
2393 Hegna, 2015). Furthermore, integration of past descriptive work is hindered by language barriers
2394 between different workers (Chinese, Russian, and English; summarized by Astrop and Hegna, 2015).

2395 For example, some poorly known fossils from the Middle Devonian of Antarctica, described as
2396 members of the genus *Cyzicus* (*Euestheria*), may be assigned to Spinicaudata (Tasch, 1987), possibly

2397 on the stem lineage of ‘non-Australian Cyzicidae’ *sensu* Schwentner et al. (2009). Characters linking
2398 the Antarctic fossils to the living clade, however, are dubious. There are reports of uncertain Late
2399 Devonian stem group members for Limnadiidae (Liu and Gao, 1985), and much more likely Permian
2400 stem Limnadiidae (Novojilov, 1970), but these fossils are insufficiently described, leaving any specific
2401 crown spinicaudatan character states debatable. Therefore we must caution that Jurassic age is likely
2402 a severe underestimate of crown spinicaudatan antiquity. Finally, the Sinemurian *Afrolimnadia*
2403 *sibiriensis* Tasch, 1987 was used to calibrate crown Spinicaudata in a divergence time analysis, but
2404 with limited justification of characters for Limnadiidae (Bellec and Rabet, 2016).

2405

2406 **63. Crown Cladocera**

2407

2408 This clade comprises Anomopoda, Ctenopoda, Onychopoda and Haplopoda, their last
2409 common ancestor and all of its descendants (**Fig. 15**). Monophyly of this clade is supported by
2410 phylogenetic analysis of housekeeping genes alone (Stenderup et al., 2006), morphology (Hegna,
2411 2012; Olesen, 2009, 2007, 1998), and six housekeeping genes plus morphology (Richter et al., 2007).

2412

2413 *63.1. Fossil specimens*

2414

2415 *Smirnovidaphnia smirnovi* Kotov, 2007, illustrated by two specimens: PIN 1873/100 (holotype,
2416 preserving the second antenna; **Fig. 16f**) and PIN 1873/105 (paratype, preserving both second
2417 antennae and mandibles).

2418

2419 *63.2. Phylogenetic justification*

2420

2421 The setal armature of the second antenna is similar to that found in extant Ctenopoda (Kotov,
2422 2007). In morphological phylogenetic analyses, *S. smirnovi* was either found in a basal polytomy with

all of crown Cladocera, or it was sister to all Cladocera except Anomopoda (Hegna, 2012). The polytomy could indicate a stem cladoceran position, but the analyses in which *S. smirnovi* was within crown Cladocera included a lesser amount of missing data, and thus may be more robust. Furthermore, Ctenopoda itself was not recovered as monophyletic in these analyses, but *S. smirnovi* was related to taxa that have been previously included in Ctenopoda (Hegna, 2012).

63.3. Age justification

S. smirnovi was found on the right bank of the Angara River, downstream of Ust'-Baley village in the Olonkovsky District of Asian Russia (Kotov, 2007). According to the presence of *Osmundacidites*-type plant spores, the Ust'-Baley outcrop of the Cheremkhovo or Cheremkhovskaya Formation is correlated to the late Toarcian stage of the Early Jurassic (Akulov et al., 2015). The upper boundary of the Toarcian is $174.1 \text{ Ma} \pm 1.0 \text{ Myr}$, therefore giving a minimum age of 173.1 Ma.

Soft maximum as for 26.3.

63.4. Discussion

Ebullitiocaris oviformis Anderson et al., 2003 from the Devonian Rhynie Chert and *E. elatus* Womack et al., 2012 from Carboniferous chert have both been described as Cladocera. Fragmentation patterns of both fossils are inconsistent with those observed from decay experiments, therefore casting doubt on their cladoceran membership (Hegna, 2012).

Other Jurassic/Cretaceous members of the fossil family Prochydoridae are known from Mongolia and Asian Russia (Kotov, 2009). However, the Prochydoridae have been proposed as a member of the stem lineage of Anomopoda, the stem of all non-Anomopoda Cladocera, as well as the stem of Cladocera itself (Kotov, 2013, 2009). Thus crown-group affinity cannot be confirmed.

2449 **64. Crown Hexapoda**

2450

2451 This clade comprises Collembola (springtails), Protura (cone heads), Diplura (two-pronged
2452 bristletails) and Insecta (insects), their last common ancestor and all of its descendants (**Fig. 17**).
2453 Monophyly of Hexapoda is established by phylogenetic analysis of nuclear protein-coding genes
2454 (Regier et al., 2010, 2005; Sasaki et al., 2013), transcriptomes (Dell’Ampio et al., 2014; Misof et al.,
2455 2014), and morphology (Legg et al., 2013).

2456

2457 *64.1. Fossil specimens*

2458

2459 *Rhyniella praecursor* Hirst and Maulik, 1926. NHMUK IN. 27765, lectotype (*fide* Ross and York,
2460 2003), head capsule with mouthparts in chert (**Fig. 2f**). Paralectotypes NHMUK IN. 38225-38227.

2461

2462 *64.2. Phylogenetic justification*

2463

2464 The Rhynie Chert taxon *R. praecursor* Hirst and Maulik, 1926, was originally identified as an
2465 insect. Re-identification as a poduromorph collembolan was made by Tillyard (1928). Additional
2466 material was examined by Scourfield (1940a, 1940b), who considered *R. praecursor* to be a possible
2467 entomobryomorph rather than a poduromorph. Subsequent studies, including some additional
2468 specimens, were made by Massoud (1967), Whalley and Jarzembowski (1981), Greenslade (1988),
2469 and Greenslade and Whalley (1986). The most recent of these investigations favour membership of at
2470 least some specimens assigned to *R. praecursor* in the extant entomobryomorph family Isotomidae
2471 (Greenslade and Whalley, 1986). Greenslade (1988) indicated that three species could be
2472 represented in the sample that is currently assigned to *R. praecursor*. Identification as an
2473 entomobryomorph underpins an assignment to the crown groups of Collembola and Hexapoda. Other
2474 taxa from the Rhynie Chert (*Rhyniognatha* and *Leverhulmia*; Engel and Grimaldi, 2004; Fayers and

2475 Trewin, 2005) and thus as old as *R. praecursor* have also been identified as Hexapoda, and more
2476 precisely as Insecta.

2477

2478 *64.3. Age justification*

2479

2480 As for 58.3.

2481

2482 **65. Crown Collembola**

2483

2484 This clade comprises Entomobryomorpha, Neelipleona, Poduromorpha, Symphypleona and
2485 Tomoceroidea, their last common ancestor and all of its descendants (**Fig. 17**). Most studies with
2486 substantial outgroup sampling are based on only one or two subclades of Collembola; however,
2487 phylogenetic analysis of ribosomal genes including all subclades (Gao et al., 2008; Xiong et al., 2008)
2488 demonstrated monophyly. Additional support with limited sampling of Collembola subclades comes
2489 from transcriptomes (Dell’Ampio et al., 2014), mitochondrial genomes (Carapelli et al., 2007), and
2490 morphology (D’Haese, 2003).

2491

2492 *65.1. Fossil specimens*

2493

2494 As for 64.1.

2495

2496 *65.2. Phylogenetic justification*

2497

2498 As for 64.2.

2499

2500 *65.3. Age justification*

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As for 58.3.

66. Crown Diplura

This clade comprises Projapygoidea, Japygoidea and Campodeoidea, their last common ancestor and all of its descendants (**Fig. 17**). Monophyly of Diplura has been demonstrated by phylogenetic analysis of ribosomal genes (Gao et al., 2008), whole mitochondrial genomes (Chen et al., 2014), and morphology (Koch, 1997).

66.1. Fossil specimens

Ferrojapyx vivax Wilson and Martill, 2001. SMNS 64276, holotype.

66.2. Phylogenetic justification

F. vivax is “morphologically indistinguishable” (Wilson and Martill, 2001) from extant Japygoidea, sharing characters such as 40-segmented antennules, abdominal tergites 1-8 with a median suture, abdominal tergite 9 significantly shorter, conical abdominal styli, and forcipate cerci with curved inner margins and lacking obvious denticles (Wilson and Martill, 2001). Monophyly of Japygoidea has been considered “beyond doubt” (Koch, 2009; Fig. 3 therein for cladogram), so a phylogenetic position for this fossil either within or closely related to that clade would place it within crown Diplura.

66.3. Age justification

2527 As for 29.3.

2528

2529 **67. Crown Insecta**

2530

2531 This clade comprises Microcoryphia (jumping bristletails), Zygentoma (silverfish) and Pterygota
2532 (winged insects), their last common ancestor and all of its descendants (**Fig. 17**). Monophyly is
2533 established by phylogenetic analysis of nuclear protein-coding genes (Regier et al., 2010, 2005;
2534 Sasaki et al., 2013), transcriptomes (Dell’Ampio et al., 2014; Misof et al., 2014), and morphology
2535 (Legg et al., 2013).

2536

2537 *67.1. Fossil specimens*

2538

2539 *Rhyniognatha hirsti* Tillyard, 1928. BMNH IN. 38234, holotype, preserving the mandibles and
2540 their articulation (**Fig. 18d**). Redescribed and imaged by Engel and Grimaldi (2004).

2541

2542 *67.2. Phylogenetic justification*

2543

2544 The only known specimen (the holotype) of *R. hirsti* demonstrates that the preserved pair of
2545 mandibles articulate at two points, i.e. are dicondylic (Engel and Grimaldi, 2004). Dicondylic mandibles
2546 are a diagnostic synapomorphy of Insecta (including Microcoryphia; Blanke et al., 2015). Although *R.*
2547 *hirsti* has not been included in numerical phylogenetic analyses, its mandibular shape implies
2548 “metapterygote” affinities (Engel and Grimaldi, 2004) and accordingly crown group membership within
2549 Insecta.

2550

2551 *67.3. Age justification*

2552

2553 As for 58.3.

2554

2555 67.4. Discussion

2556

2557 A complete body fossil of a putative insect, *Strudiella devonica* Garrouste et al., 2012, was
2558 described from the Fammenian (372-359 Ma) of Strud, Belgium. Apomorphies supporting an insect
2559 affinity (such as the structure of the mandibles and the number of legs), however, are poorly preserved
2560 and potentially over-interpreted (Hörnchemeyer et al., 2013).

2561

2562 68. Crown Microcoryphia

2563

2564 This clade comprises the families 'Machilidae' and Meinertillidae, their last common ancestor,
2565 and all of its descendants (**Fig. 17**). This clade is commonly referred to as Microcoryphia in taxonomic
2566 literature and Archaeognatha in phylogenetic literature (Gaju-Richart et al., 2015). Recently it was
2567 clarified that Archaeognatha includes the completely extinct order Monura (compound eyes not fused,
2568 paracercus only) and Microcoryphia (very small head vertex due to their fused compound eyes,
2569 terminalia composed of a median paracercus and two lateral cerci), and thus the crown group refers to
2570 Microcoryphia only (Gaju-Ricart et al., 2015). Monophyly is supported by phylogenetic analysis of
2571 transcriptomes (Misof et al., 2014), nuclear protein-coding genes (Regier et al., 2010), and
2572 morphology (Legg et al., 2013). Synapomorphies are discussed and mapped on cladograms by Larink
2573 (1997) and Koch (2003).

2574

2575 68.1. Fossil specimens

2576

2577 *Cretaceomachilis libanensis* Sturm and Poinar, 1998 (collection Milki No. 194/35, deposited at
2578 the American University of Beirut, Beirut, Lebanon), holotype, male in amber (**Fig. 18b**).

2579

2580 68.2. *Phylogenetic justification*

2581

2582 *C. libanensis* shares morphological characters with the extant family Meinertillidae. These
2583 include the the absence of scales on the scapus, pedicellus and flagellum, and the presence of a
2584 characteristic hook near the distal end of article 2 of the male maxillary palp (Sturm and Poinar, 1998).
2585 The latter character is a synapomorphy of crown Meinertillidae (Sturm and Poinar, 1998), therefore the
2586 fossil is within crown Microcoryphia.

2587

2588 68.3. *Age justification*

2589

2590 *C. libanensis* was discovered in Cretaceous amber, from a locality in Lebanon that was not
2591 recorded (Sturm and Poinar, 1998). We therefore use a minimum age constraint from the youngest of
2592 the several known Lebanese amber localities, which all bear the same age within the early Barremian
2593 (Maksoud et al., 2016). The upper boundary of the early Barremian is proposed to be the first
2594 appearance of the ammonite *Ancyloceras vandenheckii* (Ogg et al., 2012). Cyclostratigraphy dates the
2595 *A. vandenheckii* Zone beginning at 129.41 Ma (Ogg et al., 2012), providing a minimum age for Jezzine
2596 Lebanese amber fossils.

2597 Soft maximum as for 26.3.

2598

2599 68.4. *Discussion*

2600

2601 Body imprint and trackway trace fossils from the Pennsylvanian have been attributed to both
2602 Archaeognatha and Zygentoma (Getty et al., 2013). Experiments with extant species of both clades
2603 indicate that archaeognathans produced fossil body imprints, as well as trackways exhibiting opposite
2604 symmetry (Getty et al., 2013). However, it is not possible to distinguish specific crown group

2605 apomorphies for these traces.

2606 Dasyleptidae, a diverse fossil group known from the Carboniferous-Triassic, has been
2607 proposed as the sister group of Ectognatha (Collembola, Diplura, Protura) as well as part of
2608 Archaeognatha. Recent classifications place Dasyleptidae in Monura, a separate extinct suborder of
2609 Archaeognatha, and thus outside its crown group (Bechly and Stockar, 2011; Gaju-Ricart et al., 2015).

2610

2611 **69. Crown Zygentoma**

2612

2613 This clade comprises the families Lepismatidae, Nicoletiidae, Lepidotrichidae, Maindroniidae,
2614 and Protrinemuridae, their last common ancestor and all of its descendants (**Fig. 17**). Phylogenetic
2615 analyses of transcriptomes (Misof et al., 2014), protein-coding genes (Regier et al., 2010; Sasaki et
2616 al., 2013), morphology (Blanke et al., 2014), and combined molecular and morphological data (Kjer et
2617 al., 2006) with partial taxon sampling support monophyly.

2618

2619 *69.1. Fossil specimens*

2620

2621 *Burmalepisma cretacicum* Mendes and Poinar, 2008 (specimen B-TH-1 deposited in the Poinar
2622 amber collection maintained at Oregon State University; B-TH refers to Burma-Thysanura), holotype, a
2623 female in amber (**Fig. 18c**).

2624

2625 *69.2. Phylogenetic justification*

2626

2627 Although it has not been included in a phylogenetic analysis, *B. cretacicum* bears several
2628 morphological similarities to the extant family Lepismatidae. These include the presence of compound
2629 eyes, absence of ocelli, coxal, femur, and tarsal morphology, absence of a pronotal setal collar, and
2630 presence of only smooth macrochaetae (Mendes and Poinar, 2008). A phylogenetic position either on

2631 the stem or within the crown of Lepismatidae is within the crown group of Zygentoma.

2632

2633 *69.3. Age justification*

2634

2635 As for 33.3.

2636

2637 *69.4 Discussion*

2638

2639 A possible Zygentoma fossil has been recorded from the older Aptian Crato Formation of Brazil
2640 (Sturm, 1998), but is not sufficiently characterized to be a calibration fossil. Another fossil from
2641 Burmese amber, *Cretolepisma kachinicum* Mendes and Wunderlich, 2013, is also identified as
2642 Lepismatidae. This fossil is of equal age and affinity, and is therefore also an acceptable calibration for
2643 Zygentoma.

2644

2645 **70. Crown Pterygota**

2646

2647 This clade comprises Palaeoptera (mayflies, dragonflies) and Neoptera (flexible winged
2648 insects), their last common ancestor and all of its descendants (**Fig. 17**). Monophyly is established
2649 based on phylogenetic analysis of nuclear protein-coding genes (Regier et al., 2010, 2005; Sasaki et
2650 al., 2013), transcriptomes (Misof et al., 2014; Simon et al., 2012), and morphology (Legg et al., 2013).

2651

2652 *70.1. Fossil specimens*

2653

2654 *Delitzschala bitterfeldensis* Brauckmann and Schneider, 1996 (BGR X 9216), holotype,
2655 preserving a forewing, a hindwing, cerci, and part of the abdomen (**Fig. 18a**).

2656

2657 70.2. *Phylogenetic justification*

2658

2659 *D. bitterfeldensis* is considered a member of the family Spilapteridae, in the clade
2660 Palaeodictyoptera (Brauckmann and Schneider, 1996). Morphological characters supporting this
2661 relationship include the concave anterior wing margin and deeply bifurcate MA vein ending with two
2662 long branches (Brauckmann and Schneider, 1996; Li et al., 2013b). Other fossils of Spilapteridae have
2663 also preserved the distinctive colour patterns and long cerci observed in *D. bitterfeldensis* (Li et al.,
2664 2013b). Palaeodictyoptera have previously assumed to be related to extant Palaeoptera as they share
2665 the inability to fold their wings over the abdomen (a character observed in *D. bitterfeldensis*). However,
2666 a recent morphological phylogenetic analysis controversially recognized Palaeodictyoptera as the
2667 fossil sister group of Neoptera (Sroka et al., 2015). In this evolutionary scenario, palaeopterous wings
2668 are presumably a symplesiomorphy. Nonetheless, the position of Palaeodictyoptera suggested by
2669 Sroka et al. (2015) remains within crown Pterygota.

2670

2671 70.3. *Age justification*

2672

2673 *D. bitterfeldensis* was preserved in a core extracted from the locality Bore WISABAW 1315, in
2674 the Sandersdorf Formation of Bitterfeld, Germany (Brauckmann and Schneider, 1996). The core was
2675 correlated with the E2 ammonite zone, i.e. Arnsbergian (middle Namurian A) based on the co-
2676 occurrence of ostracods and conchostracans (Brauckmann et al., 1994). The Arnsbergian is further
2677 correlated to the late Serpukhovian stage at the end of the Mississippian (Pointon et al., 2012). The
2678 upper boundary of the Serpukhovian (base of the Pennsylvanian) is estimated at 323.23 Ma \pm 0.4 Myr
2679 (Davydov et al., 2012), giving a minimum age of 322.83 Ma.

2680 Soft maximum as for 26.3.

2681

2682 70.4. *Discussion*

2683

2684 An undescribed Namurian A (latest Mississippian) member of Archaeorthoptera was initially
2685 attributed to Orthoptera (Prokop et al., 2005). It was noted that the veins are strongly deformed,
2686 enough so that the authors were reluctant to make a formal systematic description (Prokop et al.,
2687 2005). Therefore, we regard the fossil as insufficiently characterized for dating. See section 67.4 for
2688 refutation of the even older *Strudiella devonica* (Garrouste et al., 2012).

2689

2690 **71. Crown Palaeoptera**

2691

2692 This clade comprises Euplectoptera (mayflies) and Odonata (dragonflies), their last common
2693 ancestor and all of its descendants (**Fig. 17**). Monophyly of this group has been challenged by
2694 morphology (Kristensen 1981) and some transcriptome data (Simon et al., 2012, 2009), though recent
2695 analyses of nuclear protein-coding genes (Regier et al., 2010) and transcriptomes have supported
2696 Palaeoptera (Misof et al., 2014; von Reumont et al., 2012), the former weakly, only in maximum
2697 likelihood analyses of the total dataset. Recent detailed morphological analyses of head morphology
2698 corroborate the monophyly of Palaeoptera (Blanke et al., 2013, 2012). Although a morphological
2699 phylogenetic analysis (Sroka et al., 2015) claims to reject palaeopteran monophyly, its constituent
2700 extant members, Euplectoptera and Odonata, are each others' closest living relative and named
2701 therein as a new clade, Euhydrolaeoptera. We therefore cautiously endorse Palaeoptera as a clade
2702 of interest for dating.

2703

2704 *71.1. Fossil specimens*

2705

2706 *Oligotypus huangheensis* Li et al., 2013a (CNU-NX2006003), holotype, a forewing.

2707

2708 *71.2. Phylogenetic justification*

2709

2710 This species was originally described as *Sinomeganeura huangheensis* within the family
2711 Meganeuridae, part of Protodonata (Ren et al., 2008). Meganeurids include the “giant” dragonflies
2712 (with wings up to 710 mm), though *O. huangheensis* is much smaller at 70 mm (Ren et al., 2008).
2713 Despite the size difference, wing venation characters are consistent with classification in Protodonata,
2714 including the fusion of stems of CuP and CuA to a single oblique vein, distinctly stronger than the
2715 crossveins (Ren et al., 2008). This character, previously assumed to be synapomorphic for
2716 Meganeuridae, is more widespread within Protodonata (Li et al., 2013a). The group “Protodonata”
2717 itself is a paraphyletic stem group to crown Odonata, together within the total group Odonatoptera,
2718 defined by the simple MP vein (Sroka et al., 2015). Regardless of the precise relationship of
2719 Protodonata to crown Odonata, its members are definitively within crown Palaeoptera.

2720

2721 71.3. Age justification

2722

2723 The insect beds where this species was located are near Xiaheyan Village in the Qilianshan
2724 Mountains, Zhongwei County, Ningxia Huizu Autonomous Region, northwest China (Zhang et al.,
2725 2013). The insect fossil deposits are within the uppermost unit of the upper Tupo Formation
2726 (synonyms Hongtuwa or Zhongwei Formation). The presence of the ammonoids *Reticuloceras*
2727 *reticulatum*, *Gastrioceras listeri* and *G. montgomeryense* and conodonts *Declingnathodus noduliferous*
2728 and *Neognathodus symmetricus* indicate a Namurian B/C age (Xie et al., 2004; Yang, 1987; Yang et
2729 al., 1988; Zhang et al., 2013). The (late) Namurian-(early) Westphalian boundary is defined by the
2730 earliest occurrence of the goniatite *Gastrioceras subcrenatum* (Waters and Davies, 2006), but lacks a
2731 precise isotopic date. Pointon et al. (2012) estimated an age of c. 319.9 Ma for the base of the
2732 Westphalian (top of the Namurian, only slightly younger than the Marsdenian) based on Milankovitch
2733 cycles of sedimentation, giving a minimum age for Xiaheyan fossils.

2734 Soft maximum as for 26.3.

2735

2736 71.4. Discussion

2737

2738 Due to the controversial status of Palaeoptera as a clade, there are several fossil groups that
2739 have been considered for membership: Palaeodictyoptera, Paoliida, stem mayflies (Ephemeroptera,
2740 see section 72), and stem dragonflies (Protodonata, including Geroptera) (Grimaldi and Engel, 2005).
2741 Each is discussed below.

2742 Palaeodictyoptera, an abundant clade from the Carboniferous and Permian, have been
2743 assumed to be related to extant Palaeoptera as they share the inability to fold their wings over the
2744 abdomen. The oldest member, *Delitzschala bitterfeldensis*, predates all other Palaeoptera (and all
2745 other Pterygota with preserved wings), as it is from the Mississippian (Brauckmann et al., 1994;
2746 Pointon et al., 2012). In cladograms in which Palaeodictyoptera is the fossil sister group of
2747 Neoptera (Sroka et al., 2015), palaeopterous wings are presumably a symplesiomorphy. The presence
2748 of nymphal wing pads is probably also a symplesiomorphy of Pterygota (Haug et al., 2016). Therefore
2749 Palaeodictyoptera may be outside the crown and even stem group of Palaeoptera.

2750 Paoliida is an extinct clade known mainly from wings of the Westphalian A stage of the
2751 Pennsylvanian. The group has been attributed to the Palaeodictyoptera and later removed (Prokop et
2752 al., 2012; Prokop and Nel, 2007). It has been subsequently proposed that Paoliida is the fossil sister
2753 group of Dictyoptera (Prokop et al., 2014), and thus are within crown Polyneoptera. This would refute
2754 a relationship with Palaeoptera or any of its members.

2755 A full body impression of a putative Carboniferous (Westphalian B/C) mayfly is subject to
2756 controversy (Benner et al., 2013; Knecht et al., 2011; Marden, 2013a, 2013b). *Bojophlebia prokopi*
2757 Kukalová-Peck, 1985 (Westphalian C) is likely outside of Palaeoptera, according to descriptions and
2758 phylogenetic analysis (Prokop et al., 2010; Sroka et al., 2015; Staniczek et al., 2011). The Stephanian
2759 B/C fossil *Triplosoba pulchella* Brongniart, 1883, originally described as a mayfly, has been
2760 redescribed as Palaeodictyoptera (Prokop and Nel, 2009). The oldest body fossils belonging to the

mayfly stem group are therefore members of the Syntonopteroidea. The oldest Syntonopteroidea are *Lithoneura lameerei* Carpenter, 1938 and *Syntonoptera schucherti* Handlirsch, 1911, from the Westphalian D Mazon Creek (younger than Xiaheyan) (Nicholson et al., 2015; Prokop et al., 2010).

Putative older members of Odonatoptera are Geroptera, represented by the species *Eugeropteron lunatum* and *Geropteron arcuatum* (both Riek and Kukalová-Peck, 1984), are known from the late Namurian of Argentina (Gutiérrez et al., 2000; Riek and Kukalová-Peck, 1984). *G. arcuatum* was included in a morphological phylogenetic analysis, but was resolved outside Protodonata, in a polytomy with Odonata, Ephemeroptera, and Neoptera, thus outside Palaeoptera (Bybee et al., 2008). It need, however, be noted that morphological characters were polarized *a priori* with respect to *G. arcuatum* (Bybee et al., 2008).

2771

2772 **72. Crown Euplectoptera**

2773

This clade comprises the families Siphuriscidae, Baetidae, Isonychiidae, Ametropodidae, Acanthametropodidae, Coloburiscidae, Siphlaenigmatidae, Ameletopsidae, Heptageniidae, Metretopodidae, Siphonuridae, Oniscigastridae, Rallidentidae, Nesameletidae, and the larger clades Carapacea and Furcatergalia, their last common ancestor and all of its descendants (**Fig. 17**). A variety of different classification schemes have been proposed (Kluge, 2004, 1998; McCafferty, 1991; Ogden and Whiting, 2005), but we follow the consensus based on combined phylogenetic analysis of two nuclear genes, two mitochondrial genes, and morphology (Ogden et al., 2009). Although the extant members are often referred to as Ephemeroptera, that clade includes a number of extinct members forming a paraphyletic grade (Kluge, 2004, 1998). As membership of fossil species within a crown group is only possible if they branch along the stem lineage of a living clade that is part of the crown itself, we treat crown 'Ephemeroptera' as equivalent to the clade Euplectoptera *sensu* Tillyard (1932).

Monophyly has been supported by the aforementioned combined data study (Ogden et al.,

2787 2009), as well as analyses of transcriptomes (with limited but representative taxon sampling: Misof et
2788 al., 2014) and morphology (Ogden et al., 2009 Fig. 4: note this is monophyletic, but the root is shown
2789 intervening).

2790

2791 72.1. Fossil specimens

2792

2793 *Triassonurus doliiformis* Sinitshenkova et al., 2005 (part of the private Louis Grauvogel
2794 collection, Ringendorf, Bas-Rhin, France, No. 9304), holotype, an incomplete nymph (**Fig. 18e**).

2795

2796 72.2. Phylogenetic justification

2797

2798 *T. doliiformis* has not been explicitly included in a phylogenetic analysis. It bears several
2799 morphological characters indicating affinity with the extant family Siphonuridae: a large nymph with a
2800 non-flattened body, head longer than short prothorax, massive mesothorax with considerably shorter
2801 metathorax, large and wide forewing pads almost completely covering the hind ones, short and
2802 slender legs, abdominal segments without sharp denticles, large rounded tergaliae, and cerci and
2803 paracercus long (Sinitshenkova et al., 2005). The family Siphonuridae is not accepted as
2804 monophyletic by all authors (J.-D. Huang et al., 2008; Kluge, 2004; McCafferty, 1991) although it is
2805 supported in total evidence and morphological analyses of Ogden et al. (2009). Siphonuridae is within
2806 the crown of Euplectoptera, in the clade of families outside Carapacea + Furcatergalia (Ogden et al.,
2807 2009). Therefore, *T. doliiformis* is also crown Euplectoptera.

2808

2809 72.3. Age justification

2810

2811 The fossil is derived from the silt-clay Grès à Meules unit (lowermost layer) of the Grès-a-
2812 Voltzia Formation, Vosges, northeastern France (Gall and Grauvogel-Stamm, 1993). Grès à Meules

2813 represents the last stage of the fluviatile facies prevalent in the Buntsandstein (Gall, 1985). Based on
2814 sequence stratigraphy, Bourquin et al. (2007, 2006) correlate the Grès-a-Voltzia Formation to the
2815 middle Anisian stage of the Triassic. Globally, the uppermost boundary of the Anisian is 241.5 ± 1 Ma
2816 (Ogg, 2012), providing a minimum age at 240.5 Ma.

2817 Because the monophyly of Palaeoptera is under debate (Simon et al., 2012, 2009), we assign
2818 a soft maximum age that allows its constituent extant orders to be older than the Rhynie Chert, as for
2819 26.3.

2820

2821 72.4. Discussion

2822

2823 The Permian fossils *Protereisma permianum* Sellards, 1907 and *Kukalova americana*
2824 Demoulin, 1970 were coded in the morphology matrix (larval and adult characters) of Odgen et al.
2825 (2009), but their relationships to the crown remain uncertain. *P. permianum* was resolved on the stem
2826 lineage of the extant families Euthyplociidae, Ephemeridae, and Potamanthidae with morphology only,
2827 but outside crown Euplectoptera in a total evidence analysis (Ogden et al., 2009). More generally,
2828 Kluge (Kluge, 2004, 1998) considered the Permian-Triassic members to form a plesion,
2829 Permoplectoptera, outside the crown group Euplectoptera. The relationship of Permoplectoptera to the
2830 crown group remains to be tested by morphological phylogenetics.

2831 Furthermore, many mayfly fossils are of nymphs, and linking characters between fossil and
2832 extant nymphs (or fossil nymphs and extant adults) is challenging, though not impossible (e.g. Haug et
2833 al., 2016; Wolfe and Hegna, 2014). The nymphal fossils include *Fuyous gregarius* and *Shantous*
2834 *lacustris* (both Zhang and Kluge, 2007), two species from the Jurassic Daohugou biota that have been
2835 used as crown group calibrations in previous divergence time analyses (Thomas et al., 2013). They
2836 are, however, younger than *T. doliiformis*.

2837

2838 73. Crown Odonata

2839

2840 This clade comprises Epiprocta (dragonflies; comprising Anisozygoptera and Anisoptera) and
2841 Zygoptera (damselflies), their last common ancestor and all of its descendants (**Fig. 17**). Monophyly of
2842 Odonata is supported by phylogenetic analysis of transcriptomes (Misof et al., 2014), combined
2843 morphology and housekeeping genes (Bybee et al., 2008), and a supertree including morphological
2844 and molecular input trees (Davis et al., 2011).

2845

2846 *73.1. Fossil specimens*

2847

2848 *Triassothemis mendozensis* Carpenter, 1960. MACN No. 18040, holotype, preserving the distal
2849 portion of two wings.

2850

2851 *73.2. Phylogenetic justification*

2852

2853 *T. mendozensis* is the oldest known member of the fossil family Triassolestidae (Nel et al.,
2854 2002; Nicholson et al., 2015). A family-level supertree, incorporating molecular and morphological
2855 input trees, found Triassolestidae within crown group Epiprocta (Davis et al., 2011, largest tree in their
2856 Fig. 1). This fossil is therefore also a member of crown group Odonata. Of all the fossil families
2857 included in the supertree analysis and placed within crown Odonata (Davis et al., 2011),
2858 Triassolestidae (represented by *T. mendozensis*) has the oldest member. Furthermore, this family (and
2859 its approximate date) was used to calibrate Odonata in multiple recent divergence time analyses
2860 (Rota-Stabelli et al., 2013a; Thomas et al., 2013).

2861

2862 *73.3. Age justification*

2863

2864 *T. mendozensis* was discovered in dark grey siltstone of the Potrerillos Formation, at Quebrada

del Durazno, Mendoza Province, Argentina (Martins-Neto et al., 2008). The insect-bearing beds are from the upper part of the Potrerillos Formation. U-Pb SHRIMP dates have been measured for zircons from tuff layers in the middle section of the Potrerillos Formation. The uppermost tuff layer estimated an age of $230.3 \text{ Ma} \pm 2.3 \text{ Myr}$ (Spalletti et al., 2009), corresponding to the Carnian, late Triassic. Thus a minimum age of *T. mendozensis* is 228.0 Ma.

Because the monophyly of Palaeoptera is under debate (Simon et al., 2009, 2012), we assign a soft maximum age that allows its constituent extant orders to be older than the Rhynie Chert, as for 26.3.

2873

2874 73.4. Discussion

2875

The internal taxonomy and placement of odonate fossils is highly contentious. Triassic members of the fossil family Triadophlebiidae are of approximately equal age to *T. mendozensis* (i.e. Carnian; Nicholson et al., 2015), however, they appear outside the crown group of Odonata in a supertree (Davis et al., 2011). Triadophlebiidae were not included in the total evidence analysis of Bybee et al. (2008). Most fossils in the latter analysis that had membership within crown Odonata were Jurassic or younger (Bybee et al., 2008).

The Madygen fauna of Kyrgyzstan yields two possible calibrations for crown group Odonata. *Triassolestodes asiaticus* Pritykina, 1981 (family Triassolestidae, preserving a hindwing) was recently justified as the oldest odonate by Kohli et al. (2016). As well, fossil members of Lestidae, crown group Odonata in the analysis of Bybee et al. (2008), are inferred from oviposition scars on plant fossils from Madygen (Moisan et al., 2012). Aside from challenges associated with interpreting crown group affinities of trace fossils, the Madygen fauna is, according to our stratigraphy, dated to the Carnian (see section 90.3), substantially younger than the 237 Ma age argued by Kohli et al. (2016) based on megaf flora. Our age would give a minimum age of 226.4 Ma for Madygen fossils, which is very slightly younger than the 228.0 Ma estimated for *T. mendozensis*. Note, however, that the mean age estimate

2891 for Madygen is 228.4 Ma (also younger than the mean of 230.3 Ma for the Potrerillos Formation).

2892 *Triassolestes epiophlebioides* Tillyard, 1918, a member of Triassolestidae used as a calibration
2893 fossil by Rota-Stabelli et al. (2013), is also known from the Carnian (Nicholson et al., 2015). Another
2894 fossil, *Pseudotriassothemis nipponensis* Bechly, 1997 (formerly *Triassoneura okafujii*), from the
2895 Carnian of Japan is also approximately coeval. We select *T. mendozensis* because its preservation is
2896 better, and radiometric dates for the Potrerillos Formation may be more precise.

2897

2898 **74. Crown Neoptera**

2899

2900 This clade comprises Polyneoptera (**Figs. 19 and 20**) and Eumetabola, their last common
2901 ancestor and all of its descendants (**Fig. 21**). Monophyly is supported by phylogenetic analysis of
2902 transcriptomes (Letsch and Simon, 2013; Misof et al., 2014), protein-coding genes (Ishiwata et al.,
2903 2011; Sasaki et al., 2013), and combined molecular and morphological data (Terry and Whiting, 2005).

2904

2905 *74.1. Fossil specimens*

2906

2907 *Protoprosbole straeleni* Laurentiaux, 1952. IRSNB a9885, holotype, preserving a forewing.
2908 Figured in Nel et al. (A. Nel et al., 2012), Fig. 3h.

2909

2910 *74.2. Phylogenetic justification*

2911

2912 The original description of *P. straeleni* as a member of Hemiptera by Laurentiaux (1952) has
2913 been rejected several times (Hennig, 1981; A. Nel et al., 2012; Shcherbakov, 1995). Nel et al. (2012)
2914 summarize the phylogenetic position of *P. straeleni* as being within Paraneoptera (a clade
2915 unsupported by recent molecular studies, but comprising Psocodea and Condylgnatha). The cua-cup
2916 contact with CuP and the flexion or nodal line following the course of RA are both similar to those

2917 observed in extant Hemiptera (A. Nel et al., 2012). However, the presence of three veins in the anal
2918 area is argued as a hemipteran autapomorphy that is lacking in *P. straeleni* (A. Nel et al., 2012).
2919 Conservatively, this fossil species can be thus assigned to the stem group of Condylgnatha, and thus
2920 crown Eumetabola and Neoptera.

2921

2922 74.3. Age justification

2923

2924 *P. straeleni* was discovered in Charbonnage de Monceau-Fontaine, Charleroi Coal Basin,
2925 Belgium (Brauckmann et al., 1994). The specimen was likely found in latest Marsdenian strata about 3
2926 m below the base of the Yeadonian (discussed by Brauckmann et al., 1994). The fossil-bearing
2927 deposits are assigned to the late Namurian B (Marsdenian) based on the *Bilinguites superbilinguis*
2928 R2c2 subzone of goniatite ammonoid stratigraphy (Brauckmann et al., 1994). The (late) Namurian-
2929 (early) Westphalian boundary is defined by the earliest occurrence of the goniatite *Gastrioceras*
2930 *subcrenatum* (Waters and Davies, 2006), but lacks a precise isotopic date. Pointon et al. (2012)
2931 estimated an age of c. 319.9 Ma for the base of the Westphalian (top of the Namurian, only slightly
2932 younger than the Marsdenian) based on Milankovitch cycles of sedimentation, giving a minimum age
2933 for *P. straeleni*.

2934 Soft maximum as for 26.3.

2935

2936 74.4. Discussion

2937

2938 *Qilianiblatia namurensis* Zhang et al., 2013 has an equal claim to being the earliest record of
2939 Neoptera (as *Q. namurensis* is a member of crown Polyneoptera), but it is of equal age to *P. straeleni*.
2940 The Qilianshan entomofauna at Xiaheyan, China, yields many other likely neopterans (e.g. Béthoux et
2941 al., 2011; Liu et al., 2009a; Prokop and Nel, 2007; Zhang et al., 2013).

2942 *Ctenoptilus elongatus* Béthoux and Nel, 2005 from the Stephanian B/C of France has been

2943 used as the putative oldest calibration fossil for crown Neoptera (e.g. O'Reilly et al., 2015). However,
2944 the Stephanian is a European stage of the Pennsylvanian, corresponding to the globally used
2945 Gzhelian, which is substantially younger than the Bashkirian age of both *P. straeleni* and *Q.*
2946 *namurensis* (with an upper boundary of 298.75 Ma).

2947

2948 **75. Crown Polyneoptera**

2949

2950 This clade comprises Zoraptera (ground lice), Dermaptera (earwigs), Plecoptera (stoneflies),
2951 Orthoptera (crickets, katydids), Notoptera, Eukinolabia and Dictyoptera, their last common ancestor
2952 and all of its descendants (**Fig. 19**). Monophyly has been demonstrated by phylogenetic analysis of
2953 transcriptomes (Letsch and Simon, 2013; Misof et al., 2014), protein-coding genes (Ishiwata et al.,
2954 2011), and wing morphology (Yoshizawa, 2011). This clade is not recognized in GenBank taxonomy.

2955

2956 *75.1. Fossil specimens*

2957

2958 *Qilianiblatia namurensis* Zhang et al., 2013. GNCB 04GNX1001-1, holotype, preserving the
2959 right forewing. We also refer to a second specimen (CNU-NX1-303; **Fig. 20a**), preserving paired
2960 forewings and hindwings (Guo et al., 2013).

2961

2962 *75.2. Phylogenetic justification*

2963

2964 *Q. namurensis* has not been included in formal phylogenetic analysis, but the fossil exhibits
2965 some apomorphic characters uniting it with crown group Blattodea, specifically presence of a deeply
2966 concave CuP in the forewing (Prokop et al., 2014). Additional data from forewings of the CNU
2967 specimen shows the RA with branches translocated to RP, as in cockroaches, suggesting this species
2968 could be stem Blattodea (Guo et al., 2013). However, there has not been a cladistic analysis of wing

2969 venation characters for both fossil and extant Blattodea and/or Dictyoptera, thus we agree with the
2970 more conservative view (Kjer et al., 2015; Legendre et al., 2015; Prokop et al., 2014) that roachoids
2971 likely represent a diverse and speciose fauna on the stem group of Dictyoptera. See also section 82.4.
2972 Nonetheless, placement of *Q. namurensis* on the stem lineage of Dictyoptera identifies it as a member
2973 of crown Polyneoptera.

2974

2975 75.3. Age justification

2976

2977 Minimum as for 71.3.

2978 A soft maximum age is estimated from *R. praecursor*, the oldest hexapod, from the Early
2979 Devonian (Pragian) Rhynie Chert of Aberdeenshire, Scotland. Spore assemblages of the Windyfield
2980 and stratigraphically underlying Rhynie Chert are dated to the early but not earliest Pragian to early
2981 (earliest?) Emsian (polygonalis-emsensis Spore Assemblage Biozone) (Parry et al., 2011).
2982 Radiometric dating of the underlying Milton of Noth Andesite at ca. 411 Ma (Parry et al., 2013, 2011)
2983 has been subject to a dispute over its temporal relationship to hot spring activity associated with the
2984 cherts (Mark et al., 2013, 2011) and predates the biostratigraphic dating of the Rhynie Chert relative to
2985 the global dating of the base of the Pragian Stage. Therefore, a soft maximum constraint may be
2986 defined at 411 Ma for the Rhynie Chert.

2987

2988 76. Crown Dermaptera

2989

2990 This clade comprises Protodermaptera and Epidermaptera, their last common ancestor and all
2991 of its descendants (**Fig. 19**). Monophyly is supported based on phylogenetic analysis of
2992 transcriptomes (Misof et al., 2014), nuclear genes (Kocarek et al., 2013), and combined molecular and
2993 morphological data (Jarvis et al., 2005).

2994

2995 76.1. Fossil specimens

2996

2997 *Rhadinolabis phoenicica* Engel et al., 2011. Holotype preserving a female in amber, 1013 in the
2998 private collection of D. Azar in Fanar (Matn), Lebanon (**Fig. 20e**). Provisionally housed at MNHN.

2999

3000 76.2. Phylogenetic justification

3001

3002 *R. phoenicica* is assigned only to Neodermaptera (= Protodermaptera + Epidermaptera), and
3003 not to any extant family. Membership within Neodermaptera is based on the presence of
3004 morphological characters: trimerous tarsi, absence of a well-developed ovipositor, and tarsal structure
3005 (Engel et al., 2011). These characters are sufficient to confirm the fossil belongs within crown
3006 Dermaptera.

3007

3008 76.3. Age justification

3009

3010 This fossil was discovered in amber from the Mdeyrij-Hammana outcrop of the Baabda district,
3011 Mount Lebanon (Azar et al., 2010). Recent revision of the stratigraphy of Lebanese amber deposits
3012 places the Hammana fossils in the upper interval of the Grès du Liban (Maksoud et al., 2016). This is
3013 below the Jezzian regional stage (Maksoud et al., 2014) and above the Banc de Mrejatt subunit
3014 (indicated as Ba3-Ba4 in Fig. 4 of Maksoud et al., 2016). Despite the lack of microfossils to further
3015 constrain the oldest boundary of the Jezzian within the late Barremian, there is evidence that later
3016 Lebanese amber deposits bear the same age as Jezzine amber (see 26.3) because the amber itself
3017 has been reworked (Maksoud et al., 2016). We adopt the early Barremian minimum age proposed by
3018 Maksoud et al. (2016). The upper boundary of the early Barremian is proposed to be the first
3019 appearance of the ammonite *Ancyloceras vandenheckii* (Ogg et al., 2012). Cyclostratigraphy dates the
3020 *A. vandenheckii* Zone beginning at 129.41 Ma (Ogg et al., 2012), providing a minimum age for Jezzine

3021 Lebanese amber fossils.

3022 Soft maximum as for 75.3.

3023

3024 **77. Crown Plecoptera**

3025

3026 This clade comprises Antartoperlaria, Euholognatha and Systellognatha, their last common
3027 ancestor and all of its descendants (**Fig. 19**). This classification and its morphological evidence is
3028 reviewed by Zwick (2000). Monophyly of Plecoptera is supported by phylogenetic analysis of
3029 transcriptomes (Misof et al., 2014) and combined ribosomal genes, H3, and morphology (Terry and
3030 Whiting, 2005).

3031

3032 *77.1. Fossil specimens*

3033

3034 *Palaeotaeniopteryx elegans* Sharov, 1961. PIN 1197/333, holotype, preserving a forewing.

3035

3036 *77.2. Phylogenetic justification*

3037

3038 *P. elegans* is classified in the fossil family Palaeonemouridae, suborder Nemourina
3039 (Sinitshenkova, 1987). At that time, Nemourina was one of only two suborders, the other being Perlina
3040 (Rasnitsyn and Quicke, 2002). Zwick (2000) summarized Nemourina as containing the (extant)
3041 families Notonemouridae, Nemouridae, Taeniopterygidae, Capniidae, and Leuctridae, therefore
3042 equivalent to the new suborder Euholognatha. Grimaldi and Engel (2005; Fig. 7.6) prefer a placement
3043 of Palaeonemouridae outside the crown group of Plecoptera, on the basis that diagnostic characters
3044 for crown group suborders within Plecoptera are rarely preserved (e.g. muscles, cellular structures).
3045 While no formal phylogenetic hypothesis illustrates the relationship of Palaeonemouridae to other
3046 Euholognatha, synapomorphies are identified linking *P. elegans* to the crown group of Plecoptera

3047 (Béthoux, 2005, pers. comm.).

3048

3049 *77.3. Age justification*

3050

3051 The oldest specimen of *P. elegans* was discovered from the Mitino Horizon at the Kaltan
3052 locality in the Kuznetsk Basin, Kemerovo, Russia (Sharov, 1961; Shcherbakov, 2000). Correlation of
3053 insect faunas suggests the Kaltan locality is late early Kazanian (Lozovsky et al., 2009; Shcherbakov,
3054 2008). The Kazanian is a regional stage of the Russian Permian, which has been correlated to both
3055 the Wordian (Menning et al., 2006) and the Roadian global Stages (Lozovsky et al., 2009). Evidence
3056 for an age in the Roadian is stronger, demarcated by presence of ammonites such as *Sverdrupites*
3057 *harkeri* and *S. amundseni* (Lozovsky et al., 2009). These ammonites, and associated conodonts
3058 *Kamagnathus khalimbadzhai* and *K. volgensis*, correlate globally to the Roadian (Barskov et al., 2014;
3059 Leonova, 2007; Leonova and Shilovsky, 2007). The upper boundary of the Roadian is 268.8 Ma \pm 0.5
3060 Myr, so a minimum age is 268.3 Ma.

3061 Soft maximum as for 75.3.

3062

3063 *77.4. Discussion*

3064

3065 *Gulou carpenteri* Béthoux et al., 2011, from the Pennsylvanian Qilianshan entomofauna of
3066 China, is identified as a member of the stem group to Plecoptera (Béthoux et al., 2011), and thus
3067 cannot be used to calibrate a minimum age of the crown group. Moreover, other Permian plecopterans
3068 had terrestrial nymphs; an aquatic nymph is a symapomorphy uniting crown group Plecoptera (Zwick,
3069 2000), relegating any fossil without it to the stem group.

3070 O. Béthoux (pers. comm.) cautioned that a Jurassic minimum age for crown Plecoptera, as
3071 used by Misof et al. (2014), would underestimate their age significantly. The calibrating fossil
3072 *Pronemoura angustithorax* Liu et al., 2011 used by Misof et al. (2014), from the Daohugou Beds, is

3073 likely a member of total group Euholognatha (Liu et al., 2011). Other crown Plecoptera groups are also
3074 known from the same locality (Liu et al., 2009b), suggesting diversification of the crown group was
3075 significantly earlier.

3076

3077 **78. Crown Orthoptera**

3078

3079 This clade comprises Ensifera (crickets, katydids) and Caelifera (grasshoppers), their last
3080 common ancestor and all of its descendants (**Fig. 19**). Monophyly is demonstrated by phylogenetic
3081 analysis of transcriptomes (Misof et al., 2014), mitochondrial genomes plus four nuclear genes (Song
3082 et al., 2015), morphology (Béthoux and Nel, 2002), and combined molecular and morphological data
3083 (Terry and Whiting, 2005).

3084

3085 *78.1. Fossil specimens*

3086

3087 *Raphogla rubra* Béthoux et al., 2002. Ld LAP 415 B, holotype, preserving the counterpart of a
3088 forewing (**Fig. 20c**).

3089

3090 *78.2. Phylogenetic justification*

3091

3092 Although no cladistic analysis exists combining extant and fossil Ensifera, *R. rubra* may be
3093 assigned to crown Ensifera based on forewing venation characters (Béthoux et al., 2002). It likely
3094 belongs to the stem group of the clade (Gryllidea + Tettigoniidea), based on the following characters:
3095 very broad area between anterior margin and Sc; RS moderately long basal of a short fusion with the
3096 anterior branch MA1a of MA; MP + CuA1 with only one simple anterior branch (Béthoux et al., 2002).
3097 As both Gryllidea and Tettigoniidea are crown clades within crown Ensifera, *R. rubra* is within crown
3098 group Orthoptera.

3099

3100 *78.3. Age justification*

3101

3102 *R. rubra* was found at the fossiliferous site F21 D, at “Le Moural D”, in the basal Mérifrons
3103 Member of the Salagou Formation (Saxonian Group), near village Octon, Lodève Basin, Hérault,
3104 France (Béthoux et al., 2002; Nel et al., 1999; Schneider et al., 2006). U-Pb dates have been recently
3105 measured from zircons lying in tuff beds near the lower two-thirds of the Salagou Formation (Octon
3106 Member), in the Artinskian (Michel et al., 2015). The Mérifrons Member, overlying the Octon, is
3107 therefore inferred to be Artinskian at its base but continuing up through the Kungurian (Michel et al.,
3108 2015). As the exact stratum of the F21 site is not indicated within the Mérifrons member (Michel et al.,
3109 2015; Schneider et al., 2006), we apply a conservative minimum estimate from the upper boundary of
3110 the Kungurian (272.3 Ma \pm 0.5 Myr), at 271.8 Ma.

3111 Soft maximum as for 75.3.

3112

3113 *78.4. Discussion*

3114

3115 An undescribed Namurian member of Archaeorthoptera was initially attributed to crown group
3116 Orthoptera (Prokop et al., 2005). However, an affinity with Archaeorthoptera is supported in the stem
3117 group of Orthoptera based on phylogenetic analysis (Béthoux and Nel, 2002), thus it cannot be used
3118 to calibrate the crown. Similarly, *Oedischia williamsoni* Brongniart, 1885, from the Pennsylvanian of
3119 France, is recognized as a stem group member of Orthoptera by cladistic analysis (Béthoux and Nel,
3120 2002). Together these fossils suggest a long stem branch for Orthoptera.

3121 The fossil *Eolocustopsis primitiva* Riek, 1976 from Natal, South Africa was listed as the oldest
3122 crown group member of Caelifera, and thus another Permian crown group member of Orthoptera
3123 (Song et al., 2015). However, the fossil comes from strata of the Normandien Formation,
3124 Changhsingian stage, latest Permian (due to the co-occurrence of the vertebrate fossil *Dicynodon*;

3125 e.g. Catuneanu et al., 2005), which is younger than the Kungurian.

3126

3127 **79. Crown Notoptera**

3128

3129 This clade comprises Mantophasmatodea (rock crawlers) and Grylloblattodea (ice crawlers),
3130 their last common ancestor and all of its descendants (**Fig. 19**). The monophyly of Notoptera is
3131 supported by phylogenetic analysis of transcriptomes (Misof et al., 2014), morphology (Wipfler et al.,
3132 2011), and combined molecular and morphological data (Terry and Whiting, 2005).

3133

3134 *79.1. Fossil specimens*

3135

3136 *Juramantophasma sinica* D. Huang et al., 2008. NIGP 142171, holotype, preserving a nearly
3137 complete adult female (**Fig. 20g**).

3138

3139 *79.2. Phylogenetic justification*

3140

3141 *J. sinica* has several characters in common with crown Mantophasmatodea. These include: a
3142 third tarsomere with a sclerotized elongated dorsal process, enlarged and fanlike pretarsal arolia, last
3143 tarsomere at right angle to the others, female gonoplasts short and claw shaped, and egg with a
3144 circular ridge (D. Huang et al., 2008). As no morphological matrix exists for Mantophasmatodea,
3145 relationships to extant lineages are not possible to test (D. Huang et al., 2008). The fossil is excluded
3146 from the crown group of Grylloblattodea as it lacks segmented cerci. Thus, conservatively, a position
3147 on the stem lineage of Mantophasmatodea is likely (although *J. sinica* could be amended to within the
3148 crown of Mantophasmatodea). This would, in any case, mean it is a member of crown Notoptera.

3149

3150 *79.3. Age justification*

3151

3152 This fossil was found in deposits of the Daohugou Beds, Ningcheng County, Inner Mongolia,
3153 China (D. Huang et al., 2008). There has been controversy about the accuracy and precise age and
3154 stratigraphic position of the Daohugou Beds (Gao and Ren, 2006; Wang et al., 2005; Zhang, 2015).
3155 The beds consist of 100–150 m thick succession of grey-white or locally reddish, thinly bedded
3156 claystones, shales, siltstones and sandy mudstones with intercalated ash-fall tuffs and ignimbrites.
3157 Ages have been proposed from Aalenian (Middle Jurassic) to Early Cretaceous (Liu et al., 2014; Wang
3158 et al., 2000), with several studies converging on Callovian-Oxfordian (Late Jurassic; Zhang, 2015).
3159 Radiometric dating of the ignimbrites with $^{40}\text{Ar}/^{39}\text{Ar}$ and SHRIMP U-Pb variously yields dates
3160 between $165 \text{ Ma} \pm 2.5 \text{ Myr}$ and $158.7 \text{ Ma} \pm 0.6 \text{ Myr}$ (Chang et al., 2009b; Gao and Ren, 2006; He et
3161 al., 2004; Peng et al., 2012). The fossiliferous shales overlay the volcanic deposits (Gao and Ren,
3162 2006), and are thus younger. The isotopic dates nonetheless provide a reasonable refutation of
3163 Cretaceous age estimates. Furthermore, the Daohugou Beds may be correlated to sediments from
3164 Oxfordian localities in China and Kazakhstan (Zhang, 2015). The most conservative (i.e. youngest) of
3165 the direct radiometric dates is 158.1 Ma (within the Oxfordian), giving a minimum age.

3166 Soft maximum as for 75.3.

3167

3168 *79.4. Discussion*

3169

3170 Stem group Grylloblattodea are uncommon, and extant grylloblattids (and mantophasmids) are
3171 wingless (Wipfler et al., 2014). A putative grylloblattid insect was described from the Pennsylvanian
3172 Montceau-les-Mines Lagerstätte, about 130 Myr older than *J. sinica* (Béthoux and Nel, 2010);
3173 however, the fossil preserved only the wings. We take the parsimonious view that there was a single
3174 loss of wings in the common ancestor of Grylloblattodea and Mantophasmatodea, i.e. in the crown
3175 group of Notoptera (Grimaldi and Engel, 2005). Therefore, any fossil bearing wings, such as the
3176 Pennsylvanian and Permian members, would be on the stem branch of Notoptera.

3177

3178 **80. Crown Eukinolabia**

3179

3180 This clade comprises Embioptera (webspinners) and Phasmatodea (stick and leaf insects),
3181 their last common ancestor and all of its descendants (**Fig. 19**). Monophyly of Eukinolabia is
3182 supported by phylogenetic analyses of transcriptomes (Letsch and Simon, 2013; Misof et al., 2014)
3183 and ribosomal and H3 sequences (Terry and Whiting, 2005).

3184

3185 *80.1. Fossil specimens*

3186

3187 *Cretophasmomima melanogramma* Wang et al., 2014. CNU-PHA-NN2012002, holotype,
3188 preserving a male (**Fig. 20d**).

3189

3190 *80.2. Phylogenetic justification*

3191

3192 *C. melanogramma* shares the 'shoulder pad' structure, and twig-like appearance (elongated
3193 meso- and metathorax) diagnostic of total group Phasmatodea (Wang et al., 2014). Crown
3194 membership within Phasmatodea is questionable, as important synapomorphies, the vomer and
3195 forceps-like extensions of the 10th abdominal tergum, are absent from *C. melanogramma* (Wang et
3196 al., 2014). The position of *C. melanogramma* on the stem lineage of Phasmatodea therefore places it
3197 within the crown group of Eukinolabia.

3198

3199 *80.3. Age justification*

3200

3201 As for 76.3.

3202

3203 80.4. Discussion

3204

3205 *Renphasma sinica* Nel and Delfosse, 2011 is of equal age, also from the Yixian Formation, and
3206 also a member of stem Phasmatodea, and thus crown Eukinolabia.

3207

3208 **81. Crown Phasmatodea**

3209

3210 This clade comprises Timematodea and Euphasmatodea, their last common ancestor and all
3211 of its descendants (**Fig. 19**). Monophyly of Phasmatodea is supported by phylogenetic analyses of
3212 transcriptomes (Misof et al., 2014), ribosomal and H3 sequences (Terry and Whiting, 2005), and
3213 morphology (Friedemann et al., 2012).

3214

3215 81.1 Fossil specimens

3216

3217 *Echinosomiscus primoticus* Engel et al., 2016c. NIGP 163536, holotype, preserving a male in
3218 amber (**Fig. 20f**).

3219

3220 81.2 Phylogenetic justification

3221

3222 Until recently, no Mesozoic fossil qualified for membership in the crown group of Phasmatodea
3223 (Bradler and Buckley, 2011). *E. primoticus* bears morphological characters shared with extant
3224 members of Euphasmatodea, in particular Heteropterygidae and Aschiphasmataidae, but lack the area
3225 apicalis on the tibiae (Engel et al., 2016c). It also shares characters with Lonchodinae, such as absent
3226 areole on all tibiae, comparatively long antennae, the absence of wings, and the division of the tenth
3227 abdominal tergum into moveable hemitergites (Engel et al., 2016c). Although a new family was
3228 erected to accommodate the unique character combination for *E. primoticus*, it is very clearly within

3229 Euphasmatodea (Phasmatidae s.l.), and thus a member of crown Phasmatodea (Engel et al., 2016c).

3230

3231 *81.3 Age justification*

3232

3233 Minimum as for 12.3. Soft maximum as for 75.3.

3234

3235 **82. Crown Dictyoptera**

3236

3237 This clade comprises Mantodea (praying mantids) and Blattodea (cockroaches, termites), their
3238 last common ancestor and all of its descendants (**Fig. 19**). Phylogenetic analysis of transcriptomes
3239 (Misof et al., 2014), mitochondrial genes (Legendre et al., 2015), and combined molecular and
3240 morphological data (Djernæs et al., 2015; Ware et al., 2008), support monophyly of Dictyoptera.

3241

3242 *82.1. Fossil specimens*

3243

3244 *Valditermes brenanae* Jarzembowski, 1981. BMNH In. 64588, holotype, preserving a forewing.

3245

3246 *82.2. Phylogenetic justification*

3247

3248 The position of *V. brenanae* was confirmed by morphological phylogenetic analysis (Engel et
3249 al., 2009). *V. brenanae* was resolved on the stem lineage of Mastotermitidae (Engel et al., 2009). This
3250 position was separately found for a congeneric species in the combined morphological and molecular
3251 phylogeny of Ware et al. (2010). Mastotermitidae is a monotypic family, sister to all other termites
3252 (Djernæs et al., 2015; Ware et al., 2010), so this phylogeny would also place *V. brenanae* in the
3253 crowns of Isoptera and Blattodea.

3254

3255 82.3. Age justification

3256

3257 The fossil is from the Clockhouse Brickworks pit site, Surrey, England (Jarzembowski, 1981).
3258 The Clockhouse Brickworks belongs to the Lower Weald Clay, as indicated by the presence of the
3259 ostracods *Cytheridea clavata*, *C. tuberculata*, and *C. valdensis* (Anderson, 1985). Of these, *C.*
3260 *tuberculata* has the narrowest range, and is restricted to the middle portion of the Lower Weald Clay,
3261 at BGS Bed 3a (Anderson, 1985; Ross and Cook, 1995). This faunal Zone is now assigned to the
3262 lower portion of the *C. pumila* Subzone of the *Theriosynoecum fittoni* Zone (Horne, 1995). Based on
3263 palynomorph stratigraphy, the boundary between Lower and Upper Weald Clay at the base of BGS
3264 Bed 3a corresponds accurately to the boundary between the Hauterivian and Barremian Stages (Ross
3265 and Cook, 1995). The upper boundary of the Hauterivian is 130.8 Ma \pm 0.5 Myr (Ogg et al., 2012a),
3266 therefore a minimum age of the Lower Weald Clay is 130.3 Ma.

3267 Soft maximum as for 75.3.

3268

3269 82.4. Discussion

3270

3271 There is ongoing debate over whether various Palaeozoic “roachoid” fossils, such as
3272 *Qilianiblattea namurensis* and *Homocladus grandis* Carpenter, 1966 (known only from wing venation
3273 characters), truly represent crown group members of Dictyoptera (e.g. Guan et al., 2016; Kjer et al.,
3274 2015; Legendre et al., 2015; Tong et al., 2015). If roachoids are indeed within crown group
3275 Dictyoptera, their antiquity may push back the origins of crown Dictyoptera and crown Polyneoptera by
3276 80-88 Myr (Legendre et al., 2015; Tong et al., 2015). However, wing venation alone may be insufficient
3277 to place most fossils within the crown group of Blattodea or even Dictyoptera. Particularly in
3278 cockroaches, asymmetry at the individual level and convergence at higher taxonomic levels are
3279 impediments to wing venation taxonomy, as well as the paucity of comparative venation data for extant
3280 species (e.g. Béthoux et al., 2010; Béthoux and Wieland, 2009; Garwood and Sutton, 2010; Gorochov,

3281 2013; Guan et al., 2016).

3282 In the absence of detailed cladistic analysis of fossil roachoid wings together with extant
3283 Dictyoptera and other outgroups, we take the conservative view (Guan et al., 2016; Kjer et al., 2015;
3284 Prokop et al., 2014) that roachoids (including the family Anthracoptilidae/Strephocladidae, containing
3285 *H. grandis*) likely represent a diverse and speciose fauna on the stem group of Dictyoptera, perhaps
3286 with some members on the stem group of Neoptera or Polyneoptera (Grimaldi and Engel, 2005). At
3287 least some such roachoids may be used to calibrate crown group Polyneoptera (as done herein by
3288 assigning *Q. namurensis*), but they cannot calibrate crown Dictyoptera. As a consequence, many
3289 recent analyses have begun to rewrite the traditional assumption of extremely old crown ages for
3290 Dictyoptera, with crown origins likely in the Jurassic (Misof et al., 2014).

3291 Morphological phylogenetic analyses have excluded all Cretaceous fossils from the crown
3292 group of Mantodea, although they remain as likely crown Dictyoptera (Delclòs et al., 2016; Grimaldi,
3293 2003). Given that the analysed morphological matrix has fewer characters than taxa and has
3294 substantial missing data, it is not definitive (Delclòs et al., 2016). A recently discovered fossil from
3295 Crato (Aptian of Brazil), *Cretophotina santanensis* Lee, 2014, may be a stem group Chaeteessidae,
3296 which may be the most basal crown family of Mantodea (Svenson and Whiting, 2009). The position of
3297 Chaeteessidae may be within polyphyletic Mantidae (Legendre et al., 2015), but we exercise caution
3298 and do not place *C. santanensis* in the crown group, as recommended by Lee (2014).

3299

3300 **83. Crown Blattodea**

3301

3302 This clade comprises Lamproblattidae, Blaberoidea, Blattidae, Nocticolidae, Polyphagidae,
3303 Cryptocercidae and Isoptera, their last common ancestor and all of its descendants (**Fig. 19**). The
3304 position of Isoptera (termites) within a paraphyletic Blattodea was first identified by Inward et al. (2007)
3305 with six molecular loci. Further support for the monophyly of the new concept of Blattodea comes from
3306 transcriptomes (Misof et al., 2014), mitochondrial genes (Legendre et al., 2015), housekeeping genes

3307 (Djernæs et al., 2012), and combined molecular and morphological data (Djernæs et al., 2015; Ware
3308 et al., 2008).

3309

3310 *83.1. Fossil specimens*

3311

3312 As for 82.1.

3313

3314 *83.2. Phylogenetic justification*

3315

3316 As for 82.2.

3317

3318 *83.3. Age justification*

3319

3320 As for 82.3.

3321

3322 *83.4. Discussion*

3323

3324 *Baissatermes lapideus* Engel et al., 2007 is a crown group member of Isoptera, and
3325 *Mastotermes nepropadyom* Vršanský and Aristov, 2014 is crown Blattodea (Engel et al., 2016a); both
3326 have been used to calibrate Isoptera and Blattodea (Djernæs et al., 2015; Ware et al., 2010). Note that
3327 fossil *Mastotermes* are likely polyphyletic (Engel et al., 2016a). Although these are appropriate
3328 calibration fossils, they are not the oldest Blattodea. *B. lapideus* is from the Zaza Formation
3329 (Transbaikalian Russia), and *M. nepropadyom* is from Chernovskie Kopi, also in Transbaikalia and
3330 similar in age to the Turga Formation (Sukatsheva and Vassilenko, 2011; Vršanský and Aristov, 2014).
3331 The Turga Formation has been correlated to the Baissa locality, Zaza Formation; this is based on
3332 shared presence of *Asteropollis asteroides* spores (Vakhrameev and Kotova, 1977). As discussed in

3333 section 86.3, the Zaza Formation may be much younger than initially described, with a minimum age
3334 of Campanian (71.9 Ma). Therefore both Russian fossils are younger than *V. brenanae*.

3335

3336 **84. Crown Eumetabola**

3337

3338 This clade comprises Condylgnatha, Psocodea and Holometabola, their last common
3339 ancestor and all of its descendants (**Fig. 21**). Monophyly of the clade is supported by transcriptomes
3340 (Letsch and Simon, 2013; Misof et al., 2014) and protein-coding genes (Ishiwata et al., 2011). Some
3341 morphological analyses do not support monophyly of Eumetabola (Kristensen, 1981; Wheeler et al.,
3342 2001), although it is recovered (Kristensen, 1991; Kukalová-Peck, 1991) and assumed (Yoshizawa
3343 and Saigusa, 2001) in other analyses. Note also that support for Psocodea as the sister clade of
3344 Holometabola was statistically weak in analyses of transcriptomes (Misof et al., 2014), although
3345 monophyly of Eumetabola was well supported.

3346

3347 *84.1. Fossil specimens*

3348

3349 As for 74.1.

3350

3351 *84.2. Phylogenetic justification*

3352

3353 As for 74.2.

3354

3355 *84.3. Age justification*

3356

3357 Minimum as for 74.3. Soft maximum as for 75.3.

3358

3359 **85. Crown Condylgnatha**

3360

3361 This clade comprises Hemiptera (true bugs) and Thysanoptera (thrips), their last common
3362 ancestor and all of its descendants (**Fig. 21**). Monophyly is determined by phylogenetic analysis of
3363 transcriptomes (Misof et al., 2014), nuclear protein-coding genes (Ishiwata et al., 2011), and wing
3364 morphology (Yoshizawa and Saigusa, 2001).

3365

3366 *85.1. Fossil specimens*

3367

3368 *Aviorrhyncha magnifica* Nel et al., 2013, holotype Avion No. 2 (provisionally stored in the
3369 collection of Entomological Laboratory, MNHN; to be deposited in the Musée Géologique Pierre Vetter,
3370 Decazeville, France), preserving a single forewing (**Fig. 22a**).

3371

3372 *85.2. Phylogenetic justification*

3373

3374 Nel et al. (2013) diagnose *A. magnifica* as stem Euhemiptera (the clade sister to
3375 Sternorrhyncha containing all other living Hemiptera; Cryan and Urban, 2012; Cui et al., 2013). At least
3376 two forewing characters in *A. magnifica* are synapomorphies of Euhemiptera, including presence of an
3377 ambient vein and a well-developed concave CP (its presence is a synapomorphy) (Nel et al., 2013).
3378 Unlike many extant Euhemiptera, the cua-cup vein is not zigzagged. Given that much of fossil insect
3379 taxonomy is conducted with only preserved wings, an assignment to the crown group of Hemiptera
3380 and thus Condylgnatha is reasonable.

3381

3382 *85.4. Age justification*

3383

3384 *A. magnifica* was found in “Terril No. 7”, a layer containing rocks from the slag heap of coal

3385 mines 3 and 4 of Liévin, in the Avion outcrop of Pas-de-Calais, France (Nel et al., 2013). The coal
3386 mines are dated to the Westphalian C/D, or Bolsovian/Asturian, which has a youngest boundary
3387 equivalent to the latest Moscovian stage of the Pennsylvanian (Nel et al., 2013; Richards, 2013). As
3388 the upper boundary of the Moscovian is $307.0 \text{ Ma} \pm 0.1 \text{ Myr}$, this provides a minimum age of 306.9
3389 Ma.

3390 Soft maximum as for 75.3.

3391

3392 **86. Crown Thysanoptera**

3393

3394 This clade comprises Tubulifera and Terebrantia, their last common ancestor and all of its
3395 descendants (**Fig. 21**). Monophyly is established based on phylogenetic analysis of transcriptomes
3396 (Misof et al., 2014) and five nuclear protein-coding genes (Buckman et al., 2013). There is no
3397 adequate phylogenetic test of thysanopteran monophyly using morphology (reviewed by Mound and
3398 Morris, 2007).

3399

3400 *86.1. Fossil specimens*

3401

3402 *Fusithrips crassipes* Shmakov, 2009. PIN 3064/8547, holotype, preserving a female body (**Fig.**
3403 **22b**).

3404

3405 *86.2. Phylogenetic justification*

3406

3407 *F. crassipes* has not been included in a phylogenetic analysis, however, Shmakov (2009)
3408 describes characters placing it in the crown of Thysanoptera. In particular, Rs1 and M2 as crossveins
3409 rather than oblique veins suggest membership in the family Aeolothripidae (Shmakov, 2009). Whether
3410 crown or stem Aeolothripidae, the family is a part of Terebrantia, indicating crown group membership in

3411 Thysanoptera.

3412

3413 86.3. *Age justification*

3414

3415 The fossil *F. crassipes* was found in Layer 31 on the left bank of the Vitim River, 3 km
3416 downstream from the mouth of the Baissa River, Buryatia, Transbaikalian Russia (Shmakov, 2009).
3417 The fossiliferous lacustrine deposits are part of the Zaza Formation, Baissa locality. The Zaza
3418 Formation was once assigned to the Valanginian, based on correlation of fossil insect species,
3419 however palynological data from the appearance of *Asteropollis* spores suggests a younger date
3420 (O'Reilly et al., 2015; Zherikhin et al., 1998). *A. asteroides*, one of the earliest angiosperms, has a
3421 worldwide distribution during the Early and mid Cretaceous (Friis et al., 2005), and has been
3422 biostratigraphically assigned to the Barremian-Aptian (Friis et al., 1999; Zherikhin et al., 1998). This
3423 range has since been completely revised to Albian-Campanian, on the basis of pollen morphology
3424 (Doyle and Endress, 2014) and younger appearances of *Asteropollis* (Dettmann and Thomson, 1987;
3425 Eklund et al., 2004; Martínez et al., 2013). A minimum age can thus be estimated by the upper
3426 boundary of the Campanian, 72.1 Ma \pm 0.2 Myr, or 71.9 Ma.

3427 Soft maximum as for 75.3.

3428

3429 86.4. *Discussion*

3430

3431 *Triassothrips virginicus* Grimaldi et al., 2004 was described from the Late Triassic of Virginia.
3432 Although it was used as a calibration for Thysanoptera by Misof et al. (2014), *T. virginicus* is found in a
3433 basal polytomy outside of any crown group members in a morphological phylogeny (P. Nel et al.,
3434 2012). *Liassothrips crassipes* Martynov, 1927 is known from the Late Jurassic of Kazakhstan, but is
3435 classified in an extinct family, Liassothripidae (Shmakov, 2008). While Shmakov (2008) suggests
3436 Liassothripidae is the oldest family in the Tubulifera, making it crown Thysanoptera, characters are

3437 also listed linking it with Terebrantia; without a phylogenetic analysis it is difficult to assess their
3438 polarity and thus crown affinity.

3439

3440 **87. Crown Hemiptera**

3441

3442 This clade comprises Sternorrhyncha (aphids, scale insects), Fulgoromorpha (planthoppers),
3443 Cicadomorpha (cicadas, leafhoppers, treehoppers), Coleorrhyncha (moss bugs) and Heteroptera
3444 (typical bugs), their last common ancestor and all of its descendants (**Fig. 21**). Monophyly of
3445 Hemiptera is established by phylogenetic analysis of housekeeping genes (Cryan and Urban, 2012),
3446 whole mitochondrial genomes (Cui et al., 2013), transcriptomes (Misof et al., 2014; Simon et al.,
3447 2012), and wing morphology (Yoshizawa and Saigusa, 2001).

3448

3449 *87.1. Fossil specimens*

3450

3451 As for 85.1.

3452

3453 *87.2. Phylogenetic justification*

3454

3455 As for 85.2.

3456

3457 *87.3. Age justification*

3458

3459 As for 85.3.

3460

3461 **88. Crown Psocodea**

3462

3463 This clade comprises Psocoptera (barklice) and Phthiraptera (true lice), their last common
3464 ancestor and all of its descendants (**Fig. 21**). Monophyly of this clade is supported by phylogenies of
3465 transcriptomes (Misof et al., 2014), nuclear protein-coding genes (Ishiwata et al., 2011), mitochondrial
3466 genes (Yoshizawa and Johnson, 2003), and morphology (Lyal, 1985).

3467

3468 *88.1. Fossil specimens*

3469

3470 *Cretoscelis burmitica* Grimaldi and Engel, 2006. AMNH Bu912, holotype, female in amber.

3471

3472 *88.2. Phylogenetic justification*

3473

3474 In a morphological phylogenetic analysis, *C. burmitica* was a stem group member of
3475 Liposcelididae (Grimaldi and Engel, 2006). Liposcelididae is an extant family of Psocoptera, thus
3476 within the crown group of Psocodea.

3477

3478 *88.3. Age justification*

3479

3480 As for 81.3.

3481

3482 **89. Crown Holometabola**

3483

3484 This clade comprises Hymenoptera (sawflies, ants, bees, wasps) and Aparaglossata, their last
3485 common ancestor and all of its descendants (**Figs. 23 and 24**). Support for monophyly comes from
3486 phylogenetic analysis of transcriptomes (Misof et al., 2014; Peters et al., 2014), morphology (Beutel et
3487 al., 2011), and morphology plus molecules (Oakley et al., 2013). This clade exists in GenBank, but as
3488 Endopterygota.

3489

3490 *89.1. Fossil specimens*

3491

3492 *Westphalomerope maryvonneae* Nel et al., 2007. MNHN-LP-R.55181, holotype, preserving a
3493 hindwing. Pictured in Nel et al. (2007; Fig. 1a).

3494

3495 *89.2. Phylogenetic justification*

3496

3497 *W. maryvonneae* has not been included in a phylogenetic analysis, nor have any other
3498 members of its family, Protomeropidae. Mostly Permian members of Protomeropidae have been
3499 proposed to have affinities with a variety of holometabolan clades, including the total groups of
3500 Trichoptera, Mecoptera, and more generally Amphiesmenoptera or Antliophora (Grimaldi and Engel,
3501 2005; Kukalova-Peck and Willmann, 1990; Morse, 1997; Nel et al., 2013, 2007; Sukatsheva et al.,
3502 2007). Crown amphiesmenopteran (and thus trichopteran) affinity may be unlikely, as Protomeropidae
3503 lack a key synapomorphy, a true 'double-Y loop' arrangement of the anal veins on the forewing
3504 (Labandeira, 2011; Minet et al., 2010). However, Permian Protomeropidae possess Carpenter's
3505 organs in the male, a probable apomorphy for total group Mecoptera (Minet et al., 2010).
3506 Protomeropidae (with a younger date) was subsequently used to calibrate the basal split of
3507 Mecopterida for divergence time estimation (Rehm et al., 2011). Pending phylogenetic analysis of
3508 wing morphology, it is difficult to assign a specific placement for Protomeropidae, however, even with a
3509 conservative view all these possibilities are within crown Aparaglossata, and therefore crown
3510 Holometabola.

3511

3512 *89.3. Age justification*

3513

3514 *W. maryvonneae* was collected from black shales in the "Terril no. 5" horizon at the "Faisceau

de Modeste", "Veine Maroc" locality in Bruay-la-Bussière, Pas-de-Calais, France (Nel et al., 2007). The locality is dated as early Langsettian (Nel et al., 2007), equivalent to the Westphalian A stage (Pointon et al., 2012). There is a SHRIMP U-Pb date within the middle Langsettian estimated at 317.63 Ma \pm 0.12 Myr, however, the stratigraphy of Bruay-la-Bussière is not precise enough to determine when in the Westphalian A the fossil occurred (Nel et al., 2007; Pointon et al., 2012). Therefore, we use a date inclusive of the upper boundary of the Westphalian A, which is the upper boundary of Westphalian B. U-Pb dating of zircons constrains the upper boundary of the Westphalian B to 313.78 Ma \pm 0.08 Myr (Pointon et al., 2012), so a minimum age for *W. maryvonneae* is 313.70 Ma.

Soft maximum as for 75.3.

89.4. Discussion

Srokalarva berthei Haug et al., 2015 is a putative holometabolan larva, from the Mazon Creek and thus younger than *W. maryvonneae*. *S. berthei* has been interpreted as both an antliophoran (Labandeira, 2011) and a neuropterid (Haug et al., 2015), both positions within the crown group of Holometabola. *S. berthei*, however, remains informative about the evolutionary timing of insect metamorphosis.

90. Crown Hymenoptera

This clade comprises Symphyta (sawflies) and Apocrita (itself comprising Apoidea, Formicidae, and a paraphyletic group of wasps), their last common ancestor and all of its descendants (**Fig. 23**). Monophyly is supported by phylogenetic analysis of transcriptomes (Misof et al., 2014), morphology (Beutel et al., 2011), and morphology analysed together with molecular data (Ronquist et al., 2012).

3541 90.1. Fossil specimens

3542
3543 *Triassoxyela foveolata* Rasnitsyn, 1964. PIN 2070/1, holotype (**Fig. 25a**).
3544

3545 90.2. Phylogenetic justification

3546
3547 In the total-evidence phylogenetic analysis of Ronquist et al. (2012), *T. foveolata* was found as
3548 a stem group member of the family Xyelidae. As Xyelidae is a crown group family of sawflies, it is thus
3549 crown Hymenoptera.
3550

3551 90.3. Age justification

3552
3553 *T. foveolata* was found in the Madygen Formation, south of the Fergana Valley, Kyrgyzstan.
3554 Key plant fossils *Scytophyllum* and *Neocalamites* correlate the Madygen to the *Scytophyllum* flora of
3555 the upper Keuper lithographic unit, of Ladinian-Carnian age (Dobruskina, 1995). The *Scytophyllum*
3556 flora is correlated with the Cortaderitian Stage of Gondwana due to the abundance of *Scytophyllum*
3557 (Morel et al., 2003). The Cortaderitian Stage is divided into 3 Biozones; a ⁴⁰Ar/³⁹Ar radiometric date
3558 for the middle biozone of the Cortaderitian Stage of 228.5 Ma ± 0.3 Myr was measured by Rogers et
3559 al. (1993), falling within the Carnian (O'Reilly et al., 2015). The Gondwanan Puesto Viejo Formation,
3560 part of the Barrealian Stage underlying the Cortaderitian Stage (and therefore the *Scytophyllum* flora)
3561 has been radiometrically dated to 232 Ma ± 4 Myr, also within the Carnian (Valencio et al., 1975).
3562 Recently calculated SHRIMP U-Pb dates dispute this age, instead constraining the Puesto Viejo
3563 Formation to 235.8 Ma ± 2.0 Myr (Ottone et al., 2014). This suggests the Cortaderitian Stage is no
3564 older than 237.8 Ma, and therefore the *Scytophyllum* flora and Madygen Formation can be no older
3565 than this age, still within the Carnian. Note that a GSSP for the Carnian-Norian boundary has not yet
3566 been identified; radioisotopic ages may suggest a younger boundary at ~220 Ma (Lucas et al., 2012).

3567 Nevertheless, a commonly accepted date for the Carnian upper boundary is estimated at 228.4 Ma \pm
3568 2 Myr based on cyclostratigraphy and a candidate GSSP (e.g. Ogg, 2012; Ogg et al., 2014), so this
3569 provides a minimum age at 226.4 Ma.

3570 Soft maximum as for 75.3.

3571

3572 90.1 Discussion

3573

3574 Previous work has suggested *Archexyela* ipswichensis Engel, 2005 from the Mt. Crosby
3575 Formation, Ipswich Coal Measures of Queensland, Australia may be the oldest hymenopteran (e.g.
3576 Nicholson et al., 2015). However, the stratigraphy of the Ipswich Basin also provides a minimum age
3577 of uppermost Carnian (Purdy and Cranfield, 2013), thus we calibrate crown Hymenoptera with the
3578 equally old *T. foveolata*, which has been included in landmark total-evidence phylogenies (O'Reilly et
3579 al., 2015; Ronquist et al., 2012).

3580

3581 91. Crown Aparaglossata

3582

3583 This clade comprises Neuropterida, Coleopterida and Mecopterida, their last common ancestor
3584 and all of its descendants (**Fig. 23**). The clade was first named by Peters et al. (2014) based on
3585 support from phylogenetic analysis of transcriptomes.

3586

3587 91.1. Fossil specimens

3588

3589 As for 89.1.

3590

3591 91.2. Phylogenetic justification

3592

3593 As for 89.2.

3594

3595 91.3. *Age justification*

3596

3597 As for 89.3.

3598

3599 **92. Crown Neuropterida**

3600

3601 This clade comprises Raphidioptera (snakeflies), Megaloptera (fishflies), Neuroptera (net-
3602 winged insects), their last common ancestor and all of its descendants (**Fig. 23**). Monophyly is
3603 established by phylogenetic analysis of transcriptomes (Misof et al., 2014; Peters et al., 2014), protein-
3604 coding genes (Wiegmann et al., 2009), morphology (Beutel et al., 2011), and combined molecular and
3605 morphological data (Winterton et al., 2010).

3606

3607 92.1. *Fossil specimens*

3608

3609 *Elmothone martynovae* Carpenter, 1976. MCZ 5585, holotype, a forewing (**Fig. 25b**). Figured
3610 by Prokop et al. (2015; Fig. 7A).

3611

3612 92.2. *Phylogenetic justification*

3613

3614 A morphological phylogenetic analysis placed the Permithonidae *sensu lato* as a stem group to
3615 the extant Neuroptera (Ren et al., 2009; shown in supplementary information therein). A position on
3616 the stem lineage of Neuroptera is thus part of the crown group of Neuropterida. As the coding was
3617 done at a family level, we note with caution that monophyly of the Permithonidae and the exact
3618 relationships of its member species with Neuroptera has not been examined in a phylogenetic context

3619 and remain obscure (Prokop et al., 2015). Nonetheless, most members of Permithonidae possess the
3620 character states coded by Ren et al. (2009), so we take the oldest well-described member, *E.*
3621 *martynovae*, as a calibration fossil.

3622

3623 92.3. Age justification

3624

3625 This fossil occurs in the Carlton Limestone Member of the Wellington Formation in the Sumner
3626 Group of Elmo, Dickinson County, central Kansas (Prokop et al., 2015; Zambito et al., 2012). The
3627 insect-bearing locality is correlated with the Leonardian regional Stage (Sawin et al., 2008; Zambito et
3628 al., 2012) on the basis of conchostracan biostratigraphy (Tasch, 1962). The Leonardian spans the
3629 Artinskian and the younger Kungurian Stage (Henderson et al., 2012). The upper boundary of the
3630 Kungurian is $272.3 \text{ Ma} \pm 0.5 \text{ Myr}$, thus providing a conservative minimum age estimate of 271.8 Ma.

3631 Soft maximum as for 75.3.

3632

3633 92.4. Discussion

3634

3635 A younger member of the Permithonidae, *Permithone belmontensis* Tillyard, 1922
3636 (Changhsingian or latest Permian of Belmont, Australia), was previously used as a calibration fossil for
3637 Neuropterida (Misof et al., 2014).

3638

3639 93. Crown Megaloptera

3640

3641 This clade comprises Sialidae and Corydalidae, their last common ancestor and all of its
3642 descendants (**Fig. 23**). Monophyly is established by phylogenetic analysis of full mitochondrial
3643 genomes (Wang et al., 2012), transcriptomes (Misof et al., 2014), and morphology of the wing base
3644 (Zhao et al., 2014).

3645

3646 93.1. *Fossil specimens*

3647

3648 *Eochauliodes striolatus* Liu et al., 2012. CNU-MEG-NN2011004 P/C, holotype part/counterpart,
3649 laterally preserving an adult including forewing and hindwing (**Fig. 25c**).

3650

3651 93.2. *Phylogenetic justification*

3652

3653 *E. striolatus* was included in a phylogenetic analysis of morphology, encompassing characters
3654 from wing venation, adult genitalia, and larval morphology where possible (Liu et al., 2012). *E.*
3655 *striolatus* was found within the crown Corydalidae, at the base of the 'Protochauliodes clade'
3656 (comprising extant species). This position is therefore within crown Megaloptera. The bifurcated
3657 anterior branch of the Rs vein is a relevant synapomorphy (Liu et al., 2012).

3658

3659 93.3. *Age justification*

3660

3661 As for 79.3.

3662

3663 93.4. *Discussion*

3664

3665 Another fossil from the Daohugou fauna, *Jurochauliodes ponomarenkoi* Wang and Zhang,
3666 2010 was found in a slightly more basal position within the Corydalidae (and thus Megaloptera) crown
3667 group (Liu et al., 2012). As it is of equal age to *E. striolatus*, it is also an acceptable calibration fossil
3668 for this clade.

3669

3670 **94. Crown Neuroptera**

3671

3672 This clade comprises Hemerobiiformia, Nevrothiformia and Myrmeleontiformia, their last
3673 common ancestor and all of its descendants (**Fig. 23**). Monophyly is supported by phylogenetic
3674 analysis of ribosomal and mitochondrial genes (Haring and Aspöck, 2004), housekeeping genes
3675 (Wiegmann et al., 2009), and morphology (Beutel et al., 2011; Zhao et al., 2014).

3676

3677 *94.1. Fossil specimens*

3678

3679 *Liassochrysa stigmatica* Ansorge and Schlüter, 1990. MBA.I 5046 (formerly from the Ansorge
3680 collection, Dobbertin, Germany: No. LDA301), holotype, preserving a forewing. Imaged in (Wedmann
3681 and Makarkin, 2007: Fig. 5a).

3682

3683 *94.2. Phylogenetic justification*

3684

3685 *L. stigmatica* was coded in the morphological matrix for the total evidence phylogeny of Liu et
3686 al. (2015). In that tree, it was a member of crown group Mantispidae, a family within Hemerobiiformia,
3687 and therefore crown Neuroptera (Liu et al., 2015). This fossil was also the oldest calibration used for
3688 Neuroptera in the divergence time analysis of Winterton et al. (2010).

3689

3690 *94.3. Age justification*

3691

3692 The fossil was recovered from the former clay pit of Schwinz, near Dobbertin, Mecklenburg,
3693 northeast Germany (Ansorge and Schlüter, 1990). Multiple associated ammonites (*Eleganticeras*
3694 *elegantulum*, *Lobolytoceras siemensii*, *Harpoceras capellatum*) indicate that the locality is correlated to
3695 the lower part of the *H. falciferum* ammonite Zone, early Toarcian (Ansorge and Schlüter, 1990;
3696 O'Reilly et al., 2015; Pálffy et al., 2002, 2000). The Boreal *falciferum* Zone is equivalent to the Tethyan

3697 *H. serpentinum* ammonoid Zone (Macchioni, 2002), and succeeded by the *Hildoceras bifrons*
3698 ammonoid Zone. The base of the *bifrons* Zone has been dated to 180.36 Ma \pm 0.7 Myr (Ogg et al.,
3699 2012b). From this, an upper boundary of the *falciferum* Zone can be derived, and thus a minimum age
3700 for Dobbertin, at 179.66 Ma.

3701 Soft maximum as for 75.3.

3702

3703 **95. Crown Coleoptera**

3704

3705 This clade comprises Strepsiptera (twisted wing parasites) and Coleoptera (beetles), their last
3706 common ancestor and all of its descendants (**Fig. 23**). Monophyly of this clade is an extremely well-
3707 examined question in systematics, often used to illustrate the principle of long branch attraction (e.g.
3708 Boussau et al., 2014; Carmean and Crespi, 1995; Huelsenbeck, 1998, 1997; Niehuis et al., 2012;
3709 Siddall and Whiting, 1999; Whiting et al., 1997; Wiegmann et al., 2009). However, recent analyses of
3710 genomes and transcriptomes have consistently converged on a sister group relationship between
3711 Strepsiptera and Coleoptera (Boussau et al., 2014; Misof et al., 2014; Niehuis et al., 2012).

3712

3713 *95.1. Fossil specimens*

3714

3715 *Adiphebia lacoana* Scudder, 1885. USNM 38140, holotype, preserving a forewing. Imaged in
3716 Béthoux (2009: Fig. 1(3-5)).

3717

3718 *95.2. Phylogenetic justification*

3719

3720 *A. lacoana* has not been included in formal cladistic analysis to test its phylogenetic position.
3721 Variation in forewing venation within species provides a challenge to homology statements (Béthoux,
3722 2009; Garwood and Sutton, 2010). However, *A. lacoana* shares a forewing character with the crown

3723 beetle suborder Archostemata, specifically: "the areas between ScP, RA, branches of RP, M, branches
3724 of CuA, and AA filled with a regular network of quadrangular to pentagonal cells forming intercalary
3725 longitudinal pseudo-veins" (Béthoux, 2009). Intercalary pseudo-veins are also observed in fossils
3726 throughout Pterygota, suggesting this is either a symplesiomorphic or homoplastic state. However,
3727 some of the wing regions exhibiting intercalary veins (ScP and RA) are restricted to fossil Coleoptera
3728 (Béthoux, 2009). *A. lacoana* has thus been designated as a sister group to all crown Coleoptera, i.e. a
3729 member of its stem lineage (Béthoux, 2009), and thus a crown group member of Coleopterida. This
3730 assignment is also supported by putative larval material (Labandeira, 2011).

3731 There has been debate, however, about the taphonomy of the network of wing veins,
3732 suggesting they are clumps of clay instead of morphological characters (Kukalova-Peck and Beutel,
3733 2012). Alternative placements were on the stem lineage of Neuroptera or Neuropterida (Kukalova-
3734 Peck and Beutel, 2012), or outside Holometabola altogether (Guan et al., 2016; Nel et al., 2013).

3735

3736 *95.3. Age justification*

3737

3738 Minimum as for 31.3. Soft maximum as for 75.3.

3739

3740 **96. Crown Coleoptera**

3741

3742 This clade comprises Archostemata, Myxophaga, Adephaga (ground beetles, tiger beetles,
3743 diving beetles, whirligig beetles) and Polyphaga (ladybugs, longhorn beetles, weevils, fireflies,
3744 scarabs, stag beetles, rove beetles), their last common ancestor and all of its descendants (**Fig. 23**).
3745 Monophyly is supported by phylogenetic analysis of nuclear protein-coding genes (McKenna et al.,
3746 2015) and morphology (Beutel et al., 2011).

3747

3748 *96.1. Fossil specimens*

3749

3750 *Triadogyrus sternalis* Ponomarenko, 1977. PIN 3320/13, holotype (**Fig. 25d**), an exoskeleton
3751 without head, prothorax, or legs (Arnol'di et al., 1992).

3752

3753 *96.2. Phylogenetic justification*

3754

3755 In the morphological phylogenetic analysis of Beutel et al. (2013), *T. sternalis* is a stem group
3756 member of the family Gyrinidae. As Gyrinidae is part of Adephaga, crown membership within both
3757 Adephaga and Coleoptera is justified.

3758

3759 *96.3. Age justification*

3760

3761 *T. sternalis* was recovered from the mouth of Bereni River near Garazhokva settlement,
3762 Khar'kov oblast, Izyum region, Ukraine (Arnol'di et al., 1992). Fossiliferous strata are lacustrine
3763 claystone, part of the Protopivka Formation, estimated as Late Carnian-Early Norian age within the
3764 late Triassic (Arnol'di et al., 1992; Rasnitsyn and Quicke, 2002; Shcherbakov, 2008). The upper Norian
3765 boundary is estimated at ~208.5 Ma, so this provides a conservative minimum age.

3766 Soft maximum as for 75.3.

3767

3768 *96.4. Discussion*

3769

3770 The Pennsylvanian (Mazon Creek) fossil *A. lacoana* is a member of the stem lineage of
3771 Coleoptera (Béthoux, 2009). Recent divergence time analyses (McKenna et al., 2015; Misof et al.,
3772 2014) have therefore elected not to calibrate the crown group of Coleoptera with *A. lacoana*. Resulting
3773 age estimates for crown Coleoptera ranged from 250-280 Ma, substantially younger than *A. lacoana*
3774 itself.

3775 The Permian *Coleopsis archaica* Kirejtshuk et al., 2014 was noted as a stem group fossil,
3776 potentially Protocoleoptera (stem Coleoptera) (McKenna et al., 2015). Thus it was not used as a
3777 calibration. However, using younger internal calibrations (the oldest from Madygen, 225 Ma in their
3778 dataset), the crown origin of Coleoptera was estimated around 250 Ma (McKenna et al., 2015).
3779 Accounting for error bars, the crown group may have originated shortly before (or shortly after) the
3780 end-Permian extinction, timing that is compatible with *C. archaica* as a very early representative.

3781

3782 **97. Crown Mecopterida**

3783

3784 This clade comprises Amphiesmenoptera and Antliophora, their last common ancestor and all
3785 of its descendants (**Fig. 24**). Phylogenetic support for monophyly of Mecopterida comes from
3786 genomes (Niehuis et al., 2012), transcriptomes (Misof et al., 2014) and morphology (Beutel et al.,
3787 2011). Note that the clade we refer to as Mecopterida was called Panorpida by Grimaldi and Engel
3788 (2005), because they used Mecopterida to refer to paraphyletic Mecoptera containing Siphonaptera
3789 (and excluding Diptera). Our clade Mecopterida was also referred to as Panorpoidea by several
3790 sources, including Ren et al. (2009). Analyses relying on molecular data alone do not support the
3791 paraphyly of Mecoptera (Misof et al., 2014; Peters et al., 2014; Wiegmann et al., 2009), and these
3792 tend to utilize our conception of Mecopterida.

3793

3794 *97.1. Fossil specimens*

3795

3796 *Permopanorpa inaequalis* Tillyard, 1926. YPM IP 005058, holotype, a wing (**Fig. 25e**).

3797

3798 *97.2. Phylogenetic justification*

3799

3800 *P. inaequalis* is the oldest member of the family Permopanorpidae, which was coded (at the

3801 family level) in the morphological matrix of Ren et al. (2009). In that tree, it was part of the total group
3802 of Antliophora (although the figure label indicated it was inside crown Antliophora, the topology clearly
3803 indicates it was on the stem lineage; Ren et al., 2009). As a stem group member of Antliophora, *P.*
3804 *inaequalis* is thus crown group Mecopterida.

3805

3806 *97.3. Age justification*

3807

3808 As for 92.3.

3809

3810 *97.4. Discussion*

3811

3812 *W. maryvonneae* (family Protomeropidae), from the Bashkirian of France, has been proposed
3813 as an “amphiesmenopteran or antliophoran”, which may mean it belongs on the stem lineage of one of
3814 those clades and thus in crown Mecopterida. It has also been drawn onto a phylogram as a stem
3815 member of Mecoptera (Nel et al., 2013). However, the evidence for any particular placement within
3816 Mecopterida is ambiguous, and thus it is possible the fossil is only stem Mecopterida. See 89.2 for
3817 greater detail.

3818 Conversely, the early to middle Permian family Kaltanidae has been included in a phylogenetic
3819 analysis, and shown to fall on the stem lineage of Amphiesmenoptera (Ren et al., 2009). Although
3820 Kaltanidae have been previously discussed as calibration fossils for Mecopterida (e.g. Benton and
3821 Donoghue, 2007), their oldest members are from the Kungurian Stage of Russia, the same age as
3822 Elmo (Bashkuev, 2008). Additionally, the family Belmontiidae is within crown Mecopterida in a
3823 phylogenetic analysis (Ren et al., 2009), but its oldest fossil is from the late Permian (Changhsingian)
3824 of Australia (Grimaldi and Engel, 2005).

3825

3826 **98. Crown Amphiesmenoptera**

3827

3828 This clade comprises Trichoptera (caddisflies) and Lepidoptera (butterflies, moths), their last
3829 common ancestor and all of its descendants (**Fig. 24**). Monophyly is supported by phylogenetic
3830 analysis of transcriptomes (Misof et al., 2014), nuclear protein-coding genes (Wiegmann et al., 2009),
3831 and morphology (Beutel et al., 2011; Kristensen, 1991).

3832

3833 *98.1. Fossil specimens*

3834

3835 *Archaeolepis mane* Whalley, 1985. BMNH In. 59397, holotype, preserving a hindwing (**Fig.**
3836 **25f**).

3837

3838 *98.2. Phylogenetic justification*

3839

3840 *A. mane* has been used to calibrate the lepidopteran root in previous molecular dating
3841 analyses (e.g. Wahlberg et al., 2013), where this relationship is based on two lines of evidence: wing
3842 scales and wing venation. The preservation of extremely rare scales completely covering the hindwing
3843 excludes *A. mane* from crown Trichoptera (Whalley, 1986, 1985) because Trichoptera only bear scales
3844 on the forewing. The presence of scales across the entirety of a wing with panorpoid venation can only
3845 signal amphiesmenopteran affinity.

3846 The Sc vein (with one visible branch) of *A. mane* is unlikely to represent the ancestral state for
3847 Lepidoptera, as the number of Sc vein branches varies in early-diverging moths, but is usually two
3848 branches, and this vein is multi-branched ancestrally in Amphiesmenoptera (Kukalova-Peck and
3849 Willmann, 1990; Minet et al., 2010; Sukatsheva and Vassilenko, 2011; Schachat and Brown, 2016).
3850 Although Trichoptera tend to have more wing veins than Lepidoptera, it is likely that fewer veins were
3851 lost by ancestral moths than is currently accepted in the literature, making distinctions between
3852 amphiesmenopteran branches difficult for Mesozoic fossils (Schachat and Brown, 2015, 2016). As

3853 reconstructed by Whalley (1986), the wing venation of *A. mane* differs markedly from the venation of
3854 crown Lepidoptera: there is a single, branched Cubitus vein, with CuP apparently absent, and all three
3855 branches of the anal vein reach the dorsum. In contrast, basal crown Lepidoptera nearly always have
3856 a CuP vein, and the anal vein becomes fused before reaching the dorsum (Common, 1973; Schachat
3857 and Brown, 2016). A position for *A. mane* within the crown group of Lepidoptera thus cannot be
3858 confirmed, but an identity as stem Lepidoptera is highly likely based on the wing scales in particular, in
3859 agreement with Whalley (1986). This fossil would therefore be within the crown group of
3860 Amphiesmenoptera.

3861

3862 98.3. Age justification

3863

3864 Whalley (1985) noted the locality as Black Ven, Charmouth, Dorset, on the Jurassic Coast of
3865 England. This was further specified as calcareous flatstone, probably from Bed 75a, of the *Caenisites*
3866 *turneri* ammonoid Zone (Sohn et al., 2012), or *Microderoceras birchi* Nodular of the “Shales with Beef”
3867 (Lang et al., 1923). Chemostratigraphy places the *C. turneri* (and *M. birchi*) Zones within the middle
3868 Sinemurian (Jenkyns et al., 2002). The upper boundary of the *C. turneri* Zone is thus dated to 195.31
3869 Ma (Ogg et al., 2012b), providing a minimum age.

3870 Soft maximum as for 75.3.

3871

3872 99. Crown Trichoptera

3873

3874 This clade comprises 'Spicipalpia', Annulipalpia and Integripalpia their last common ancestor
3875 and all of its descendants (**Fig. 24**). Monophyly is supported by phylogenetic analysis of
3876 transcriptomes (Misof et al., 2014), housekeeping genes (Kjer et al., 2002, 2001; Malm et al., 2013),
3877 and morphology (Beutel et al., 2011).

3878

3879 99.1. *Fossil specimens*

3880

3881 *Liadotaulius maior* Handlirsch, 1906. Handlirsch (1906) did not designate a holotype, thus we
3882 refer to three specimens figured by Ansorge (2002): (Ansorge collection, to be deposited at MBA: LGA
3883 1995; **Fig. 25g**), female forewing, (LGA 672), male forewing, and (LGA 1710), hindwing.

3884

3885 99.2. *Phylogenetic justification*

3886

3887 Taxonomic placement of *L. maior* requires apomorphies from the male wings, as female wings
3888 have many plesiomorphic venation characters (Ansorge, 2002). Further studies of a younger
3889 congeneric, *L. daohugouensis* Wu and Huang, 2012, reveal new characters shared with crown group
3890 Trichoptera. These include the apical part of Cu2 bending towards the wing margin, its
3891 desclerotisation, and complete anal veins (Ansorge, 2002; Wu and Huang, 2012). These apomorphies
3892 place the genus *Liadotaulius* in Philopotamidae, a family within crown group Annulipalpa, and thus
3893 Trichoptera (Wu and Huang, 2012).

3894

3895 99.3. *Age justification*

3896

3897 The fossils were recovered from Grimmen, northeast Germany (Ansorge, 2002). Further age
3898 information as for 94.3.

3899

3900 99.4. *Discussion*

3901

3902 Possible caddisfly larval cases were recently described from the early Permian of Brazil (Mouro
3903 et al., 2016). The cases are tubular in form, and particulate matter is stuck to some of the cases
3904 (Mouro et al., 2016). Of the two most basal extant trichopteran families that construct larval cases, the

Hydroptilidae construct tubular cases and the Glossosomatidae construct their cases from particulate matter (Malm et al., 2013). However, various types of larval cases, including tubular cases, are constructed by caddisflies belonging to distantly-related lineages (Malm et al., 2013); at present, it cannot be assumed that tubular larval cases have originated only once within the Trichoptera. Assuming the Permian fossils are indeed insect larval cases, therefore, does not confirm the phylogenetic position of their inhabitants within crown versus stem Trichoptera, as larval cases might have evolved in the stem group.

3912

3913 **100. Crown Lepidoptera**

3914

This clade comprises Zeugloptera, Aglossata, Heterobathmiina and Glossata (itself comprising six infraorders, over 100 families, and over 160,000 species), their last common ancestor and all of its descendants (**Fig. 24**). The list of lepidopteran subclades comes from a recently published consensus (van Nieukerken et al., 2011), although some molecular analyses have not recovered these clades (Regier et al., 2013). Monophyly is supported by nuclear protein-coding genes (Regier et al., 2013), transcriptomes (Misof et al., 2014), and morphology (Beutel et al., 2011).

3921

3922 *100.1. Fossil specimens*

3923

Parasabatinca aftimacrai Whalley, 1978. Although the holotype (the specimen to which we refer; **Fig. 25h**) and two paratypes were attributed to the NHMUK (Sohn et al., 2012), they are now housed as part of the Acra collection, curated by D. Azar, pending construction of a fossil museum at the Lebanese University in Fanar (Matn), Lebanon (D. Azar, pers. comm.).

3928

3929 *100.2. Phylogenetic justification*

3930

3931 Although not included in formal phylogenetic analysis, morphological characters (morphology
3932 of the antennae with ascoids, number and shape of tibial spurs, mouthpart and maxillary palp
3933 morphology) support the position of *P. aftimacrai* in what was formerly known as the 'Sabatinca' group
3934 of genera within Micropterigidae (Kristensen and Skalski, 1998; D. Azar, pers. comm.). As *P. aftimacrai*
3935 has an unbranched R vein and because Rs_4 terminates below the apex, the wing venation of *P.*
3936 *aftimacrai* most closely resembles that of the extant species *Austromartyria porphyrodes*, which
3937 belongs to what is now known as the 'Southern sabatinoid' lineage of Micropterigidae (Gibbs, 2010).
3938 Based on the above morphological characters, *P. aftimacrai* is supported as the oldest crown group
3939 member in multiple summaries of the fossil record of Lepidoptera (Grimaldi and Engel, 2005, Fig.
3940 13.13; Sohn et al., 2015, Fig. 2). Membership either within the crown or stem of Micropterigidae places
3941 the fossil within crown Zeugloptera and crown Lepidoptera.

3942

3943 100.3. Age justification

3944

3945 As for 76.3.

3946

3947

3948 100.4. Discussion

3949

3950 A number of older fossils have been assigned to Lepidoptera, but their position within the
3951 crown is ambiguous. *A. mane*, from the Early Jurassic of Dorset, England, has been used to calibrate
3952 the lepidopteran root in previous molecular dating analyses (e.g. Wahlberg et al., 2013). See 98.2 for
3953 exclusion of *A. mane* from the lepidopteran crown.

3954 Sohn et al. (2015) suggested that two undescribed fossil species are members of the
3955 Micropterigidae stem lineage (and thus crown Zeugloptera and crown Lepidoptera). These are from
3956 the Toarcian (Early Jurassic) Grüne Series of Grimmen, Germany (Ansorge, 2002), but they are too

3957 poorly characterized to be confidently used as calibration fossils.

3958

3959 **101. Crown Antliophora**

3960

3961 This clade comprises Siphonaptera (fleas), Mecoptera (scorpionflies) and Diptera (flies), their
3962 last common ancestor and all of its descendants (**Fig. 24**). Support for monophyly comes from
3963 phylogenetic analysis of transcriptomes (Misof et al., 2014; Peters et al., 2014) and morphology
3964 (Beutel et al., 2011). A recent analysis of mitochondrial genomes finds Amphiesmenoptera within
3965 Antliophora under some analytical conditions, potentially challenging antliophoran monophyly (Song et
3966 al., 2016).

3967

3968 *101.1. Fossil specimens*

3969

3970 *Pseudonannochorista willmanni* Novokshonov, 1994. PIN 966/21, holotype, preserving a
3971 forewing (**Fig. 25i**).

3972

3973 *101.2. Phylogenetic justification*

3974

3975 Pseudonannochoristinae is a subfamily of the Permochoristidae (Bashkuev, 2011;
3976 Novokshonov, 1994), however, a morphological phylogenetic analysis indicates polyphyly of this family
3977 (Ren et al., 2009). While the Permochoristinae (the other subfamily of Permochoristidae) fall on the
3978 stem lineage of Antliophora, Pseudonannochoristinae are part of the stem lineage of Mecoptera (Ren
3979 et al., 2009). Therefore, *P. willmanni*, as a member of Pseudonannochoristinae, is part of the crown
3980 group of Antliophora.

3981

3982 *101.3. Age justification*

3983

3984 Minimum as for 77.3. Soft maximum as for 75.3.

3985

3986 101.4. *Discussion*

3987

3988 Other fossils from the families Permotanyderidae, Permotipulidae, and Nannochoristinae are
3989 all demonstrably within crown group Antliophora (Ren et al., 2009). However, the localities from which
3990 they are known are younger, of Changhsingian age (Belmont, Australia and Mooi River, South Africa).

3991 Fossils of Siphonaptera from the Jurassic (Gao et al., 2012) and Cretaceous (Gao et al., 2014;
3992 Huang, 2015), suggested to parasitise dinosaurs, have been excluded from the crown group in a
3993 recent molecular phylogenetic analysis (Zhu et al., 2015). The molecular clock analysis (which was
3994 calibrated with better established fossils from Dominican and Baltic amber, of Miocene and Eocene
3995 age, respectively) estimated the origins of crown Siphonaptera in the Valanginian to Aptian stages of
3996 the Early Cretaceous (Zhu et al., 2015). Furthermore, none of the Mesozoic fossils possess a
3997 diagnostic character combination for the crown group (Dittmar et al., 2016). As siphonapteran
3998 parasites of dinosaurs would require a strong assumption that piercing mouthparts must be used for
3999 blood-feeding (Dittmar et al., 2016), we do not include any crown fossil calibrations.

4000

4001 **102. Crown Mecoptera**

4002

4003 This clade comprises Apteropanorpidae, Bittacidae, Boreidae, Choristidae, Eomeropidae,
4004 Meropeidae, Nannochoristidae, Panorpidae, and Panorpididae, their last common ancestor and all of
4005 its descendants (**Fig. 24**). Paraphyly of the traditional concept of Mecoptera (i.e. inclusion of
4006 Siphonaptera) was proposed by Whiting (2002) on the basis of four nuclear genes. This was, however,
4007 contradicted by analysis of six nuclear genes (Wiegmann et al., 2009), transcriptomes (Misof et al.,
4008 2014; Peters et al., 2014), and morphology (Beutel et al., 2011). Each of the latter studies recovered a

4009 monophyletic Mecoptera as the sister group of Siphonaptera.

4010

4011 *102.1. Fossil specimens*

4012

4013 *Burmomerope eureka* Grimaldi and Engel, 2013 (collection of James Zigras, available for study
4014 at AMNH: JZC Bu-84), holotype in amber.

4015

4016 *102.2. Phylogenetic justification*

4017

4018 *B. eureka* was assigned to the stem group of the extant family Meropeidae, based on several
4019 wing venation characters, including loss of slanted portion of CuA in forewing and R-Rs fork basal
4020 (Grimaldi and Engel, 2013). A position on the stem lineage of Meropeidae is therefore within the crown
4021 group of Mecoptera.

4022

4023 *102.3. Age justification*

4024

4025 As for 87.3.

4026

4027 **103. Crown Diptera**

4028

4029 This clade comprises Tipulomorpha (crane flies), Psychodomorpha (moth flies, sand flies),
4030 Culicomorpha (mosquitoes, black flies), Bibionomorpha (march flies, fungus gnats) and Brachycera
4031 (horse flies, robber flies, fruit flies, house flies, blow flies, etc.), their last common ancestor and all of
4032 its descendants (**Fig. 24**). Monophyly of Diptera has been supported in many phylogenetic analyses,
4033 including those based on transcriptomes (Misof et al., 2014), mitochondrial genomes and microRNA
4034 presence (Wiegmann et al., 2011), and morphology (Beutel et al., 2011; Wiegmann et al., 2011).

4035

4036 103.1. *Fossil specimens*

4037

4038 *Grauvogelia arzvilleriana* Krzeminski et al., 1994 (part of the private Louis Grauvogel collection,
4039 Ringendorf, Bas-Rhin, France, No. 5514), holotype (**Fig. 25j**).

4040

4041 103.2. *Phylogenetic justification*

4042

4043 *G. arzvilleriana* was included in the morphological cladistic analysis of Blagoderov et al. (2007).
4044 In that analysis, it was supported on the stem group of Psychodomorpha (Blagoderov et al., 2007).
4045 Although the original description assigned *G. arzvilleriana* to its own family, several wing venation
4046 characters were noted as similarities with families of Psychodomorpha (Krzeminski et al., 1994). The
4047 stem group of Psychodomorpha is within crown Diptera.

4048

4049 103.3. *Age justification*

4050

4051 Minimum as for 72.3. Soft maximum as for 75.3.

4052

4053 103.4. *Discussion*

4054

4055 A number of other dipteran fossils have been described from Grès à Voltzia; of special interest
4056 is *Voltziapupa tentata* Lukashevich et al., 2010, known only from well-preserved pupae, while *G.*
4057 *arzvilleriana* is known only from adult wings. The venation of the wing sheath in *V. tentata* is not well
4058 preserved, preventing a clear link of characters with *G. arzvilleriana* (Lukashevich et al., 2010).

4059

4060 **104. Conclusions**

4061

4062 Based on this compilation, qualitative trends in the fossil record of arthropod crown group
4063 members can be described. Patchiness in our taxonomic coverage results from differential
4064 preservation potential, with a notable scarcity of taxa living in habitats with poorly preserved facies
4065 (e.g. intertidal barnacles or pelagic copepods). More completely preserved fossils representing ancient
4066 divergences are well represented in our list of calibrations, perhaps owing to the attention devoted to
4067 phylogenetic analysis of deep fossil relationships within arthropods (e.g. Garwood and Dunlop, 2014 ;
4068 Lee et al., 2013; Legg et al., 2013; Oakley et al., 2013; Rota-Stabelli et al., 2011). However because
4069 our review is focused on crown groups, about half of our calibrations are from mid-Palaeozoic
4070 localities, making them much more numerous than those from Cambrian Burgess Shale-type biotas.
4071 Throughout the dataset, there is less of a relationship between 'hard part' preservation (calcified body
4072 parts, such as ostracod carapaces) and phylogenetic accuracy than might be expected.

4073 Particular Konservat-Lagerstätten, such as Herefordshire (Silurian), Rhynie Chert (Devonian),
4074 Mazon Creek (Carboniferous), Crato (Cretaceous) and Burmese amber (Cretaceous), provide several
4075 calibrations representing different arthropod clades, presumably owing to their preservation of non-
4076 biomineralised tissues required to identify arthropods to the ordinal level. These sites are critically
4077 important for the arthropod fossil record because of their relatively low preservation potential of many
4078 groups, as is particularly the case for terrestrial arthropods, being less well mineralised than many of
4079 the marine groups. This is reflected in the low level of congruence between the order of appearance of
4080 lineages in the fossil record (stratigraphic appearance) and the order of phylogenetic branching (Wills,
4081 2001; O'Connor and Wills, 2016) in arthropods, as compared to more congruent datasets such as
4082 tetrapods (Benton et al., 1999, 2000; Norell and Novacek, 1992). Clustering of calibrations at
4083 Konservat-Lagerstätten localities may lead to highly variable lengths of ghost lineages for the different
4084 taxa that are preserved together at these sites, and indeed many of the clades in our database have
4085 soft maxima that are substantially older than their hard minimum date. Konservat-Lagerstätten
4086 localities are, however, fairly regularly spaced throughout the Middle to Late Palaeozoic and the

4087 Mesozoic, and interim periods of time are punctuated by numerous other fossil localities yielding fewer
4088 calibration points. This results in our database having good coverage throughout the Phanerozoic
4089 with fossil localities occurring on average every 4-10 million years. A notable exception is the 43.2
4090 million year gap in the Ordovician, during which no definite earliest appearances of any crown-group
4091 orders have been identified in our study, despite this period being known as the Ordovician
4092 biodiversification event (Servais et al., 2008, 2010). Numerous arthropod stem lineage taxa were
4093 abundant during the Ordovician (e.g. trilobites), while the possible crown group taxa that have been
4094 described, e.g. ostracods (Siveter et al., 2014; Williams et al., 2008), barnacles (Van Roy et al., 2010),
4095 pycnogonids (Rudkin et al., 2013), xiphosurans (Lamsdell, 2013; Rudkin et al., 2008; Van Roy et al.,
4096 2010), and acariform mites (Bernini et al., 2002) do not meet the rigorous standards employed herein
4097 for determining calibration points. From the Late Devonian through the Mississippian (382.7 to 323.2
4098 Ma) our dataset has another large gap during which we have only one calibration point, which
4099 interestingly corresponds with one of the largest mass extinctions events known in the fossil record
4100 (McGhee, 2013).

4101 The field of divergence time estimation itself is rapidly advancing. New methodologies to
4102 incorporate fossil morphology and stratigraphy into the model of diversification (Heath et al., 2014;
4103 Wilkinson et al., 2011) and the phylogenetic topology itself ('tip-dating'; Ronquist et al., 2012) are
4104 growing in popularity. Precision and accuracy of date estimates are improved with the inclusion of as
4105 many *a priori* justified fossils as possible in tip- (Lee et al., 2013; Ronquist et al., 2012; Zhang et al.,
4106 2016) or node-dating studies (Heath et al., 2014; Ho and Phillips, 2009; Warnock et al., 2012, 2015;
4107 Yang and Rannala, 2006). When examined in the context of geological and evolutionary history, the
4108 distribution of fossil calibrations in our dataset are comprehensive, and have been rigorously vetted to
4109 ensure they meet *a priori* requirements (Parham et al., 2012; Warnock et al., 2015). Following their
4110 use in molecular clock analyses, *a posteriori* methods such as cross-validation could be employed to
4111 explore the impact of calibrations on the resulting divergence time estimates (e.g. Battistuzzi et al.,
4112 2015; Dornburg et al., 2011; Marshall, 2008; Near et al., 2005), although these methods cannot justify

4113 removal of individual constraints (Warnock et al., 2015). Fossils mentioned in Discussion sections
4114 occupy key positions along clade stems, and should also be considered in divergence time
4115 applications. To this end, we have compiled a robust list of over 100 fossil calibrations covering much
4116 of the arthropod Tree of Life. We hope this summary will inspire further work clarifying the
4117 phylogenetic relationships of fossil arthropods, and morphological studies of characters linking them to
4118 their crown clades.

4119

4120

4121

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4144 **REFERENCES**

4145

4146 Abele, L.G., Spears, T., Kim, W., Applegate, M., 1992. Phylogeny of Selected Maxillopodan and Other
4147 Crustacean Taxa Based on 18S Ribosomal Nucleotide Sequences: A Preliminary Analysis. *Acta*
4148 *Zool.* 73, 373–382.

4149 Ahyong, S.T., 1997. Phylogenetic analysis of the Stomatopoda (Malacostraca). *J. Crustac. Biol.* 17,
4150 695–715.

4151 Ahyong, S.T., Harling, C., 2000. The phylogeny of the stomatopod Crustacea. *Aust. J. Zool.* 48, 607–
4152 642.

4153 Aitkin, J.D., 1997. Stratigraphy of the Middle Cambrian platformal succession, southern Rocky
4154 Mountains, Geological Survey of Canada Bulletin, 322 pp.

4155 Akulov, N.I., Frolov, A.O., Mashchuk, I.M., Akulova, V.V., 2015. Jurassic deposits of the southern part
4156 of the Irkutsk sedimentary basin. *Stratigr. Geol. Correl.* 23, 387–409.

4157 Almeida, W.O., Christoffersen, M.L., 1999. A Cladistic Approach to Relationships in Pentastomida. *J.*
4158 *Parasitol.* 85, 695–704.

4159 Alonso, J., Arillo, A., Barrón, E., Corral, J.C., Grimalt, J., López, J.F., Lopez, R., Martínez-Delclòs, X.,
4160 Ortuño, V., Peñalver, E., Trincao, P.R., 2000. A new fossil resin with biological inclusions in
4161 Lower Cretaceous deposits from Álava (Northern Spain, Basque-Cantabrian Basin). *J.*
4162 *Paleontol.* 74, 158-178.

4163 Anderson, F.W., 1985. Ostracod faunas in the Purbeck and Wealden of England. *J.*
4164 *Micropalaeontology* 4, 1–67.

4165 Anderson, L.I., Trewin, N.H., 2003. An Early Devonian arthropod fauna from the Windyfield cherts,
4166 Aberdeenshire, Scotland. *Palaeontology* 46, 467–509.

4167 Anderson, L.I., Crighton, W.R., Hass, H., 2003. A new univalve crustacean from the Early Devonian
4168 Rhynie chert hot-spring complex. *Trans. R. Soc. Edinb. Earth Sci.* 94, 355–369.

- 4169 Andrew, D.R., 2011. A new view of insect–crustacean relationships II. Inferences from expressed
4170 sequence tags and comparisons with neural cladistics. *Arthropod Struct. Dev.* 40, 289–302.
- 4171 Ansorge, J., 2002. Upper Liassic Amphiesmenopterans (Trichoptera + Lepidoptera) from Germany—a
4172 review. *Acta Zool. Cracoviensia* 46, 285–290.
- 4173 Ansorge, J., Schlüter, T., 1990. The earliest chrysopid: *Liassochrysa stigmatica* n.g., n. sp. from the
4174 Lower Jurassic of Dobbertin, Germany. *Neuroptera Int.* 6, 87–93.
- 4175 Arabi, J., Cruaud, C., Couloux, A., Hassanin, A., 2010. Studying sources of incongruence in arthropod
4176 molecular phylogenies: Sea spiders (Pycnogonida) as a case study. *Comptes Rendus Biol.*
4177 333, 438–453.
- 4178 Arango, C.P., Wheeler, W.C., 2007. Phylogeny of the sea spiders (Arthropoda, Pycnogonida) based
4179 on direct optimization of six loci and morphology. *Cladistics* 23, 255–293.
- 4180 Arnol'di, L.V., Zherikhin, V.V., Nikritin, L.M., Ponomarenko, A.G., 1992. Mesozoic Coleoptera. Oxonian
4181 Press, New Delhi.
- 4182 Astrop, T.I., Hegna, T.A., 2015. Phylogenetic relationships between living and fossil spinicaudatan taxa
4183 (Branchiopoda Spinicaudata): reconsidering the evidence. *J. Crustac. Biol.* 35, 339–354.
- 4184 Avise, J.C., Nelson, W.S., Sugita, H., 1994. A speciation history of “living fossils”: molecular
4185 evolutionary patterns in horseshoe crabs. *Evolution* 1986–2001.
- 4186 Azar, D., Geze, R., Acra, F., 2010. Lebanese amber, in: Penney, D. (Ed.), *Biodiversity of Fossils in*
4187 *Amber from the Major World Deposits*. Siri Scientific Press, pp. 271–298.
- 4188 Babcock, L.E., Peng, S., Geyef, G., Shergold, J.H., 2005. Changing perspectives on Cambrian
4189 chronostratigraphy and progress toward subdivision of the Cambrian System. *Geosci. J.* 9,
4190 101–106.
- 4191 Baird, G.C., Sroka, S.D., Shabica, C.W., Beard, T.L., 1985. Mazon Creek-type fossil assemblages in
4192 the U.S. midcontinent Pennsylvanian: their recurrent character and palaeoenvironmental
4193 significance. *Philos. Trans. R. Soc. B Biol. Sci.* 311, 87–99.

- 4194 Bamber, R.N., 2007. A holistic re-interpretation of the phylogeny of the Pycnogonida Latreille, 1810
4195 (Arthropoda). Zootaxa 1668, 295–312.
- 4196 Baptista, C., Santiago-Blay, J.A., Soleglad, M.E., Fet, V., 2006. The Cretaceous Scorpion Genus,
4197 *Archaeobuthus*, Revisited (Scorpiones: Archaeobuthidae). Euscorpius 35, 1–28.
- 4198 Barrón, E., Elorza, L., Rengifo, M.J.C., 2001. Contribuciones al estudio palinológico del Cretácico
4199 Inferior de la Cuenca Vasco-Cantábrica: los afloramientos ambarígenos de Peñacerrada
4200 (España). Coloq. Paleontol. 135–156.
- 4201 Barrón, E., Peyrot, D., Rodríguez-López, J.P., Meléndez, N., López del Valle, R., Najarro, M., Rosales,
4202 I., Comas-Rengifo, M.J., 2015. Palynology of Aptian and upper Albian (Lower Cretaceous)
4203 amber-bearing outcrops of the southern margin of the Basque-Cantabrian basin (northern
4204 Spain). Cretac. Res. 52, 292–312.
- 4205 Barskov, I.S., Leonova, T.B., Shilovsky, O.P., 2014. Middle Permian cephalopods of the Volga-Ural
4206 Region. Paleontol. J. 48, 1331–1414.
- 4207 Bashkuev, A.S., 2008. The first record of Kaltanidae (Insecta: Mecoptera: Kaltanidae) from the
4208 Permian of European Russia. Paleontol. J. 42, 401–405.
- 4209 Bashkuev, A.S., 2011. Nedubroviidae, a new family of Mecoptera: the first Paleozoic long-proboscid
4210 scorpionflies. Zootaxa 2895, 47–57.
- 4211 Batten, D.J., 2007. Spores and pollen from the Crato Formation: biostratigraphic and
4212 palaeoenvironmental implications, in: The Crato Fossil Beds of Brazil: Window into an Ancient
4213 World. Cambridge University Press, Cambridge, pp. 566–573.
- 4214 Battistuzzi, F.U., Billing-Ross, P., Murillo, O., Filipinski, A., Kumar, S., 2015. A Protocol for Diagnosing
4215 the Effect of Calibration Priors on Posterior Time Estimates: A Case Study for the Cambrian
4216 Explosion of Animal Phyla. Mol. Biol. Evol. 32, 1907–1912.
- 4217 Bechly, G., 1997. New fossil Odonata from the Upper Triassic of Italy, with a redescription of
4218 *Italophlebia gervasutti*, and a reclassification of Triassic dragonflies. Riv. Mus. Civ. Sci. Nat. E
4219 Caffi 19, 31–70.

- 4220 Bechly, G., Stockar, R., 2011. The first Mesozoic record of the extinct apterygote insect genus
4221 *Dasyleptus* (Insecta: Archaeognatha: Monura: Dasyleptidae) from the Triassic of Monte San
4222 Giorgio (Switzerland). *Palaeodiversity* 4, 23–37.
- 4223 Becker, R.T., Gradstein, F.M., Hammer, O., 2012. The Devonian Period, in: *The Geologic Time Scale*.
4224 Elsevier, pp. 559–601.
- 4225 Bellec, L., Rabet, N., 2016. Dating of the Limnadiidae family suggests an American origin of
4226 *Eulimnadia*. *Hydrobiologia* 773, 149–161.
- 4227 Benner, J.S., Knecht, R.J., Engel, M.S., 2013. Comment on Marden (2013): “Reanalysis and
4228 experimental evidence indicate that the earliest trace fossil of a winged insect was a surface
4229 skimming neopteran.” *Evolution* 67, 2142–2149.
- 4230 Benton, M.J., Donoghue, P.C.J., 2007. Paleontological Evidence to Date the Tree of Life. *Mol. Biol.*
4231 *Evol.* 24, 26–53.
- 4232 Benton, M.J., Donoghue, P.C., Asher, R.J., Friedman, M., Near, T.J., Vinther, J., 2015. Constraints on
4233 the timescale of animal evolutionary history. *Palaeontol. Electron.* 18, 1–106.
- 4234 Benton, M.J., Hitchin, R., Wills, M.A., 1999. Assessing congruence between cladistics and
4235 stratigraphic data. *Syst. Biol.* 48, 581–596.
- 4236 Benton, M.J., Wills, M.A., Hitchin, R., 2000. Quality of the fossil record through time. *Nature* 403, 534–
4237 537.
- 4238 Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C., Dronov, A., 2009. The new chronostratigraphic
4239 classification of the Ordovician System and its relations to major regional series and stages
4240 and to $\delta^{13}\text{C}$ chemostratigraphy. *Lethaia* 42, 97–107.
- 4241 Bernini, F., 1986. Current ideas on the phylogeny and the adaptive radiations of Acarida. *Bolletino*
4242 *Zool.* 53, 279–313.
- 4243 Bernini, F., Carnevale, G., Bagnoli, G., Stouge, S., 2002. An early Ordovician oribatid mite (Acari:
4244 Oribatida) from the island of Öland, Sweden, in: *Acarid Phylogeny and Evolution: Adaptation in*
4245 *Mites and Ticks*. Springer, pp. 45–47.

- 4246 Béthoux, O., 2005. Wing venation pattern of Plecoptera (Insecta: Neoptera). *Illiesia* 1, 52–81.
- 4247 Béthoux, O., 2009. The Earliest Beetle Identified. *J. Paleontol.* 83, 931–937.
- 4248 Béthoux, O., Beckemeyer, R.J., Engel, M.S., Hall, J.D., 2010. New data on *Homocladus grandis*, a
4249 Permian stem-mantodean (Polyneoptera: Dictyoptera). *J. Paleontol.* 84, 746–753.
- 4250 Béthoux, O., Cui, Y., Kondratieff, B., Stark, B., Ren, D., 2011. At last, a Pennsylvanian stem-stonefly
4251 (Plecoptera) discovered. *BMC Evol. Biol.* 11, 248.
- 4252 Béthoux, O., Nel, A., 2002. Venation pattern and revision of Orthoptera *sensu nov.* and sister groups.
4253 Phylogeny of Palaeozoic and Mesozoic Orthoptera *sensu nov.* *Zootaxa* 96, 1–88.
- 4254 Béthoux, O., Nel, A., 2005. Some Palaeozoic “Protorthoptera” are “ancestral” orthopteroids: Major
4255 wing braces as clues to a new split among the “Protorthoptera” (Insecta). *J. Syst. Palaeontol.*
4256 2, 285–309.
- 4257 Béthoux, O., Nel, A., 2010. Description of a new grylloblattidan insect from Montceau-les-Mines (Late
4258 Carboniferous; France) and definition of *Phenopterum* Carpenter, 1950. *Syst. Entomol.* 35,
4259 546–553.
- 4260
- 4261 Béthoux, O., Nel, A., Lapeyrie, J., Gand, G., Galtier, J., 2002. *Raphogla rubra* gen. n., sp. n., the oldest
4262 representative of the clade of modern Ensifera (Orthoptera: Tettigoniidea, Gryllidea). *Eur. J.*
4263 *Entomol.* 99, 111–116.
- 4264 Béthoux, O., Wieland, F., 2009. Evidence for Carboniferous origin of the order Mantodea (Insecta:
4265 Dictyoptera) gained from forewing morphology. *Zool. J. Linn. Soc.* 156, 79–113.
- 4266 Beutel, R.G., Friedrich, F., Hörnschemeyer, T., Pohl, H., Hünefeld, F., Beckmann, F., Meier, R., Misof,
4267 B., Whiting, M.F., Vilhelmsen, L., 2011. Morphological and molecular evidence converge upon
4268 a robust phylogeny of the megadiverse Holometabola. *Cladistics* 27, 341–355.
- 4269 Beutel, R.G., Wang, B., Tan, J.-J., Ge, S.-Q., Ren, D., Yang, X.-K., 2013. On the phylogeny and
4270 evolution of Mesozoic and extant lineages of Adephaga (Coleoptera, Insecta). *Cladistics* 29,
4271 147–165.

- 4272 Bill, P.C., 1914. Über crustaceen aus dem Voltziensandstein des Elasses. Mitteilungen der
4273 Geologischen Landesanstalt von Elsaß-Lothringen, Strassburg. 8, 289-338.
- 4274 Bird, T.L., Wharton, R.A., Prendini, L., 2015. Chelicer al Morphology in Solifugae (Arachnida): Primary
4275 Homology, Terminology, and Character Survey. Bull. Am. Mus. Nat. Hist. 394, 1–355.
- 4276 Blagoderov, V., Grimaldi, D.A., Fraser, N.C., 2007. How Time Flies for Flies: Diverse Diptera from the
4277 Triassic of Virginia and Early Radiation of the Order. Am. Mus. Novit. 3572, 1–39.
- 4278 Blanke, A., Greve, C., Wipfler, B., Beutel, R.G., Holland, B.R., Misof, B., 2013. The Identification of
4279 Concerted Convergence in Insect Heads Corroborates Palaeoptera. Syst. Biol. 62, 250–263.
- 4280 Blanke, A., Koch, M., Wipfler, B., Wilde, F., Misof, B., 2014. Head morphology of *Tricholepidion*
4281 *gertschi* indicates monophyletic Zygentoma. Front. Zool. 11, 1.
- 4282 Blanke, A., Machida, R., Szucsich, N.U., Wilde, F., Misof, B., 2015. Mandibles with two joints evolved
4283 much earlier in the history of insects: dicondyl y is a synapomorphy of bristletails, silverfish and
4284 winged insects. Syst. Entomol. 40, 357–364.
- 4285 Blanke, A., Wesener, T., 2014. Revival of forgotten characters and modern imaging techniques help to
4286 produce a robust phylogeny of the Diplopoda (Arthropoda, Myriapoda). Arthropod Struct. Dev.
4287 43, 63–75.
- 4288 Blanke, A., Wipfler, B., Letsch, H., Koch, M., Beckmann, F., Beutel, R., Misof, B., 2012. Revival of
4289 Palaeoptera-head characters support a monophyletic origin of Odonata and Ephemeroptera
4290 (Insecta) Cladistics 28, 560–581.
- 4291 Bonato, L., Drago, L., Murienne, J., 2014a. Phylogeny of Geophilomorpha (Chilopoda) inferred from
4292 new morphological and molecular evidence. Cladistics 30, 485–507.
- 4293 Bonato, L., Edgecombe, G.D., Minelli, A., 2014b. Geophilomorph centipedes from the Cretaceous
4294 amber of Burma. Palaeontology 57, 97–110.
- 4295 Bond, J.E., Garrison, N.L., Hamilton, C.A., Godwin, R.L., Hedin, M., Agnarsson, I., 2014.
4296 Phylogenomics Resolves a Spider Backbone Phylogeny and Rejects a Prevailing Paradigm for
4297 Orb Web Evolution. Curr. Biol. 24, 1765–1771.

- 4298 Bourquin, S., Durand, M., Diez, J.B., Broutin, J., Fluteau, F., 2007. El limite Permico-Triasico y la
4299 sedimentacion durante el Triasico inferior en las cuencas de Europa occidental: una vision
4300 general. *J. Iber. Geol.* 221–237.
- 4301 Bourquin, S., Peron, S., Durand, M., 2006. Lower Triassic sequence stratigraphy of the western part of
4302 the Germanic Basin (west of Black Forest): Fluvial system evolution through time and space.
4303 *Sediment. Geol.* 186, 187–211.
- 4304 Boussau, B., Walton, Z., Delgado, J.A., Collantes, F., Beani, L., Stewart, I.J., Cameron, S.A., Whitfield,
4305 J.B., Johnston, J.S., Holland, P.W.H., Bachtrog, D., Kathirithamby, J., Huelsenbeck, J.P., 2014.
4306 Strepsiptera, Phylogenomics and the Long Branch Attraction Problem. *PLoS ONE* 9, e107709.
- 4307 Boyko, C.B., Bruce, N.L., Merrin, K.L., Ota, Y., Poore, G.C.B., Taiti, S., Schotte, M., Wilson, G.D.F.,
4308 2008. World marine, freshwater and terrestrial isopod crustaceans database.
4309 <http://www.marinespecies.org/isopoda> (accessed 23.03.16).
- 4310 Bracken, H.D., Toon, A., Felder, D.L., Martin, J.W., Finley, M., Rasmussen, J., Palero, F., Crandall,
4311 K.A., 2009. The decapod tree of life: compiling the data and moving toward a consensus of
4312 decapod evolution. *Arthropod Syst. Phylogeny* 67, 99–116.
- 4313 Bracken-Grissom, H.D., Ah Yong, S.T., Wilkinson, R.D., Feldmann, R.M., Schweitzer, C.E., Breinholt,
4314 J.W., Bendall, M., Palero, F., Chan, T.-Y., Felder, D.L., Robles, R., Chu, K.-H., Tsang, L.-M.,
4315 Kim, D., Martin, J.W., Crandall, K.A., 2014. The Emergence of Lobsters: Phylogenetic
4316 Relationships, Morphological Evolution and Divergence Time Comparisons of an Ancient
4317 Group (Decapoda: Achelata, Astacidea, Glypheidea, Polychelida). *Syst. Biol.* 63, 457–479.
- 4318 Bracken-Grissom, H.D., Cannon, M.E., Cabezas, P., Feldmann, R.M., Schweitzer, C.E., Ah Yong, S.T.,
4319 Felder, D.L., Lemaitre, R., Crandall, K.A., 2013. A comprehensive and integrative
4320 reconstruction of evolutionary history for Anomura (Crustacea: Decapoda). *BMC Evol. Biol.* 13,
4321 128.

- 4322 Bradler, S., Buckley, T.R., 2011. Stick insect on unsafe ground: does a fossil from the early Eocene of
4323 France really link Mesozoic taxa with the extant crown group of Phasmatodea? Syst. Entomol.
4324 36, 218–222.
- 4325 Brauckmann, C., Brauckmann, B., Groning, E., 1994. The stratigraphical position of the oldest known
4326 Pterygota (Insecta. Carboniferous, Namurian). Ann. Société Géologique Belg. 117, 47–56.
- 4327 Brauckmann, C., Koch, L., 1983. *Prothelyphonus naufragus* n. sp., a new whip scorpion (Arachnida:
4328 Thelyphonida: Thelyphonidae) from the Namurian (lower Upper Carboniferous) of West
4329 Germany. Entomol. Gen. 9, 63–73.
- 4330 Brauckmann, C., Schneider, J., 1996. Ein unter-karbonisches Insekt aus dem Raum
4331 Bitterfeld/Delitzsch (Pterygota, Arnsbergium, Deutschland). Neues Jahrb. Geol. Palaontologie-
4332 Monatshefte 17–30.
- 4333 Brewer, M.S., Swafford, L., Spruill, C.L., Bond, J.E., 2013. Arthropod phylogenetics in light of three
4334 novel millipede (Myriapoda: Diplopoda) mitochondrial genomes with comments on the
4335 appropriateness of mitochondrial genome sequence data for inferring deep level relationships.
4336 PLoS ONE 8, e68005.
- 4337 Briggs, D.E.G., Collins, D., 1988. A Middle Cambrian chelicerate from Mount Stephen, British
4338 Columbia. Palaeontology 31, 779–798.
- 4339 Briggs, D.E.G., Liu, H.P., McKay, R.M., Witzke, B.J., 2015. Bivalved arthropods from the Middle
4340 Ordovician Winneshiek Lagerstätte, Iowa, USA. J. Paleontol. 89, 991–1006.
- 4341 Briggs, D.E.G., Siveter, D.J., Siveter, D.J., Sutton, M.D., Garwood, R.J., Legg, D., 2012. Silurian
4342 horseshoe crab illuminates the evolution of arthropod limbs. Proc. Natl. Acad. Sci. 109, 15702–
4343 15705.
- 4344 Briggs, D.E.G., Sutton, M.D., Siveter, D.J., Siveter, D.J., 2004. A new phyllocarid (Crustacea:
4345 Malacostraca) from the Silurian Fossil-Lagerstätte of Herefordshire, UK. Proc. R. Soc. B Biol.
4346 Sci. 271, 131–138.

- 4347 Briggs, D.E., Sutton, M.D., Siveter, D.J., Siveter, D.J., 2005. Metamorphosis in a Silurian barnacle.
4348 Proc. R. Soc. B Biol. Sci. 272, 2365–2369.
- 4349 Brongniart, C., 1883. Recherches pour servir à l'histoire des insectes fossiles des temps primaires
4350 précédées d'une étude sur la nervation des ailes des insectes. Bull. Société d'Industrie Min.
4351 Saint-Etienne, 7, 1–491.
- 4352 Brongniart, C., 1885. Les Insectes fossiles des terrains primaires. Coup d'oeil rapide sur la faune
4353 entomologique des terrains paléozoïques. Bull. Société Amis Sci. Nat. Rouen 1885, 50–68.
- 4354 Brydone, R.M., 1912. The stratigraphy of the chalk of Hampshire, with map and palaeontological
4355 notes. Dulau, London.
- 4356 Buckeridge, J.S., 1983. Fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia. N.Z.
4357 Geol. Surv. Paleontol. Bull. 50, 1–151.
- 4358 Buckeridge, J.S., 1979. The fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia.
4359 (PhD). University of Auckland, Auckland.
- 4360 Buckeridge, J.S., Newman, W.A., 2006. A revision of the Iblidae and the stalked barnacles (Crustacea:
4361 Cirripedia: Thoracica), including new ordinal, familial and generic taxa, and two new species
4362 from New Zealand and Tasmanian waters. Zootaxa 1136, 1–38.
- 4363 Buckman, R.S., Mound, L.A., Whiting, M.F., 2013. Phylogeny of thrips (Insecta: Thysanoptera) based
4364 on five molecular loci. Syst. Entomol. 38, 123–133.
- 4365 Budd, G.E., Jensen, S., 2000. A critical reappraisal of the fossil record of the bilaterian phyla. Biol. Rev.
4366 75, 253–295.
- 4367 Bull, E.E., Loydell, D.K., 1995. Uppermost Telychian graptolites from the North Esk Inlier, Pentland
4368 Hills, near Edinburgh. Scottish Journal of Geology 31, 163–170.
- 4369 Bybee, S.M., Bracken-Grissom, H., Haynes, B.D., Hermansen, R.A., Byers, R.L., Clement, M.J., Udall,
4370 J.A., Wilcox, E.R., Crandall, K.A., 2011. Targeted Amplicon Sequencing (TAS): A Scalable
4371 Next-Gen Approach to Multilocus, Multitaxa Phylogenetics. Genome Biol. Evol. 3, 1312–1323.

- 4372 Bybee, S.M., Ogden, T.H., Branham, M.A., Whiting, M.F., 2008. Molecules, morphology and fossils: a
4373 comprehensive approach to odonate phylogeny and the evolution of the odonate wing.
4374 Cladistics 24, 477–514.
- 4375 Calvet, F., Tucker, M.E., 1995. Mud-mounds with reefal caps in the upper Muschelkalk (Triassic),
4376 eastern Spain, in: Monty, C.L.V., Bosence, D.W.J., Bridges, P.H., Pratt, B.R. (Eds.), Carbonate
4377 Mud-Mounds: Their Origin and Evolution, Int. Assoc. Sediment. Spec. Publ. Blackwell Science,
4378 pp. 311–333.
- 4379 Camacho, A.I., Rey, I., Dorda, B.A., Machordom, A., Valdecasas, A.G., 2002. A note on the systematic
4380 position of the Bathynellacea (Crustacea, Malacostraca) using molecular evidence. Contrib.
4381 Zool. 71, 123–129.
- 4382 Campbell, L.I., Rota-Stabelli, O., Edgecombe, G.D., Marchioro, T., Longhorn, S.J., Telford, M.J.,
4383 Philippe, H., Rebecchi, L., Peterson, K.J., Pisani, D., 2011. MicroRNAs and phylogenomics
4384 resolve the relationships of Tardigrada and suggest that velvet worms are the sister group of
4385 Arthropoda. Proc. Natl. Acad. Sci. 108, 15920–15924.
- 4386 Campos, D.R.B., 1986. Primeiro registro fóssil de Scorpionoidea na chapada do Araripe (Cretáceo
4387 Inferior), Brasil. An. Acad. Bras. Ciênc. 58, 135–137.
- 4388 Cao, Z., Yu, Y., Wu, Y., Hao, P., Di, Z., He, Y., Chen, Z., Yang, W., Shen, Z., He, X., Sheng, J., Xu, X.,
4389 Pan, B., Feng, J., Yang, X., Hong, W., Zhao, W., Li, Z., Huang, K., Li, T., Kong, Y., Liu, H.,
4390 Jiang, D., Zhang, B., Hu, J., Hu, Y., Wang, B., Dai, J., Yuan, B., Feng, Y., Huang, W., Xing, X.,
4391 Zhao, G., Li, X., Li, Y., Li, W., 2013. The genome of *Mesobuthus martensii* reveals a unique
4392 adaptation model of arthropods. Nat. Commun. 4, 2602.
- 4393 Carapelli, A., Liò, P., Nardi, F., van der Wath, E., Frati, F., 2007. Phylogenetic analysis of mitochondrial
4394 protein coding genes confirms the reciprocal paraphyly of Hexapoda and Crustacea. BMC
4395 Evol. Biol. 7, S8.
- 4396 Carmean, D., Crespi, B.J., 1995. Do long branches attract flies? Nature 373, 666.

- 4397 Caron, J.-B., Gaines, R.R., Mángano, M.G., Streng, M., Daley, A.C., 2010. A new Burgess Shale–type
4398 assemblage from the “thin” Stephen Formation of the southern Canadian Rockies. *Geology* 38,
4399 811–814.
- 4400 Carpenter, F.M., 1938. Two Carboniferous insects from the vicinity of Mazon Creek, Illinois. *Am. J. Sci.*
4401 216, 445–452.
- 4402 Carpenter, F.M., 1960. A Triassic odonate from Argentina. *Psyche* 67, 71–75.
- 4403 Carpenter, F.M., 1966. The Lower Permian insects of Kansas. Part II. The orders Protorthoptera and
4404 Orthoptera. *Psyche* 73, 46–88.
- 4405 Carpenter, F.M., 1976. Lower Permian insects of Kansas. 12. Protorthoptera (continued), Neuroptera,
4406 additional Palaeodictyoptera, and families of uncertain position. *Psyche* 83, 336–376.
- 4407 Carvalho, M. d. G.P., Lourenço, W.R., 2001. A new family of fossil scorpions from the Early Cretaceous
4408 of Brazil. *Comptes Rendus Académie Sci.-Ser. IIA-Earth Planet. Sci.* 332, 711–716.
- 4409 Castellani, C., Maas, A., Waloszek, D., Haug, J.T., 2011. New pentastomids from the Late Cambrian of
4410 Sweden - deeper insight of the ontogeny of fossil tongue worms. *Palaeontogr. Abt. A* 95–145.
- 4411 Catuneanu, O., Wopfner, H., Eriksson, P.G., Cairncross, B., Rubidge, B.S., Smith, R.M.H., Hancox,
4412 P.J., 2005. The Karoo basins of south-central Africa. *J. Afr. Earth Sci.* 43, 211–253.
- 4413 Chang, S., Zhang, H., Renne, P.R., Fang, Y., 2009a. High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ age for the Jehol Biota.
4414 *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 280, 94–104.
- 4415 Chang, S., Zhang, H., Renne, P.R., Fang, Y., 2009b. High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ age constraints on the
4416 basal Lanqi Formation and its implications for the origin of angiosperm plants. *Earth Planet.*
4417 *Sci. Lett.* 279, 212–221.
- 4418 Chen, P.J., Hudson, J.D., 1991. The conchostracan fauna of the Great Estuarine Group, Middle
4419 Jurassic, Scotland. *Palaeontology* 34, 515–545.
- 4420 Chen, P., Li, G., Batten, D.J., 2007. Evolution, migration and radiation of late Mesozoic
4421 conchostracans in East Asia. *Geol. J.* 42, 391–413.

- 4422 Chen, W.-J., Koch, M., Mallatt, J.M., Luan, Y.-X., 2014. Comparative Analysis of Mitochondrial
4423 Genomes in Diplura (Hexapoda, Arthropoda): Taxon Sampling Is Crucial for Phylogenetic
4424 Inferences. *Genome Biol. Evol.* 6, 105–120.
- 4425 Chernyshev, B.I., 1930. Cirripeden aus den Basin des Donetz und von Kusnetsk. *Zool. Anz.* 92, 26–
4426 28.
- 4427 Chilton, C., 1929. Note on a fossil shrimp from Hawkesbury sandstones. *J. R. Soc. New South Wales*
4428 62, 366–368.
- 4429 Collette, J.H., Hagadorn, J.W., 2010a. Three-dimensionally preserved arthropods from Cambrian
4430 Lagerstätten of Quebec and Wisconsin. *J. Paleontol.* 84, 646–667.
- 4431 Collette, J.H., Hagadorn, J.W., 2010b. Early evolution of phyllocarid arthropods: phylogeny and
4432 systematics of Cambrian-Devonian archaeostracans. *J. Paleontol.* 84, 795–820.
- 4433 Common, I.F.B., 1973. A new family of Dacnonypha (Lepidoptera) based on three new species from
4434 southern Australia, with notes on the Agathiphaeidae. *Aust. J. Entomol.* 12, 11–73.
- 4435 Condon, D.J., Zhu, M., Bowring, S., Wang, W., Yang, A., Jin, Y., 2005. U-Pb Ages from the
4436 Neoproterozoic Doushantuo Formation, China. *Science* 308, 92–95.
- 4437 Cressey, R., Boxshall, G., 1989. *Kabatarina pattersoni*, a fossil parasitic copepod (Dichelesthidae)
4438 from a Lower Cretaceous fish. *Micropaleontology* 35, 150–167.
- 4439 Crimes, T.P., 1987. Trace fossils and correlation of late Precambrian and early Cambrian strata. *Geol.*
4440 *Mag.* 124, 97–119.
- 4441 Crimes, T.P., Jiang, Z., 1986. Trace fossils from the Precambrian–Cambrian boundary candidate at
4442 Meishucun, Jinning, Yunnan, China. *Geol. Mag.* 123, 641–649.
- 4443 Crowson, R.A., 1985. Comments on Insecta of the Rhynie Chert. *Entomol. Gen.* 97–98.
- 4444 Cryan, J.R., Urban, J.M., 2012. Higher-level phylogeny of the insect order Hemiptera: is
4445 Auchenorrhyncha really paraphyletic? *Syst. Entomol.* 37, 7–21.

- 4446 Cui, Y., Xie, Q., Hua, J., Dang, K., Zhou, J., Liu, X., Wang, G., Yu, X., Bu, W., 2013. Phylogenomics of
4447 Hemiptera (Insecta: Paraneoptera) based on mitochondrial genomes. *Syst. Entomol.* 38, 233–
4448 245.
- 4449 Dahms, H.-U., 2004. Postembryonic apomorphies proving the monophyletic status of the Copepoda.
4450 *Zool. Stud.* 43, 446–453.
- 4451 Darwin, C., 1851. A Monograph on the Fossil Lepadidae, Or, Pedunculated Cirripedes of Great Britain.
4452 Palaeontographical Society.
- 4453 Davis, R.B., Nicholson, D.B., Saunders, E.L., Mayhew, P.J., 2011. Fossil gaps inferred from
4454 phylogenies alter the apparent nature of diversification in dragonflies and their relatives. *BMC*
4455 *Evol. Biol.* 11, 252.
- 4456 Davydov, V.I., Korn, D., Schmitz, M.D., Gradstein, F.M., Hammer, O., 2012. The Carboniferous Period,
4457 in: *The Geologic Time Scale*. Elsevier, pp. 603–651.
- 4458 De Grave, S., Chan, T.-Y., Chu, K.H., Yang, C.-H., Landeira, J.M., 2015. Phylogenetics reveals the
4459 crustacean order Amphionidacea to be larval shrimps (Decapoda: Caridea). *Sci. Rep.* 5,
4460 17464.
- 4461 Delclòs, X., Peñalver, E., Arillo, A., Engel, M.S., Nel, A., Azar, D., Ross, A., 2016. New mantises
4462 (Insecta: Mantodea) in Cretaceous ambers from Lebanon, Spain, and Myanmar. *Cretac. Res.*
4463 60, 91–108.
- 4464 Dell'Ampio, E., Meusemann, K., Szucsich, N.U., Peters, R.S., Meyer, B., Borner, J., Petersen, M.,
4465 Aberer, A.J., Stamatakis, A., Walz, M.G., Minh, B.Q., von Haeseler, A., Ebersberger, I., Pass,
4466 G., Misof, B., 2014. Decisive Data Sets in Phylogenomics: Lessons from Studies on the
4467 Phylogenetic Relationships of Primarily Wingless Insects. *Mol. Biol. Evol.* 31, 239–249.
- 4468 Demoulin, G., 1970. Remarques critiques sur des larves “éphéméromorphes” du Permien. *Bull. Inst.*
4469 *R. Sci. Nat. Belg.* 46, 1–10.
- 4470 Dettmann, M.E., Thomson, M.R.A., 1987. Cretaceous palynomorphs from the James Ross Island
4471 area, Antarctica. A pilot study. *Bull.-Br. Antarct. Surv.* 13–59.

- 4472 D'Haese, C.A., 2003. Morphological appraisal of Collembola phylogeny with special emphasis on
4473 Poduromorpha and a test of the aquatic origin hypothesis. *Zool. Scr.* 32, 563–586.
- 4474 Diedrich, C.G., 2011. Middle Triassic horseshoe crab reproduction areas on intertidal flats of Europe
4475 with evidence of predation by archosaurs. *Biol. J. Linn. Soc.* 103, 76–105.
- 4476 Dittmar, K., Zhu, Q., Hastriter, M.W., Whiting, M.F., 2016. On the probability of dinosaur fleas. *BMC*
4477 *Evol. Biol.* 16.
- 4478 Dixon, C.J., Ah Yong, S.T., Schram, F.R., 2003. A new hypothesis of decapod phylogeny. *Crustaceana*
4479 76, 935–975.
- 4480 Djernæs, M., Klass, K.-D., Eggleton, P., 2015. Identifying possible sister groups of Cryptocercidae +
4481 Isoptera: A combined molecular and morphological phylogeny of Dictyoptera. *Mol. Phylogenet.*
4482 *Evol.* 84, 284–303.
- 4483 Djernæs, M., Klass, K.-D., Picker, M.D., Damgaard, J., 2012. Phylogeny of cockroaches (Insecta,
4484 Dictyoptera, Blattodea), with placement of aberrant taxa and exploration of out-group sampling.
4485 *Syst. Entomol.* 37, 65–83.
- 4486 Dobruskina, I.A., 1995. Keuper (Triassic) Flora from Middle Asia (Madygen, Southern Fergana):
4487 Bulletin 5. New Mexico Museum of Natural History and Science, Albuquerque.
- 4488 Dohle, W., 2001. Are the insects terrestrial crustaceans? A discussion of some new facts and
4489 arguments and the proposal of the proper name “Tetraconata” for the monophyletic unit
4490 Crustacea + Hexapoda, in: *Annales de La Société Entomologique de France*. Presented at the
4491 Symposium on the Origin of the Hexapoda, Société entomologique de France, pp. 85–103.
- 4492 Dornburg, A., Beaulieu, J.M., Oliver, J.C., Near, T.J., 2011. Integrating Fossil Preservation Biases in
4493 the Selection of Calibrations for Molecular Divergence Time Estimation. *Syst. Biol.* 60, 519-
4494 527.
- 4495 Doyle, J.A., Endress, P.K., 2014. Integrating Early Cretaceous Fossils into the Phylogeny of Living
4496 Angiosperms: ANITA Lines and Relatives of Chloranthaceae. *Int. J. Plant Sci.* 175, 555–600.
- 4497 Drumm, D.T., 2010. Phylogenetic Relationships of Tanaidacea (Eumalacostraca: Peracarida) Inferred

4498 from Three Molecular Loci. J. Crustac. Biol. 30, 692–698.

4499 Drygant, D., Szaniawski, H., 2012. Lochkovian conodonts from Podolia, Ukraine, and their
4500 stratigraphic significance. Acta Palaeontol. Pol. 57, 833-861.

4501 Dubinin, V.B., 1962. Class Acaromorpha: mites or gnathosomic chelicerate arthropods. Fundam.
4502 Palaeontol. 447–473.

4503 Dunlop, J.A., 2010. Geological history and phylogeny of Chelicerata. Arthropod Struct. Dev. 39, 124–
4504 142.

4505 Dunlop, J.A., Anderson, L.I., Braddy, S.J., 2004. A redescription of *Chasmataspis laurencii* Caster and
4506 Brooks, 1956 (Chelicerata: Chasmataspidida) from the Middle Ordovician of Tennessee, USA,
4507 with remarks on chasmataspid phylogeny. Trans. R. Soc. Edinb. Earth Sci. 94, 207-225.

4508 Dunlop, J.A., Anderson, L.I., Kerp, H., Hass, H., 2003. A harvestman (Arachnida: Opiliones) from the
4509 Early Devonian Rhynie cherts, Aberdeenshire, Scotland. Trans. R. Soc. Edinb. Earth Sci. 94,
4510 341–354.

4511 Dunlop, J.A., Selden, P.A., 2009. Calibrating the chelicerate clock: a paleontological reply to
4512 Jeyaprakash and Hoy. Exp. Appl. Acarol. 48, 183–197.

4513 Dunlop, J.A., Zhou, G.R.S., Braddy, S.J., 2007. The affinities of the Carboniferous whip spider
4514 *Graeophonus anglicus* Pocock, 1911 (Arachnida: Amblypygi). Earth Environ. Sci. Trans. R.
4515 Soc. Edinb. 98, 165–178.

4516 Edgecombe, G.D., 2004. Morphological data, extant Myriapoda, and the myriapod stem-group.
4517 Contrib. Zool. 73, 267–252.

4518 Edgecombe, G.D., 2010. Palaeomorphology: fossils and the inference of cladistic relationships. Acta
4519 Zool. 91, 72–80.

4520 Edgecombe, G.D., 2011. Chilopoda—the fossil history, in: Treatise on Zoology-Anatomy, Taxonomy,
4521 Biology. The Myriapoda. pp. 355–361.

- 4522 Edgecombe, G.D., Giribet, G., 2004. Adding mitochondrial sequence data (16S rRNA and cytochrome
4523 c oxidase subunit I) to the phylogeny of centipedes (Myriapoda: Chilopoda): an analysis of
4524 morphology and four molecular loci. *J. Zool. Syst. Evol. Res.* 42, 89–134.
- 4525 Eklund, H., Doyle, J.A., Herendeen, P.S., 2004. Morphological phylogenetic analysis of living and
4526 fossil Chloranthaceae. *Int. J. Plant Sci.* 165, 107–151.
- 4527 Engel, M.S., 2005. A new sawfly from the Triassic of Queensland (Hymenoptera: Xyelidae). *Mem.*
4528 *Queensl. Mus.* 51.2, 558.
- 4529 Engel, M.S., Barden, P., Riccio, M.L., Grimaldi, D.A., 2016a. Morphologically Specialized Termite
4530 Castes and Advanced Sociality in the Early Cretaceous. *Curr. Biol.* 26, 522-530.
- 4531 Engel, M.S., Breitkreuz, L.C.V., Cai, C., Alvarado, M., Azar, D., Huang, D., 2016b. The first Mesozoic
4532 microwhip scorpion (Palpigradi): a new genus and species in mid-Cretaceous amber from
4533 Myanmar. *Sci. Nat.* 103, 1-7.
- 4534 Engel, M.S., Grimaldi, D.A., 2004. New light shed on the oldest insect. *Nature* 427, 624–627.
- 4535 Engel, M.S., Grimaldi, D., Krishna, K., 2007. Primitive termites from the Early Cretaceous of Asia
4536 (Isoptera). *Stuttg. Beitr. Naturk. Ser. B* 371.
- 4537 Engel, M.S., Grimaldi, D.A., Krishna, K., 2009. Termites (Isoptera): their phylogeny, classification, and
4538 rise to ecological dominance. *Am. Mus. Novit.* 3650, 1–27.
- 4539 Engel, M.S., Ortega-Blanco, J., Azar, D., 2011. The earliest earwigs in amber (Dermaptera): A new
4540 genus and species from the Early Cretaceous of Lebanon. *Insect Syst. Evol.* 42, 139-148.
- 4541 Engel, M.S., Wang, B., Alqarni, A.S. 2016c. A thorny, ‘anareolate’ stick-insect (Phasmatidae s.l.) in
4542 Upper Cretaceous amber from Myanmar, with remarks on diversification times among
4543 Phasmatodea. *Cretac. Res.* 63, 45-53.
- 4544 Enghoff, H., 1984. Phylogeny of millipedes—a cladistic analysis. *J. Zool. Syst. Evol. Res.* 22, 8–26.
- 4545 Enghoff, H., Short, M., Stoev, P., Wesener, T., 2015. Diplopoda—Taxonomic Overview, in: *Treatise on*
4546 *Zoology-Anatomy, Taxonomy, Biology. The Myriapoda.* p. 363.

- 4547 Farrell, Ú.C., Briggs, D.E.G., Gaines, R.R., 2011. Paleoecology of the Olenid Trilobite *Triarthrus*: New
4548 Evidence from Beecher's Trilobite Bed and Other Sites of Pyritization. *Palaios* 26, 730–742.
- 4549 Farrell, Ú.C., Martin, M.J., Hagadorn, J.W., Whiteley, T., Briggs, D.E., 2009. Beyond Beecher's
4550 Trilobite Bed: Widespread pyritization of soft tissues in the Late Ordovician Taconic foreland
4551 basin. *Geology* 37, 907–910.
- 4552 Fayers, S.R., Trewin, N.H., 2005. A hexapod from the early Devonian Windyfield chert, Rhynie,
4553 Scotland. *Palaeontology* 48, 1117–1130.
- 4554 Feldmann, R.M., Osgood Jr, R.G., Szmuc, E.J., Meinke, D.W., 1978. *Chagrinichnites brooksi*, a new
4555 trace fossil of arthropod origin. *J. Paleontol.* 287–294.
- 4556 Feldmann, R.M., Schweitzer, C.E, Hu, S., Huang, J., Zhou, C., Zhang, Q., Wen, W., Xie, T., Maguire,
4557 E., 2015. Spatial distribution of Crustacea and associated organisms in the Luoping Biota
4558 (Anisian, Middle Triassic), Yunnan Province, China: evidence of periodic mass kills. *J.*
4559 *Paleontol.* 89, 1022-1037.
- 4560 Fernández, R., Edgecombe, G.D., Giribet, G., 2016 (in press). Exploring phylogenetic relationships
4561 within Myriapoda and the effects of matrix composition and occupancy on phylogenomic
4562 reconstruction. *Syst. Biol.*
- 4563 Fernández, R., Giribet, G., 2015. Unnoticed in the tropics: phylogenomic resolution of the poorly
4564 known arachnid order Ricinulei (Arachnida). *R. Soc. Open Sci.* 2, 150065.
- 4565 Fernández, R., Hormiga, G., Giribet, G., 2014a. Phylogenomic Analysis of Spiders Reveals
4566 Nonmonophyly of Orb Weavers. *Curr. Biol.* 24, 1772–1777.
- 4567 Fernández, R., Laumer, C.E., Vahtera, V., Libro, S., Kaluziak, S., Sharma, P.P., Pérez-Porro, A.R.,
4568 Edgecombe, G.D., Giribet, G., 2014b. Evaluating Topological Conflict in Centipede Phylogeny
4569 Using Transcriptomic Data Sets. *Mol. Biol. Evol.* 31, 1500–1513.
- 4570 Filipiak, P., Zatoń, M., Szaniawski, H., Wrona, R., Racki, G., 2012. Palynology and Microfacies of
4571 Lower Devonian Mixed Carbonate-Siliciclastic Deposits in Podolia, Ukraine. *Acta Palaeontol.*
4572 *Pol.* 57, 863–877.

- 4573 Fletcher, T.P., Collins, D.H., 1998. The middle Cambrian Burgess Shale and its relationship to the
4574 Stephen Formation in the southern Canadian Rocky Mountains. *Can. J. Earth Sci.* 35, 413–
4575 436.
- 4576 Fletcher, T.P., Collins, D.H., 2003. The Burgess Shale and associated Cambrian formations west of the
4577 Fossil Gully Fault Zone on Mount Stephen, British Columbia. *Can. J. Earth Sci.* 40, 1823–1838.
- 4578 Friedemann, K., Wipfler, B., Bradler, S., Beutel, R.G., 2012. On the head morphology of *Phyllium* and
4579 the phylogenetic relationships of Phasmatodea (Insecta). *Acta Zool.* 93, 184–199.
- 4580 Friis, E.M., Pedersen, K.R., Crane, P.R., 1999. Early angiosperm diversification: the diversity of pollen
4581 associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal.
4582 *Ann. Mo. Bot. Gard.* 259–296.
- 4583 Friis, E.M., Pedersen, K.R., Crane, P.R., 2005. When Earth started blooming: insights from the fossil
4584 record. *Curr. Opin. Plant Biol.* 8, 5–12.
- 4585 Gaju-Ricart, M., Baltanás, R.M., Bach de Roca, C., 2015. Forward without wings: Current progress
4586 and future perspectives in the study of Microcoryphia and Zygentoma. *Soil Org.* 87, 183–195.
- 4587 Gale, A.S., 1996. Turonian correlation and sequence stratigraphy of the Chalk in southern England.
4588 *Geol. Soc. Lond. Spec. Publ.* 103, 177–195.
- 4589 Gale, A.S., 2015. Origin and phylogeny of verruciform barnacles (Crustacea, Cirripedia, Thoracica).
4590 *J. Syst. Palaeontol.* 13, 753–789.
- 4591 Gale, A.S., Sørensen, A.M., 2015. Origin of the balanomorph barnacles (Crustacea, Cirripedia,
4592 Thoracica): new evidence from the Late Cretaceous (Campanian) of Sweden. *J. Syst.*
4593 *Palaeontol.* 13, 791–824.
- 4594 Gallego, O.F., 2010. A new crustacean clam shrimp (Spinicaudata: Eosestheriidae) from the Upper
4595 Triassic of Argentina and its importance for “conchostracan” taxonomy. *Alcheringa* 34, 179–
4596 195.

- 4597 Gall, J.-C., 1985. Fluvial depositional environment evolving into deltaic setting with marine influences
4598 in the Buntsandstein of Northern Vosges (France), in: Aspects of Fluvial Sedimentation in the
4599 Lower Triassic Buntsandstein of Europe. Springer, pp. 449–477.
- 4600 Gall, J.-C., Grauvogel-Stamm, L., 1993. Buntsandstein (lower Triassic) of Eastern France. Nonmarine
4601 Triassic Bull. 3 3, 141.
- 4602 Gao, K., Ren, D., 2006. Radiometric Dating of Ignimbrite from Inner Mongolia Provides no Indication
4603 of a Post-Middle Jurassic Age for the Daohugou Beds. *Acta Geol. Sin.* 80, 42–45.
- 4604 Gao, T., Shih, C., Rasnitsyn, A.P., Xu, X., Wang, S., Ren, D., 2014. The first flea with fully distended
4605 abdomen from the Early Cretaceous of China. *BMC Evol. Biol.* 14, 168.
- 4606 Gao, T., Shih, C., Xu, X., Wang, S., Ren, D., 2012. Mid-Mesozoic Flea-like Ectoparasites of Feathered
4607 or Haired Vertebrates. *Curr. Biol.* 22, 732–735.
- 4608 Gao, Y., Bu, Y., Luan, Y.-X., 2008. Phylogenetic Relationships of Basal Hexapods Reconstructed from
4609 Nearly Complete 18S and 28S rRNA Gene Sequences. *Zoolog. Sci.* 25, 1139–1145.
- 4610 Garrison, N.L., Rodriguez, J., Agnarsson, I., Coddington, J.A., Griswold, C.E., Hamilton, C.A., Hedin,
4611 M., Kocot, K.M., Ledford, J.M., Bond, J.E., 2016. Spider phylogenomics: untangling the Spider
4612 Tree of Life. *PeerJ* 4, e1719.
- 4613 Garrouste, R., Clément, G., Nel, P., Engel, M.S., Grandcolas, P., D’Haese, C., Lagebro, L., Denayer,
4614 J., Gueriau, P., Lafaité, P., Olive, S., Prestianni, C., Nel, A., 2012. A complete insect from the
4615 Late Devonian period. *Nature* 488, 82–85.
- 4616 Garwood, R.J., Dunlop, J., 2014. Three-dimensional reconstruction and the phylogeny of extinct
4617 chelicerate orders. *PeerJ* 2, e641.
- 4618 Garwood, R.J., Dunlop, J.A., Giribet, G., Sutton, M.D., 2011. Anatomically modern Carboniferous
4619 harvestmen demonstrate early cladogenesis and stasis in Opiliones. *Nat. Commun.* 2, 444.
- 4620 Garwood, R.J., Sharma, P.P., Dunlop, J.A., Giribet, G., 2014. A Paleozoic Stem Group to Mite
4621 Harvestmen Revealed through Integration of Phylogenetics and Development. *Curr. Biol.* 24,
4622 1017–1023.

- 4623 Garwood, R., Sutton, M., 2010. X-ray micro-tomography of Carboniferous stem-Dictyoptera: new
4624 insights into early insects. *Biol. Lett.* 6, 699–702.
- 4625 Gehling, J.G., Jago, J.B., Paterson, J.R., García-Bellido, D.C., Edgecombe, G.D., 2011. The geological
4626 context of the lower Cambrian (Series 2) Emu Bay Shale Lagerstätte and adjacent
4627 stratigraphic units, Kangaroo Island, South Australia. *Aust. J. Earth Sci.* 58, 243–257.
- 4628 Getty, P.R., Sproule, R., Wagner, D.L., Bush, A.M., 2013. Variation in Wingless Insect Trace Fossils:
4629 Insights from Neoichnology and the Pennsylvanian of Massachussetts. *Palaios* 28, 243–258.
- 4630 Gibbs, G., 2010. Micropterigidae (Lepidoptera) of the Southwestern Pacific: a revision with the
4631 establishment of five new genera from Australia, New Caledonia and New Zealand. *Zootaxa*
4632 2520, 1–48.
- 4633 Giles, P.S., Naylor, R.D., Ténière, P.J., 2002. A synthesis of Carboniferous stratigraphy—Cape Breton
4634 Island, Nova Scotia, with new data from southwestern Cape Breton Island. *Atlantic Geology*
4635 38, 83.
- 4636 Giribet, G., Edgecombe, G.D., 2006. Conflict between datasets and phylogeny of centipedes: an
4637 analysis based on seven genes and morphology. *Proc. R. Soc. B Biol. Sci.* 273, 531–538.
- 4638 Giribet, G., Edgecombe, G.D., 2013. Stable phylogenetic patterns in scutigeromorph centipedes
4639 (Myriapoda : Chilopoda : Scutigeromorpha): dating the diversification of an ancient lineage of
4640 terrestrial arthropods. *Invertebr. Syst.* 27, 485–501.
- 4641 Giribet, G., Edgecombe, G.D., Wheeler, W.C., 2001. Arthropod phylogeny based on eight molecular
4642 loci and morphology. *Nature* 413, 157–161.
- 4643 Giribet, G., Edgecombe, G.D., Wheeler, W.C., Babbitt, C., 2002. Phylogeny and Systematic Position of
4644 Opiliones: A Combined Analysis of Chelicerate Relationships Using Morphological and
4645 Molecular Data. *Cladistics* 18, 5–70.

- 4646 Giribet, G., McIntyre, E., Christian, E., Espinasa, L., Ferreira, R.L., Francke, Ó.F., Harvey, M.S., Isaia,
4647 M., Kováč, Ľ., McCutchen, L., Souza, M.F., Zagamajster, M., 2014. The first phylogenetic
4648 analysis of Palpigradi (Arachnida)—the most enigmatic arthropod order. *Invertebr. Syst.* 28,
4649 350–360.
- 4650 Giribet, G., Ribera, C., 2000. A Review of Arthropod Phylogeny: New Data Based on Ribosomal DNA
4651 Sequences and Direct Character Optimization. *Cladistics* 16, 204–231.
- 4652 Glenner, H., Grygier, M.J., Høeg, J.T., Jensen, P.G., Schram, F.R., 1995. Cladistic analysis of the
4653 Cirripedia Thoracica. *Zool. J. Linn. Soc.* 114, 365–404.
- 4654 Goldring, R., Jensen, S., 1996. Trace fossils and biofabrics at the Precambrian–Cambrian boundary
4655 interval in western Mongolia. *Geol. Mag.* 133, 403–415.
- 4656 Gomez, B., Martin-Closas, C., Barale, G., Sole de porta, N., Thevenard, F., Guignard, G., 2002.
4657 *Frenelopsis* (Coniferales: Cheirolepidiaceae) and related male organ genera from the Lower
4658 Cretaceous of Spain. *Palaeontology* 45, 997–1036.
- 4659 Gorochoy, A.V., 2013. No evidence for Paleozoic origin of mantises (Dictyoptera: Mantodea).
4660 *Zoosystematica Ross.* 22, 6–14.
- 4661 Gratshev, V.G., Zherikhin, V.V., 2000. New Early Cretaceous weevil taxa from Spain (Coleoptera,
4662 Curculionoidea). *Acta Geológica Hispánica* 35, 37–46.
- 4663 Greenslade, P.J.M., 1988. Reply to R. A. Crowson's "Comments on Insecta of the Rhynie Chert."
4664 *Entomol. Gen.* 13, 115–117.
- 4665 Greenslade, P., Whalley, P.E.S., 1986. The systematic position of *Rhyniella praecursor* Hirst & Maulik
4666 (Collembola), the earliest known hexapod, in: *Second International Seminar on Apterygota*.
4667 University of Siena., pp. 319–323.
- 4668 Grimaldi, D., 2003. A Revision of Cretaceous Mantises and Their Relationships, Including New Taxa
4669 (Insecta: Dictyoptera: Mantodea). *Am. Mus. Novit.* 3412, 1–47.
- 4670 Grimaldi, D., Engel, M.S., 2005. *Evolution of the Insects*. Cambridge University Press, Cambridge.
- 4671 Grimaldi, D., Engel, M.S., 2006. Fossil Liposcelididae and the lice ages (Insecta: Psocodea). *Proc. R.*

- 4672 Soc. B Biol. Sci. 273, 625–633.
- 4673 Grimaldi, D.A., Engel, M.S., 2013. The Relict Scorpionfly Family Meropeidae (Mecoptera) in
4674 Cretaceous Amber. J. Kans. Entomol. Soc. 86, 253–263.
- 4675 Grimaldi, D., Shmakov, A., Fraser, N., 2004. Mesozoic Thrips and Early Evolution of the Order
4676 Thysanoptera (Insecta). J. Paleontol. 78, 941–952.
- 4677 Guan, Z., Prokop, J., Roques, P., Lapeyrie, J., Nel, A., 2016. Revision of the enigmatic insect family
4678 Anthracoptilidae enlightens the evolution of Palaeozoic stem-dictyopterans. Acta Palaeontol.
4679 Pol. 61, 71–87.
- 4680 Gueriau, P., Charbonnier, S., Clément, G., 2014. First decapod crustaceans in a Late Devonian
4681 continental ecosystem. Palaeontology 57, 1203–1213.
- 4682 Gueriau, P., Rabet, N., Clément, G., Lagebro, L., Vannier, J., Briggs, D.E.G., Charbonnier, S., Olive, S.,
4683 Béthoux, O., 2016. A 365-Million-Year-Old Freshwater Community Reveals Morphological and
4684 Ecological Stasis in Branchiopod Crustaceans. Curr. Biol. 26, 383–390.
- 4685 Guo, Y., Béthoux, O., Gu, J., Ren, D., 2013. Wing venation homologies in Pennsylvanian
4686 “cockroachoids” (Insecta) clarified thanks to a remarkable specimen from the Pennsylvanian of
4687 Ningxia (China). J. Syst. Palaeontol. 11, 41–46.
- 4688 Gutiérrez, P.R., Muzón, J., Limarino, C.O., 2000. The earliest late Carboniferous winged insect
4689 (Insecta, Protodonata) from Argentina: geographical and stratigraphical location. Ameghiniana
4690 37, 375–378.
- 4691 Handlirsch, A., 1906. Die Fossilen Insekten und die Phylogenie der Rezenten Formen, parts I–IV. Ein
4692 Handbuch für Palaontologen und Zoologen. Engelmann, Leipzig.
- 4693 Handlirsch, A., 1911. New Paleozoic insects from the vicinity of Mazon Creek, Illinois. Am. J. Sci. 297–
4694 326.
- 4695 Haring, E., Aspöck, U., 2004. Phylogeny of the Neuropterida: a first molecular approach. Syst.
4696 Entomol. 29, 415–430.
- 4697 Harvey, M.S., 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata:

4698 Arachnida). Invertebr. Taxon. 6, 1373-1435.

4699 Harvey, T.H.P., 2008. Organic-walled microfossils from the Early Cambrian of Canada (PhD).
4700 University of Cambridge, Cambridge, UK.

4701 Harvey, T.H.P., Butterfield, N.J., 2008. Sophisticated particle-feeding in a large Early Cambrian
4702 crustacean. Nature 452, 868–871.

4703 Harvey, T.H.P., Pedder, B.E., 2013. Copepod Mandible Palynomorphs from the Nolichucky Shale
4704 (Cambrian, Tennessee): Implications for the Taphonomy and Recovery of Small Carbonaceous
4705 Fossils. Palaios 28, 278–284.

4706 Harvey, T.H.P., Vélez, M.I., Butterfield, N.J., 2012. Exceptionally preserved crustaceans from western
4707 Canada reveal a cryptic Cambrian radiation. Proc. Natl. Acad. Sci. 109, 1589–1594.

4708 Haug, C., Briggs, D.E., Mikulic, D.G., Kluessendorf, J., Haug, J.T., 2014. The implications of a Silurian
4709 and other thylacocephalan crustaceans for the functional morphology and systematic affinities
4710 of the group. BMC Evol. Biol. 14, 159.

4711 Haug, C., Haug, J.T., 2015. The ambiguous use of the prefix “Pan” in arthropod systematics. J. Zool.
4712 Sci. 3, 19–24.

4713 Haug, C., Kutschera, V., Ah Yong, S.T., Vega, F.J., Maas, A., Waloszek, D., Haug, J.T., 2013. Re-
4714 evaluation of the Mesozoic mantis shrimp *Ursquilla yehoachi* based on new material and the
4715 virtual peel technique. Palaeontol. Electron. 16, 1-14.

4716 Haug, J.T., Haug, C., Garwood, R.J., 2016. Evolution of insect wings and development - new details
4717 from Palaeozoic nymphs. Biol. Rev. 91, 53–69.

4718 Haug, J.T., Haug, C., Maas, A., Kutschera, V., Waloszek, D., 2010. Evolution of mantis shrimps
4719 (Stomatopoda, Malacostraca) in the light of new Mesozoic fossils. BMC Evol. Biol. 10, 290.

4720 Haug, J.T., Haug, C., Schweigert, G., Sombke, A., 2014. The evolution of centipede venom claws –
4721 Open questions and possible answers. Arthropod Struct. Dev. 43, 5–16.

4722 Haug, J.T., Labandeira, C.C., Santiago-Blay, J.A., Haug, C., Brown, S., 2015. Life habits, hox genes,
4723 and affinities of a 311 million-year-old holometabolan larva. BMC Evol. Biol. 15.

- 4724 He, H.Y., Wang, X.L., Zhou, Z.H., Zhu, R.X., Jin, F., Wang, F., Ding, X., Boven, A., 2004. $^{40}\text{Ar}/^{39}\text{Ar}$
 4725 dating of ignimbrite from Inner Mongolia, northeastern China, indicates a post-Middle Jurassic
 4726 age for the overlying Daohugou Bed. *Geophys. Res. Lett.* 31, L20609.
- 4727 Heath, T.A., Huelsenbeck, J.P., Stadler, T., 2014. The fossilized birth-death process for coherent
 4728 calibration of divergence-time estimates. *Proc. Natl. Acad. Sci.* 111, E2957–E2966.
- 4729 Hegna, T.A., 2012. Phylogeny and fossil record of branchiopod crustaceans: an integrative approach
 4730 (PhD). Yale University, New Haven.
- 4731 Hegna, T.A., Ren, D., 2010. Two new “notostracans”, *Chenops* gen. nov. and *Jeholops* gen. nov.
 4732 (Crustacea: Branchiopoda: ?Notostraca) from the Yixian Formation, Northeastern China. *Acta*
 4733 *Geol. Sin.* 84, 886–894.
- 4734 Helby, R., 1973. Review of Late Permian and Triassic palynology of New South Wales. *Geol. Soc.*
 4735 *Aust. Spec. Publ.* 4, 141–155.
- 4736 Henderickx, H., Boone, M., 2016. The basal pseudoscorpion family Feaellidae Ellingsen , 1906 walks
 4737 the Earth for 98.000.000 years: a new fossil genus has been found in Cretaceous Burmese
 4738 amber (Pseudoscorpiones: Feaellidae). *Entomo-Info* 27, 1-12.
- 4739 Henderson, C.M., Davydov and, V.I., Wardlaw, B.R., Gradstein, F.M., Hammer, O., 2012. The Permian
 4740 Period, in: *The Geologic Time Scale*. Elsevier, pp. 653–679.
- 4741 Hennig, W., 1981. *Insect Phylogeny*. John Wiley & Sons, Chichester, New York.
- 4742 Herbert, G., 1997. Sequence stratigraphic analysis of early and middle Triassic alluvial and estuarine
 4743 fades in the Sydney Basin, Australia. *Aust. J. Earth Sci.* 44, 125–143.
- 4744 Herrera, S., Watanabe, H., Shank, T.M., 2015. Evolutionary and biogeographical patterns of barnacles
 4745 from deep-sea hydrothermal vents. *Mol. Ecol.* 24, 673–689.
- 4746 Hirst, S., 1923. On some Arachnid remains from the Old Red Sandstone (Rhynie Chert Bed,
 4747 Aberdeenshire). *Ann. Mag. Nat. Hist.* 12, 455–474.
- 4748 Hirst, S., Maulik, S., 1926. On some arthropod remains from the Rhynie chert (Old Red Sandstone).
 4749 *Geol. Mag.* 63, 69–71.

- 4750 Ho, J., 1994. Copepod phylogeny: a reconsideration of Huys & Boxshall's "parsimony versus
4751 homology." *Hydrobiologia* 292, 31–39.
- 4752 Ho, S.Y.W., Phillips, M.J., 2009. Accounting for Calibration Uncertainty in Phylogenetic Estimation of
4753 Evolutionary Divergence Times. *Syst. Biol.* 58, 367–380.
- 4754 Høeg, J.T., Achituv, Y., Chan, B.K.K., Chan, K., Jensen, P.G., Pérez-Losada, M., 2009a. Cypris
4755 morphology in the barnacles *Ibla* and *Paralepas* (Crustacea: Cirripedia Thoracica) implications
4756 for cirripede evolution. *J. Morphol.* 270, 241–255.
- 4757 Høeg, J.T., Lagersson, N.C., Glenner, H., 2004. The complete cypris larva and its significance in
4758 thecostracan phylogeny, in: Scholtz, G. (Ed.), *Evolutionary and Developmental Biology of*
4759 *Crustacea*, Crustacean Issues. AA Balkema Publishers, Lisse, Netherlands, pp. 197-215.
- 4760 Høeg, J.T., Pérez-Losada, M., Glenner, H., Kolbasov, G.A., Crandall, K.A., 2009b. Evolution of
4761 morphology, ontogeny and life cycles within the Crustacea Thecostraca. *Arthropod Syst.*
4762 *Phylogeny* 67, 199–217.
- 4763 Hof, C.H., 1998. Late Cretaceous stomatopods (Crustacea, Malacostraca) from Israel and Jordan.
4764 *Contrib. Zool.* 67, 257–266.
- 4765 Horne, D.J., 1995. A revised ostracod biostratigraphy for the Purbeck-Wealden of England. *Cretac.*
4766 *Res.* 16, 639–663.
- 4767 Horne, D.J., Schon, I., Smith, R.J., Martens, K., 2005. What are Ostracoda? A cladistic analysis of the
4768 extant superfamilies of the subclasses Myodocopa and Podocopa (Crustacea: Ostracoda), in:
4769 Koenemann, S., Jenner, R.A. (Eds.), *Crustacea and Arthropod Relationships*, Crustacean
4770 *Issues*. CRC Press, Boca Raton, pp. 249–273.
- 4771 Hörnschemeyer, T., Haug, J.T., Béthoux, O., Beutel, R.G., Charbonnier, S., Hegna, T.A., Koch, M.,
4772 Rust, J., Wedmann, S., Bradler, S., Willmann, R., 2013. Is *Strudiella* a Devonian insect? *Nature*
4773 494, E3–E4.

- 4774 Hou, X., Williams, M., Siveter, D.J., Siveter, D.J., Aldridge, R.J., Sansom, R.S., 2010. Soft-part
4775 anatomy of the Early Cambrian bivalved arthropods *Kunyangella* and *Kunmingella*:
4776 significance for the phylogenetic relationships of Bradiriida. Proc. R. Soc. B Biol. Sci. 277,
4777 1835–1841.
- 4778 Hu, S., Zhang, Q., Chen, Z., Zhou, C., Lü, T., Xie, T., Wen, W., Huang, J., Benton, M.J., 2010. The
4779 Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-
4780 Permian mass extinction. Proc. R. Soc. B Biol. Sci. 278, 2274-2282.
- 4781 Huang, D., 2015. *Tarwinia australis* (Siphonaptera: Tarwiniidae) from the Lower Cretaceous
4782 Koonwarra fossil bed: Morphological revision and analysis of its evolutionary relationship.
4783 Cretac. Res. 52, 507–515.
- 4784 Huang, D., Nel, A., Shen, Y., Selden, P.A., Lin, Q., 2006. Discussions on the age of the Daohugou
4785 fauna--evidence from invertebrates. Prog. Nat. Sci. 16, 309–312.
- 4786 Huang, D., Nel, A., Zompro, O., Waller, A., 2008. Mantophasmatodea now in the Jurassic.
4787 Naturwissenschaften 95, 947–952.
- 4788 Huang, J.-D., Ren, D., Sinitshenkova, N.D., Shih, C.-K., 2008. New fossil mayflies (Insecta:
4789 Ephemeroptera) from the Middle Jurassic of Daohugou, Inner Mongolia, China. Insect Sci. 15,
4790 193–198.
- 4791 Huelsenbeck, J.P., 1997. Is the Felsenstein Zone a fly trap? Syst. Biol. 46, 69–74.
- 4792 Huelsenbeck, J.P., 1998. Systematic Bias in Phylogenetic Analysis: Is the Strepsiptera Problem
4793 Solved? Syst. Biol. 47, 519–537.
- 4794 Huys, R., Boxshall, G.A., 1991. Copepod Evolution. Ray Society, London.
- 4795 Huys, R., Llewellyn-Hughes, J., Conroy-Dalton, S., Olson, P.D., Spinks, J.N., Johnston, D.A., 2007.
4796 Extraordinary host switching in siphonostomatoid copepods and the demise of the
4797 Monstrilloida: Integrating molecular data, ontogeny and antennular morphology. Mol.
4798 Phylogenet. Evol. 43, 368–378.

- 4799 Ibarra-Cerdeña, C.N., Zaldívar-Riverón, A., Peterson, A.T., Sánchez-Cordero, V., Ramsey, J.M., 2014.
4800 Phylogeny and Niche Conservatism in North and Central American Triatomine Bugs
4801 (Hemiptera: Reduviidae: Triatominae), Vectors of Chagas' Disease. PLoS Negl. Trop. Dis. 8,
4802 e3266.
- 4803 Ignatov, M.S., 1992. *Bryokhutuliinia jurassica*, gen. et spec. nova, a remarkable fossil moss from
4804 Mongolia. J. Hattori Bot. Lab. p377–388.
- 4805 Ignatov, M.S., Karasev, E.V., Sinitsa, S.M., 2011. Upper Jurassic mosses from Baigul (Transbaikalia,
4806 South Siberia). Arctoa 20, 43–64.
- 4807 Inward, D., Beccaloni, G., Eggleton, P., 2007. Death of an order: a comprehensive molecular
4808 phylogenetic study confirms that termites are eusocial cockroaches. Biol. Lett. 3, 331–335.
- 4809 Isachsen, C.E., Bowring, S.A., Landing, E., Samson, S.D., 1994. New constraint on the division of
4810 Cambrian time. Geology 22, 496–498.
- 4811 Ishiwata, K., Sasaki, G., Ogawa, J., Miyata, T., Su, Z.-H., 2011. Phylogenetic relationships among
4812 insect orders based on three nuclear protein-coding gene sequences. Mol. Phylogenet. Evol.
4813 58, 169–180.
- 4814 Jaeckel, O., 1921. Einen neuen Phyllocariden aus dem Unterdevon der Bundenbacher Dachschiefer.
4815 Z. Dtsch. Geol. Ges. Monatsbericht 72, 290–292.
- 4816 Jago, J.B., García-Bellido, D.C., Gehling, J.G., 2016 (in press). An early Cambrian chelicerate from the
4817 Emu Bay Shale, South Australia. Palaeontology.
- 4818 Jago, J.B., Gehling, J.G., Paterson, J.R., Brock, G.A., Zang, W., 2012. Cambrian stratigraphy and
4819 biostratigraphy of the Flinders Range and the north coast of Kangaroo Island, South Australia.
4820 Episodes 35, 247–255.
- 4821 Jagt, J.W., Buckeridge, J.S., 2005. A case of homonymy in fossil verrucid barnacles: *Verruca withersi*
4822 (Crustacea, Thoracica). Scr. Geol. 130, 187–189.

- 4823 Jarvis, K.J., Haas, F., Whiting, M.F., 2005. Phylogeny of earwigs (Insecta: Dermaptera) based on
4824 molecular and morphological evidence: reconsidering the classification of Dermaptera. Syst.
4825 Entomol. 30, 442–453.
- 4826 Jarzembowski, E.A., 1981. An early Cretaceous termite from southern England (Isoptera:
4827 Hodotermitidae). Syst. Entomol. 6, 91–96.
- 4828 Jaume, D., Pinardo-Moya, E., Boxshall, G.A., 2013. A presumed spelaegriphacean crustacean from
4829 an upper Barremian wetland (Las Hoyas; Lower Cretaceous; Central Spain). Palaeontology 56,
4830 15-28.
- 4831 Jenkyns, H.C., Jones, C.E., Gröcke, D.R., Hesselbo, S.P., Parkinson, D.N., 2002. Chemostratigraphy
4832 of the Jurassic System: applications, limitations and implications for palaeoceanography. J.
4833 Geol. Soc. 159, 351–378.
- 4834 Jenner, R.A., Dhubhghaill, C., Ferla, M.P., Wills, M.A., 2009. Eumalacostracan phylogeny and total
4835 evidence: limitations of the usual suspects. BMC Evol. Biol. 9, 21.
- 4836 Jeram, A.J., Selden, P., Edwards, D., 1990. Land animals in the Silurian: arachnids and myriapods
4837 from Shropshire, England. Science 250, 658–661.
- 4838 Jirikowski, G.J., Richter, S., Wolff, C., 2013. Myogenesis of Malacostraca-the “egg-nauplius” concept
4839 revisited. Front. Zool. 10, 9994–10.
- 4840 Jones, W.T., Feldmann, R.M., Mikulic, D.G., 2015. Archaeostracan (Phyllocarida: Archaeostraca)
4841 antennulae and antennae: sexual dimorphism in early malacostracans and *Ceratiocaris* M'Coy,
4842 1849 as a possible stem eumalacostracan. J. Crustac. Biol. 35, 191–201.
- 4843 Jones, W.T., Feldmann, R.M., Schram, F.R., Schweitzer, C.E., Maguire, E.P., 2016. The proof is in the
4844 pouch: *Tealliocaris* is a peracarid. Palaeodiversity 9, 75-88.
- 4845 Judson, M.L., 2009. Cheliferoid pseudoscorpions (Arachnida, Chelonethi) from the Lower Cretaceous
4846 of France. Geodiversitas 31, 61–71.
- 4847 Judson, M.L., 2012. Reinterpretation of *Dracochela deprehendor* (Arachnida: Pseudoscorpiones) as a
4848 stem-group pseudoscorpion. Palaeontology 55, 261–283.

4849 Kakui, K., Katoh, T., Hiruta, S.F., Kobayashi, N., Kajihara, H., 2011. Molecular systematics of
 4850 Tanaidacea (Crustacea: Peracarida) based on 18S sequence data, with an amendment of
 4851 suborder/superfamily-level classification. *Zoolog. Sci.* 28, 749–757.

4852 Kaltenpoth, M., Roeser-Mueller, K., Koehler, S., Peterson, A., Nechitaylo, T.Y., Stubblefield, J.W.,
 4853 Herzner, G., Seger, J., Strohm, E., 2014. Partner choice and fidelity stabilize coevolution in a
 4854 Cretaceous-age defensive symbiosis. *Proc. Natl. Acad. Sci.* 111, 6359–6364.

4855 Kin, A., Blazejowski, B., 2014. The horseshoe crab of the genus *Limulus*: living fossil or stabilomorph?
 4856 PLoS ONE 9, e108036.

4857 Kirejtshuk, A.G., Poschmann, M., Prokop, J., Garrouste, R., Nel, A., 2014. Evolution of the elytral
 4858 venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera:
 4859 Tshekardocoleidae). *J. Syst. Palaeontol.* 12, 575–600.

4860 Kjellesvig-Waering, E.N., 1986. A restudy of the fossil Scorpionida of the world. *Palaeontographica*
 4861 Americana 55, 1–287.

4862 Kjer, K.M., Blahnik, R.J., Holzenthal, R.W., 2001. Phylogeny of Trichoptera (Caddisflies):
 4863 Characterization of Signal and Noise Within Multiple Datasets. *Syst. Biol.* 50, 781–816.

4864 Kjer, K.M., Blahnik, R.J., Holzenthal, R.W., 2002. Phylogeny of caddisflies (Insecta, Trichoptera). *Zool.*
 4865 Scr. 31, 83–91.

4866 Kjer, K.M., Carle, F.L., Litman, J., Ware, J.L., 2006. A molecular phylogeny of Hexapoda. *Arthropod*
 4867 Syst. Phylogeny 64, 35–44.

4868 Kjer, K.M., Ware, J.L., Rust, J., Wappler, T., Lanfear, R., Jermini, L.S., Zhou, X., Aspöck, H., Aspöck,
 4869 U., Beutel, R.G., Blanke, A., Donath, A., Flouri, T., Frandsen, P.B., Kapli, P., Kawahara, A.Y.,
 4870 Letsch, H., Mayer, C., McKenna, D.D., Meusemann, K., Niehuis, O., Peters, R.S., Wiegmann,
 4871 B.M., Yeates, D.K., von Reumont, B.M., Stamatakis, A., Misof, B., 2015. Response to
 4872 Comment on “Phylogenomics resolves the timing and pattern of insect evolution.” *Science* 349,
 4873 487–c.

- 4874 Klopstein, S., Vilhelmsen, L., Ronquist, F., 2015. A Nonstationary Markov Model Detects Directional
4875 Evolution in Hymenopteran Morphology. *Syst. Biol.* 64, 1089–1103.
- 4876 Kluge, N.J., 1998. Phylogeny and higher classification of Ephemeroptera. *Zoosystematica Ross.* 7,
4877 255–269.
- 4878 Kluge, N.J., 2004. The Phylogenetic System of Ephemeroptera (the first experience in consistently
4879 non-ranking taxonomy) Volume 1. Ephemeroptera except for Turbanoculata and Leptophlebia.
4880 Kluwer Academic Publishers, Dordrecht-Hardbound.
- 4881 Knecht, R.J., Engel, M.S., Benner, J.S., 2011. Late Carboniferous paleoichnology reveals the oldest
4882 full-body impression of a flying insect. *Proc. Natl. Acad. Sci.* 108, 6515–6519.
- 4883 Kocarek, P., John, V., Hulva, P., 2013. When the Body Hides the Ancestry: Phylogeny of
4884 Morphologically Modified Epizoic Earwigs Based on Molecular Evidence. *PLoS ONE* 8,
4885 e66900.
- 4886 Koch, M., 1997. Monophyly and phylogenetic position of the Diplura (Hexapoda). *Pedobiologia* 41, 9–
4887 12.
- 4888 Koch, M., 2003. Character evolution in the Archaeognatha: consensus and conflict. *Entomol. Abh.* 61,
4889 120–122.
- 4890 Koch, M., 2009. Diplura, in: Resh, V.H., Carde, R.T. (Eds.), *Encyclopedia of Insects*. Academic Press,
4891 London, pp. 281–283.
- 4892 Kohli, M.K., Ware, J.L., Bechly, G., 2016. How to date a dragonfly: Fossil calibrations for odonates.
4893 *Palaeontol. Electron.* 19, 1-14.
- 4894 Kornicker, L.S., 1981. Revision, distribution, ecology, and ontogeny of the Ostrocode subfamily
4895 Cyclasteropinae (Myodocopina, Cylindroleberididae). *Smithson. Contrib. Zool.* 319, 1–548.
- 4896 Kotov, A.A., 2007. Jurassic Cladocera (Crustacea, Branchiopoda) with a description of an extinct
4897 Mesozoic order. *J. Nat. Hist.* 41, 13–37.
- 4898 Kotov, A.A., 2009. A revision of the extinct Mesozoic family Prochyridae Smirnov, 1992 (Crustacea:
4899 Cladocera) with a discussion of its phylogenetic position. *Zool. J. Linn. Soc.* 155, 253–265.

- 4900 Kotov, A.A., 2013. Morphology and phylogeny of the Anomopoda (Crustacea: Cladocera). Scientific
4901 press Ltd KMK, Moscow.
- 4902 Krandijevsky, V.S., 1963. The ostracod fauna of Silurian localities of Podolia. AN. URSR, Inst. Geol.
4903 Nauk, Kiev, 1–176.
- 4904 Kristensen, N.P., 1981. Phylogeny of insect orders. Annu. Rev. Entomol. 26, 135–157.
- 4905 Kristensen, N.P., 1991. Phylogeny of extant hexapods. Insects Aust. 1, 125–140.
- 4906 Kristensen, N.P., Skalski, A.W., 1998. Palaeontology and phylogeny, in: Lepidoptera, Moths and
4907 Butterflies. pp. 7–25.
- 4908 Krzemiński, W., Krzeminska, E., Papier, F., 1994. *Grauvogelia arzvilleriana* sp. n.-the oldest Diptera
4909 species [Lower-Middle Triassic of France]. Acta Zool. Cracoviensia 2, 267-274.
- 4910 Kühne, W.G., Schlüter, T., 1985. A fair deal for the Devonian Arthropoda fauna of Rhynie. Entomol.
4911 Gen. 91–96.
- 4912 Kukalová-Peck, J., 1985. Ephemeroïd wing venation based upon new gigantic Carboniferous mayflies
4913 and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta,
4914 Ephemera). Can. J. Zool. 63, 933–955.
- 4915 Kukalová-Peck, J., 1991. Fossil history and the evolution of hexapod structures. Insects Aust. 1, 141–
4916 179.
- 4917 Kukalová-Peck, J., Beutel, R.G., 2012. Is the Carboniferous †*Adiphebia lacoana* really the “oldest
4918 beetle”? Critical reassessment and description of a new Permian beetle family. Eur. J. Entomol.
4919 109, 633–645.
- 4920 Kukalová-Peck, J., Willmann, R., 1990. Lower Permian “mecopteroid-like” insects from central Europe
4921 (Insecta, Endopterygota). Can. J. Earth Sci. 27, 459–468.
- 4922 Labandeira, C.C., 2011. Evidence for an Earliest Late Carboniferous Divergence Time and the Early
4923 Larval Ecology and Diversification of Major Holometabola Lineages. Entomol. Am. 117, 9–21.
- 4924 Lagebro, L., Gueriau, P., Hegna, T.A., Rabet, N., Butler, A.D., Budd, G.E., 2015. The oldest
4925 notostracan (Upper Devonian Strud locality, Belgium). Palaeontology 58, 497–509.

- 4926 Lamsdell, J.C., 2013. Revised systematics of Palaeozoic “horseshoe crabs” and the myth of
4927 monophyletic Xiphosura: Re-evaluating the Monophyly of Xiphosura. Zool. J. Linn. Soc. 167,
4928 1–27.
- 4929 Lamsdell, J.C., Briggs, D.E.G., Liu, H.P., Witzke, B.J., McKay, R.M., 2015. A new Ordovician arthropod
4930 from the Winneshiek Lagerstätte of Iowa (USA) reveals the ground plan of eurypterids and
4931 chasmataspids. Sci. Nat. 102.
- 4932 Lamsdell, J.C., McKenzie, S.C., 2015. *Tachypleus syriacus* (Woodward)—a sexually dimorphic
4933 Cretaceous crown limulid reveals underestimated horseshoe crab divergence times. Org.
4934 Divers. Evol. 15, 681–693.
- 4935 Lang, W.D., Spath, L.F., Richardson, W.A., 1923. Shales-with-“beef,” a Sequence in the Lower Lias of
4936 the Dorset Coast. Q. J. Geol. Soc. 79, 47–66.
- 4937 Larink, O., 1997. Apomorphic and plesiomorphic characteristics in Archaeognatha, Monura and
4938 Zygentoma. Pedobiologia 41, 3–8.
- 4939 Laurentiaux, D., 1952. Découverte d'un homoptère prosboloïde dans le namurien belge. Publications
4940 de l'Association pour l'Etude de la Paléontologie Bruxelles. 14, 16 pp.
- 4941 Laurie, M., 1899. On a Silurian Scorpion and some additional Eurypterid Remains from the Pentland
4942 Hills. Trans. R. Soc. Edinb. 39, 575–590.
- 4943 Lauterbach, K.E., 1989. The pan-monophylum—a practical help in phylogenetic systematics. Zool. Anz.
4944 223, 139–156.
- 4945 Lee, M.S.Y., Soubrier, J., Edgecombe, G.D., 2013. Rates of Phenotypic and Genomic Evolution during
4946 the Cambrian Explosion. Curr. Biol. 23, 1889–1895.
- 4947 Lee, S.-W., 2014. New Lower Cretaceous basal mantodean (Insecta) from the Crato Formation (NE
4948 Brazil). Geol. Carpathica 65, 285–292.
- 4949 Legalov, A.A., 2010. Checklist of Mesozoic Curculionoidea (Coleoptera) with description of new taxa.
4950 Balt. J. Coleopterol. 10, 71–101.

- 4951 Legendre, F., Nel, A., Svenson, G.J., Robillard, T., Pellens, R., Grandcolas, P., 2015. Phylogeny of
4952 Dictyoptera: Dating the Origin of Cockroaches, Praying Mantises and Termites with Molecular
4953 Data and Controlled Fossil Evidence. PLoS ONE 10, e0130127.
- 4954 Legg, D.A., 2014. *Sanctacaris uncata*: the oldest chelicerate (Arthropoda). Naturwissenschaften 101,
4955 1065–1073.
- 4956 Legg, D.A., Sutton, M.D., Edgecombe, G.D., 2013. Arthropod fossil data increase congruence of
4957 morphological and molecular phylogenies. Nat. Commun. 4.
- 4958 Lehmann, J., Murphy, M.A., 2001. A new placenticeratid ammonite from the Albian (Lower Cretaceous)
4959 of California and the inferred history of some placenticeratid and engonoceratid ammonites.
4960 Neues Jahrb. Geol. Palaontologie Monatshefte 343–358.
- 4961 Lehmann, W.M., 1944. *Palaeoscorpius devonicus* n.g., n. sp., ein Skorpion aus dem rheinischen
4962 Unterdevon. Neues Jahrbuch für Paläontologie, Monatshefte B 7, 177–185.
- 4963 Leonova, T.B., 2007. Correlation of the Kazanian of the Volga–Urals with the Roadian of the global
4964 Permian scale. Palaeoworld 16, 246–253.
- 4965 Leonova, T.B., Shilovsky, O.P., 2007. Evolution of the Permian family Spirolegoceratidae (Goniatitida,
4966 Ammonoidea). Paleontol. J. 41, 28–38.
- 4967 Letsch, H., Gottsberger, B., Ware, J.L., 2016. Not going with the flow: a comprehensive time-calibrated
4968 phylogeny of dragonflies (Anisoptera: Odonata: Insecta) provides evidence for the role of lentic
4969 habitats on diversification. Mol. Ecol. 25, 1340–1353.
- 4970 Letsch, H., Simon, S., 2013. Insect phylogenomics: new insights on the relationships of lower
4971 neopteran orders (Polyneoptera): Phylogenomics of Polyneoptera. Syst. Entomol. 38, 783–
4972 793.
- 4973 Li, G., Ando, H., Hasegawa, H., Yamamoto, M., Hasegawa, T., Ohta, T., Hasebe, N., Ichinnorov, N.,
4974 2014. Confirmation of a Middle Jurassic age for the Eedemt Formation in Dundgobi Province,
4975 southeast Mongolia: constraints from the discovery of new spinicaudatans (clam shrimps).
4976 Alcheringa 38, 305–316.

- 4977 Li, G., Matsuoka, A., 2012. Jurassic clam shrimp ("conchostracan") faunas in China. *Sci. Rep.*, Niigata
4978 Univ. (Geology) 27, 73–88.
- 4979 Li, Y., Béthoux, O., Pang, H., Ren, D., 2013a. Early Pennsylvanian Odonatoptera from the Xiaheyuan
4980 locality (Ningxia, China): new material, taxa, and perspectives. *Foss. Rec.* 16, 117–139.
- 4981 Li, Y., Ren, D., Pecharová, M., Prokop, J., 2013b. A new palaeodictyopterid (Insecta:
4982 Palaeodictyoptera: Spilapteridae) from the Upper Carboniferous of China supports a close
4983 relationship between insect faunas of Quilianshan (northern China) and Laurussia. *Alcheringa*
4984 37, 487–495.
- 4985 Liao, W., Ruan, Y., 2003. Devonian biostratigraphy of China, in: Zhang, W., Palmer, A.R. (Eds.),
4986 Biostratigraphy of China. Science Press, Beijing, p. 237.
- 4987 Lins, L.S.F., Ho, S.Y.W., Wilson, G.D.F., Lo, N., 2012. Evidence for Permo-Triassic colonization of the
4988 deep sea by isopods. *Biol. Lett.* 8, 979–982.
- 4989 Linse, K., Jackson, J.A., Fitzcharles, E., Sands, C.J., Buckeridge, J.S., 2013. Phylogenetic position of
4990 Antarctic Scalpelliformes (Crustacea: Cirripedia: Thoracica). *Deep Sea Res. Part Oceanogr.*
4991 Res. Pap. 73, 99–116.
- 4992 Liu, Q., Zheng, D., Zhang, Q., Wang, B., Fang, Y., Zhang, H., 2014. Two new kalligrammatids (Insecta,
4993 Neuroptera) from the Middle Jurassic of Daohugou, Inner Mongolia, China. *Alcheringa* 38, 65–
4994 69.
- 4995 Liu, S., Gao, L., 1985. Conchostracans and spores of upper Devonian Huangjiadeng Formation in
4996 Hubei Province. *Acta Geosci. Sin.* 7, 113–127.
- 4997 Liu, X., Wang, Y., Shih, C., Ren, D., Yang, D., 2012. Early Evolution and Historical Biogeography of
4998 Fishflies (Megaloptera: Chauliiodinae): Implications from a Phylogeny Combining Fossil and
4999 Extant Taxa. *PLoS ONE* 7, e40345.

- 5000 Liu, X., Winterton, S.L., Wu, C., Piper, R., Ohl, M., 2015. A new genus of mantidflies discovered in the
5001 Oriental region, with a higher-level phylogeny of Mantispidae (Neuroptera) using DNA
5002 sequences and morphology: New genus and higher phylogeny of Mantispidae. *Syst. Entomol.*
5003 40, 183–206.
- 5004 Liu, Y., Ren, D., Prokop, J., 2009a. Discovery of a new Namurian archaeorthopterid from Ningxia,
5005 China (Insecta: Archaeorthoptera). *Zootaxa* 2032, 63–68.
- 5006 Liu, Y., Sinitshenkova, N.D., Ren, D., 2009b. A revision of the Jurassic Stonefly Genera
5007 *Dobbertiniopteryx* Ansorge and *Karanemoura* Sinitshenkova (Insecta: Plecoptera), with the
5008 description of new species from the Daohugou locality, China. *Paleontol. J.* 43, 183–190.
- 5009 Liu, Y., Sinitshenkova, N.D., Ren, D., Shih, C., 2011. Pronemouridae fam. nov. (Insecta: Plecoptera),
5010 the stem group of Nemouridae and Notonemouridae, from the Middle Jurassic of Inner
5011 Mongolia, China. *Palaeontology* 54, 923–933.
- 5012 Lourenço, W.R., Gall, J.-C., 2004. Fossil scorpions from the Buntsandstein (Early Triassic) of France.
5013 *Comptes Rendus Palevol* 3, 369–378.
- 5014 Lozovsky, V.R., Minikh, M.G., Grunt, T.A., Kukhtinov, D.A., Ponomarenko, A.G., Sukacheva, I.D., 2009.
5015 The Ufimian Stage of the East European scale: Status, validity, and correlation potential.
5016 *Stratigr. Geol. Correl.* 17, 602–614.
- 5017 Lucas, S.G., Tanner, L.H., Kozur, H.W., Weems, R.E., Heckert, A.B., 2012. The Late Triassic
5018 timescale: Age and correlation of the Carnian–Norian boundary. *Earth-Sci. Rev.* 114, 1–18.
- 5019 Lukashevich, E.D., Przhiboro, A.A., Marchal-Papier, F., Grauvogel-Stamm, L., 2010. The oldest
5020 occurrence of immature Diptera (Insecta), Middle Triassic, France. *Ann. Société Entomol. Fr.*
5021 46, 4–22.
- 5022 Lyal, C.H.C., 1985. Phylogeny and classification of the Psocodea, with particular reference to the lice
5023 (Psocodea: Phthiraptera). *Syst. Entomol.* 10, 145–165.

- 5024 Macchioni, F., 2002. Myths and legends in the correlation between the Boreal and Tethyan Realms.
5025 Implications on the dating of the Early Toarcian mass extinctions and the Oceanic Anoxic
5026 Event. *Geobios* 35, 150–164.
- 5027 MacNaughton, R.B., Narbonne, G.M., 1999. Evolution and ecology of Neoproterozoic-Lower Cambrian
5028 trace fossils, NW Canada. *Palaios* 97–115.
- 5029 Maksoud, S., Azar, D., Granier, B., Gèze, R., 2016 (in press). New data on the age of the Lower
5030 Cretaceous amber outcrops of Lebanon. *Palaeoworld*.
- 5031 Maksoud, S., Granier, B., Azar, D., Gèze, R., Paicheler, J.-C., Moreno-Bedmar, J.A., 2014. Revision
5032 of “Falaise de Blanche” (Lower Cretaceous) in Lebanon, with the definition of a Jezzinian
5033 Regional Stage. *Carnets Geol.-Noteb. Geol.* 14, 401–427.
- 5034 Małkowski, K., Racki, G., Drygant, D., Szaniawski, H., 2009. Carbon isotope stratigraphy across the
5035 Silurian–Devonian transition in Podolia, Ukraine: evidence for a global biogeochemical
5036 perturbation. *Geol. Mag.* 146, 674.
- 5037 Malm, T., Johanson, K.A., Wahlberg, N., 2013. The evolutionary history of Trichoptera (Insecta): A
5038 case of successful adaptation to life in freshwater. *Syst. Entomol.* 38, 459–473.
- 5039 Marden, J.H., 2013a. Reply to “Comment on Marden (2013) regarding the interpretation of the earliest
5040 trace fossil of a winged insect.” *Evolution* 67, 2150–2153.
- 5041 Marden, J.H., 2013b. Reanalysis and experimental evidence indicate that the earliest trace fossil of a
5042 winged insect was a surface-skimming neopteran: trace fossil of a Carboniferous neopteran
5043 insect. *Evolution* 67, 274–280.
- 5044 Mark, D.F., Rice, C.M., Fallick, A.E., Trewin, N.H., Lee, M.R., Boyce, A., Lee, J.K.W., 2011. $^{40}\text{Ar}/^{39}\text{Ar}$
5045 dating of hydrothermal activity, biota and gold mineralization in the Rhynie hot-spring system,
5046 Aberdeenshire, Scotland. *Geochim. Cosmochim. Acta* 75, 555–569.
- 5047 Mark, D.F., Rice, C.M., Trewin, N.H., 2013. Discussion on “A high-precision U–Pb age constraint on
5048 the Rhynie Chert Konservat-Lagerstätte: time scale and other implications”. *J. Geol. Soc.* 170,
5049 701–703.

- 5050 Marshall, J.E.A., 1991. Palynology of the Stonehaven Group, Scotland: evidence for a Mid Silurian
5051 age and its geological implications. *Geol. Mag.* 128, 283–286.
- 5052 Marshall, C.R., 2008. A simple method for bracketing absolute divergence times on molecular
5053 phylogenies using multiple fossil calibration points. *Am. Nat.* 171, 726–742.
- 5054 Martill, D.M., 2007. The age of the Cretaceous Santana Formation fossil Konservat Lagerstätte of
5055 north-east Brazil: a historical review and an appraisal of the biochronostratigraphic utility of its
5056 palaeobiota. *Cretac. Res.* 28, 895–920.
- 5057 Martill, D.M., Bechly, G., Loveridge, R.F., 2007. The Crato fossil beds of Brazil: Window into an ancient
5058 world. Cambridge University Press, Cambridge.
- 5059 Martín-Closas, C., Clavel, B., Schroeder, R., Charollais, J., Conrad, M.-A., 2009. Charophytes from
5060 the Barremian-lower Aptian of the Northern Subalpine Chains and Jura Mountains, France:
5061 correlation with associated marine assemblages. *Cretac. Res.* 30, 49–62.
- 5062 Martín-Closas, C., López-Morón, N., 1995. The charophyte flora, in: Montsec and Montral-Alcover.
5063 Two Konservat Lagerstätten, Catalonia, Spain. II International Symposium on Lithographic
5064 Limestones Field Trip Book. pp. 29–31.
- 5065 Martínez, C., Madriñán, S., Zavada, M., Alberto Jaramillo, C., 2013. Tracing the fossil pollen record of
5066 *Hedyosmum* (Chloranthaceae), an old lineage with recent Neotropical diversification. *Grana*
5067 52, 161–180.
- 5068 Martins-Neto, R.G., Gallego, O.F., Zavattieri, A.M., 2008. The Triassic insect fauna from Argentina:
5069 Coleoptera, Hemiptera and Orthoptera from the Potrerillos Formation, south of cerro Cacheuta,
5070 Cuyana basin. *Alavesia* 2, 47–58.
- 5071 Martynov, A.V., 1927. Jurassic fossil insects from Turkestan. 7. Some Odonata, Neuroptera,
5072 Thysanoptera. *Ezhegodnik Russkogo Paleontologicheskogo Obshchestva* 21, 757–768.
- 5073 Massoud, Z., 1967. Contribution à l'étude de *Rhyniella praecursor* Hirst et Maulik 1926, Collembola
5074 fossile du Dévonien. *Rev. Ecol. Biol. Sol.* 4, 497–505.

- Mathers, T.C., Hammond, R.L., Jenner, R.A., Hänfling, B., Gómez, A., 2013. Multiple global radiations in tadpole shrimps challenge the concept of “living fossils.” *PeerJ* 1, e62.
- Ma, X., Liao, W., Wang, D., 2009. The Devonian System of China, with a discussion on sea-level change in South China. *Geol. Soc. Lond. Spec. Publ.* 314, 241–262.
- McCafferty, W.P., 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta): a commentary on systematics. *Ann. Entomol. Soc. Am.* 84, 343–360.
- McGhee, G.R., 2013. When the invasion of land failed: the legacy of the Devonian extinctions. Columbia University Press, New York.
- McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., Mchugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Slipiński, A., Maddison, D.R., Farrell, B.D., 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution: Phylogeny and evolution of Coleoptera (beetles). *Syst. Entomol.* 40, 835–880.
- Meland, K., Mees, J., Porter, M.L., Wittmann, K.J., 2015. Taxonomic review of the orders Mysida and Stygiomysida (Crustacea, Peracarida). *PLoS ONE* 10, e0124656.
- Meland, K., Willassen, E., 2007. The disunity of “Mysidacea” (Crustacea). *Mol. Phylogenet. Evol.* 44, 1083–1104.
- Melchin, M.J., Sadler, P.M., Cramer, B.D., Cooper, R.A., Gradstein, F.M., Hammer, O., 2012. The Silurian Period, in: *The Geologic Time Scale*. Elsevier, pp. 525–558.
- Mendes, L.F., Poinar, G.O., 2008. A new fossil silverfish (*Zygentoma*: Insecta) in Mesozoic Burmese amber. *Eur. J. Soil Biol.* 44, 491–494.
- Mendes, L.F., Wunderlich, J., 2013. New data on thysanurans preserved in Burmese amber (*Microcoryphia* and *Zygentoma* Insecta). *Soil Org.* 85, 11–22.

- 5099 Menning, M., Alekseev, A.S., Chuvashov, B.I., Davydov, V.I., Devuyst, F.-X., Forke, H.C., Grunt, T.A.,
5100 Hance, L., Heckel, P.H., Izokh, N.G., Jin, Y.-G., Jones, P.J., Kotlyar, G.V., Kozur, H.W.,
5101 Nemyrovska, T.I., Schneider, J.W., Wang, X.-D., Weddige, K., Weyer, D., Work, D.M., 2006.
5102 Global time scale and regional stratigraphic reference scales of Central and West Europe, East
5103 Europe, Tethys, South China, and North America as used in the Devonian–Carboniferous–
5104 Permian Correlation Chart 2003 (DCP 2003). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 240,
5105 318–372.
- 5106 Menon, F., 2007. Higher systematics of scorpions from the Crato Formation, Lower Cretaceous of
5107 Brazil. *Palaeontology* 50, 185–195.
- 5108 Meusemann, K., von Reumont, B.M., Simon, S., Roeding, F., Strauss, S., Kuck, P., Ebersberger, I.,
5109 Walz, M., Pass, G., Breuers, S., Achter, V., von Haeseler, A., Burmester, T., Hadrys, H.,
5110 Wagele, J.W., Misof, B., 2010. A Phylogenomic Approach to Resolve the Arthropod Tree of
5111 Life. *Mol. Biol. Evol.* 27, 2451–2464.
- 5112 Michel, L.A., Tabor, N.J., Montañez, I.P., Schmitz, M.D., Davydov, V.I., 2015. Chronostratigraphy and
5113 Paleoclimatology of the Lodève Basin, France: Evidence for a pan-tropical aridification event
5114 across the Carboniferous–Permian boundary. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 430,
5115 118–131.
- 5116 Michels, J., Schnack-Schiel, S.B., 2005. Feeding in dominant Antarctic copepods? Does the
5117 morphology of the mandibular gnathobases relate to diet? *Mar. Biol.* 146, 483–495.
- 5118 Miller, J.F., Loch, J.D., Taylor, J.F., 2012. Biostratigraphy of Cambrian and Lower Ordovician strata in
5119 the Llano uplift, central Texas, in: Derby, J.R., Fritz, R.D., Longacre, S.A., Morgan, W.A.,
5120 Sternbach, C.A. (Eds.), *The Great American Carbonate Bank: The Geology and Economic
5121 Resources of the Cambrian – Ordovician Sauk Megasequence of Laurentia*, AAPG Memoir.
5122 pp. 187–202.
- 5123 Minet, J., Huang, D.-Y., Wu, H., Nel, A., 2010. Early Mecoptera and the systematic position of the
5124 Microptysmatidae (Insecta: Endopterygota). *Ann. Société Entomol. Fr.* 46, 262–270.

5125 Minxiao, W., Song, S., Chaolun, L., Xin, S., 2011. Distinctive mitochondrial genome of Calanoid
 5126 copepod *Calanus sinicus* with multiple large non-coding regions and reshuffled gene order:
 5127 Useful molecular markers for phylogenetic and population studies. BMC Genomics 12, 73.

5128 Misof, B., Liu, S., Meusemann, K., Peters, R.S., Donath, A., Mayer, C., Frandsen, P.B., Ware, J.,
 5129 Flouri, T., Beutel, R.G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J.,
 5130 Aberer, A.J., Aspöck, U., Aspöck, H., Bartel, D., Blanke, A., Berger, S., Böhm, A., Buckley, T.R.,
 5131 Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang,
 5132 Y., Jermini, L.S., Kawahara, A.Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li,
 5133 Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D.D., Meng, G., Nakagaki, Y.,
 5134 Navarrete-Heredia, J.L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont,
 5135 B.M., Schütte, K., Sekiya, K., Shimizu, S., Slipinski, A., Stamatakis, A., Song, W., Su, X.,
 5136 Szucsich, N.U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein,
 5137 M., Tong, X., Uchifune, T., Walz, M.G., Wiegmann, B.M., Wilbrandt, J., Wipfler, B., Wong,
 5138 T.K.F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D.K., Yoshizawa, K., Zhang, Q.,
 5139 Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Li, Y., Xu,
 5140 X., Zhang, Y., Yang, H., Wang, J., Wang, J., Kjer, K.M., Zhou, X., 2014. Phylogenomics
 5141 resolves the timing and pattern of insect evolution. Science 346, 763–767.

5142 Miyazawa, H., Ueda, C., Yahata, K., Su, Z.-H., 2014. Molecular phylogeny of Myriapoda provides
 5143 insights into evolutionary patterns of the mode in post-embryonic development. Sci. Rep. 4,
 5144 4127.

5145 Moisan, P., Labandeira, C.C., Matushkina, N.A., Wappler, T., Voigt, S., Kerp, H., 2012. Lycopsid–
 5146 arthropod associations and odonatopteran oviposition on Triassic herbaceous *Isoetes*.
 5147 Palaeogeogr. Palaeoclimatol. Palaeoecol. 344–345, 6–15.

- 5148 Møller, O.S., Olesen, J., Avenant-Oldewage, A., Thomsen, P.F., Glenner, H., 2008. First maxillae
5149 suction discs in Branchiura (Crustacea): Development and evolution in light of the first
5150 molecular phylogeny of Branchiura, Pentastomida, and other “Maxillopoda.” *Arthropod Struct.*
5151 *Dev.* 37, 333–346.
- 5152 Morel, E.M., Artabe, A.E., Spalletti, L.A., 2003. Triassic floras of Argentina: biostratigraphy, floristic
5153 events and comparison with other areas of Gondwana and Laurasia. *Alcheringa* 27, 231–243.
- 5154 Morse, J.C., 1997. Phylogeny of Trichoptera. *Annu. Rev. Entomol.* 42, 427–450.
- 5155 Mortimore, R., 2011. A chalk revolution: what have we done to the Chalk of England? *Proc. Geol.*
5156 *Assoc.* 122, 232–297.
- 5157 Mound, L.A., Morris, D.C., 2007. The insect order Thysanoptera: Classification versus systematics.
5158 *Zootaxa* 1668, 395–411.
- 5159 Mouro, L.D., Zatoń, M., Fernandes, A.C.S., Waichel, B.L., 2016. Larval cases of caddisfly (Insecta:
5160 Trichoptera) affinity in Early Permian marine environments of Gondwana. *Sci. Rep.* 6, 19215.
- 5161 Müller, K.J., 1983. Crustacea with preserved soft parts from the Upper Cambrian of Sweden. *Lethaia*
5162 16, 93–109.
- 5163 Mundel, P., 1979. The centipedes (Chilopoda) of the Mazon Creek, in: *Mazon Creek Fossils.*
5164 Academic Press, New York, pp. 361–378.
- 5165 Murienne, J., Edgecombe, G.D., Giribet, G., 2010. Including secondary structure, fossils and molecular
5166 dating in the centipede tree of life. *Mol. Phylogenet. Evol.* 57, 301–313.
- 5167 Murienne, J., Harvey, M.S., Giribet, G., 2008. First molecular phylogeny of the major clades of
5168 Pseudoscorpiones (Arthropoda: Chelicerata). *Mol. Phylogenet. Evol.* 49, 170–184.
- 5169 Murphy, J.L., 1973. Protosalvinia (*Foerstia*) Zone in the Upper Devonian sequence of eastern Ohio,
5170 northwestern Pennsylvania, and western New York. *Geol. Soc. Am. Bull.* 84, 3405–3410.
- 5171 Narbonne, G.M., Myrow, P.M., Landing, E., Anderson, M.M., 1987. A candidate stratotype for the
5172 Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern
5173 Newfoundland. *Can. J. Earth Sci.* 24, 1277–1293.

- 5174 Near T.J., Meylan, P.A., Shaffer, H.B., 2005. Assessing concordance of fossil calibration points in
5175 molecular clock studies: an example using turtles. *Am. Nat.* 165, 137-146.
- 5176 Nel, A., Delfosse, E., 2011. A New Chinese Mesozoic Stick Insect. *Acta Palaeontol. Pol.* 56, 429–432.
- 5177 Nel, A., Gand, G., Garric, J., Lapeyrie, J., 1999. The first recorded protozygopteran insects from the
5178 Upper Permian of France. *Palaeontology* 42, 83–97.
- 5179 Nel, A., Marie, V., Schmeibner, S., 2002. Revision of the Lower Mesozoic dragonfly family
5180 Triasolestidae Tillyard, 1918 (Odonata: Epiproctophora). *Ann. Paléontol.* 88, 189-214.
- 5181 Nel, A., Prokop, J., Nel, P., Grandcolas, P., Huang, D.-Y., Roques, P., Guilbert, E., Dostál, O., Szwedó,
5182 J., 2012. Traits and evolution of wing venation pattern in paraneopteran insects. *J. Morphol.*
5183 273, 480–506.
- 5184 Nel, A., Roques, P., Nel, P., Prokin, A.A., Bourgoin, T., Prokop, J., Szwedó, J., Azar, D., Desutter-
5185 Grandcolas, L., Wappler, T., Garrouste, R., Coty, D., Huang, D., Engel, M.S., Kirejtshuk, A.G.,
5186 2013. The earliest known holometabolous insects. *Nature* 503, 257–261.
- 5187 Nel, A., Roques, P., Nel, P., Prokop, J., Steyer, J.S., 2007. The earliest holometabolous insect from the
5188 Carboniferous: a “crucial” innovation with delayed success (Insecta Protomeropina
5189 Protomeropidae). *Ann. Société Entomol. Fr.* 43, 349–355.
- 5190 Nel, P., Azar, D., Prokop, J., Roques, P., Hodebert, G., Nel, A., 2012. From Carboniferous to Recent:
5191 wing venation enlightens evolution of thysanopteran lineage. *J. Syst. Palaeontol.* 10, 385–399.
- 5192 Nguyen Duy-Jacquemin, M.N., Azar, D., 2004. The oldest records of Polyxenida (Myriapoda,
5193 Diplopoda): new discoveries from the Cretaceous ambers of Lebanon and France.
5194 *Geodiversitas* 26, 631–641.
- 5195 Nicholson, D.B., Mayhew, P.J., Ross, A.J., 2015. Changes to the Fossil Record of Insects through
5196 Fifteen Years of Discovery. *PLoS ONE* 10, e0128554.

- 5197 Niehuis, O., Hartig, G., Grath, S., Pohl, H., Lehmann, J., Tafer, H., Donath, A., Krauss, V., Eisenhardt,
5198 C., Hertel, J., Petersen, M., Mayer, C., Meusemann, K., Peters, R.S., Stadler, P.F., Beutel, R.G.,
5199 Bornberg-Bauer, E., McKenna, D.D., Misof, B., 2012. Genomic and Morphological Evidence
5200 Converge to Resolve the Enigma of Strepsiptera. *Curr. Biol.* 22, 1309–1313.
- 5201 Nielsen, A.T., Weidner, T., Terfelt, F., Høyberget, M., 2014. Upper Cambrian (Furongian)
5202 biostratigraphy in Scandinavia revisited: definition of superzones. *GFF* 136, 193–197.
- 5203 Nielsen, C., 1995. *Animal evolution: Interrelationships of living Phyla*. Oxford University Press, Oxford.
- 5204 Norell, M.A., Novacek, M.J., 1992. Congruence between superpositional and phylogenetic patterns:
5205 Comparing cladistics patterns with fossil records. *Cladistics* 8, 319–337.
- 5206 Novojilov, N.I., 1970. *Vymershie limnadioidei (Conchostraca-Limnadioidea)*. Nauka, Moscow.
- 5207 Novokshonov, V.G., 1994. Permian Scorpionflies (Insecta, Panorpidia) of the Families Kaltanidae,
5208 Permochoristidae and Robinjohniidae. *Paleontol. Zhurnal* 65–76.
- 5209 Oakley, T.H., 2003. On homology of arthropod compound eyes. *Integr. Comp. Biol.* 43, 522–530.
- 5210 Oakley, T.H., Wolfe, J.M., Lindgren, A.R., Zaharoff, A.K., 2013. Phylotranscriptomics to Bring the
5211 Understudied into the Fold: Monophyletic Ostracoda, Fossil Placement, and Pancrustacean
5212 Phylogeny. *Mol. Biol. Evol.* 30, 215–233.
- 5213 Obst, M., Faurby, S., Bussarawit, S., Funch, P., 2012. Molecular phylogeny of extant horseshoe crabs
5214 (Xiphosura, Limulidae) indicates Paleogene diversification of Asian species. *Mol. Phylogenet.*
5215 *Evol.* 62, 21–26.
- 5216 O'Connor, A., Wills, M.A., 2016 (in press). Measuring stratigraphic congruence across trees, higher
5217 taxa and time. *Syst. Biol.*
- 5218 Ogden, T.H., Gattolliat, J.L., Sartori, M., Staniczek, A.H., Soldán, T., Whiting, M.F., 2009. Towards a
5219 new paradigm in mayfly phylogeny (Ephemeroptera): combined analysis of morphological and
5220 molecular data. *Syst. Entomol.* 34, 616–634.
- 5221 Ogden, T.H., Whiting, M.F., 2005. Phylogeny of Ephemeroptera (mayflies) based on molecular
5222 evidence. *Mol. Phylogenet. Evol.* 37, 625–643.

- 5223 Ogg, J.G., 2012. Triassic, in: The Geologic Time Scale. Elsevier, pp. 681–730.
- 5224 Ogg, J.G., Hinnov, L.A., Huang, C., 2012a. Cretaceous, in: The Geologic Time Scale. Elsevier, pp.
5225 793–853.
- 5226 Ogg, J.G., Hinnov, L.A., Huang, C., 2012b. Jurassic, in: The Geologic Time Scale. Elsevier, pp. 731–
5227 791.
- 5228 Ogg, J.G., Huang, C., Hinnov, L.A., 2014. Triassic timescale status: A brief overview. *Albertiana* 41, 3–
5229 30.
- 5230 Olempska, E., Horne, D.J., Szaniawski, H., 2012. First record of preserved soft parts in a Palaeozoic
5231 podocopid (Metacopina) ostracod, *Cytherellina submagna*: phylogenetic implications. *Proc. R.*
5232 *Soc. B Biol. Sci.* 279, 564–570.
- 5233 Olesen, J., 1998. A phylogenetic analysis of the Conchostraca and Cladocera (Crustacea,
5234 Branchiopoda, Diplostraca). *Zool. J. Linn. Soc.* 122, 491–536.
- 5235 Olesen, J., 2007. Monophyly and phylogeny of Branchiopoda, with focus on morphology and
5236 homologies of branchiopod phyllopodous limbs. *J. Crustac. Biol.* 27, 165–183.
- 5237 Olesen, J., 2009. Phylogeny of Branchiopoda (Crustacea)—character evolution and contribution of
5238 uniquely preserved fossils. *Arthropod Syst. Phylogeny* 67, 3–39.
- 5239 O'Reilly, J.E., dos Reis, M., Donoghue, P.C.J., 2015. Dating tips for divergence-time estimation.
5240 *Trends Genet.* 31, 637–650.
- 5241 Orr, P.J., Briggs, D.E.G., 1999. Exceptionally preserved conchostracans and other crustaceans from
5242 the Upper Carboniferous of Ireland. *Spec. Pap. Palaeontol.* 62, 1–68.
- 5243 Ortega-Hernández, J., 2016. Making sense of “lower” and “upper” stem-group Euarthropoda, with
5244 comments on the strict use of the name Arthropoda von Siebold, 1848: Upper and lower stem-
5245 Euarthropoda. *Biol. Rev.* 91, 255–273.

- 5246 Ottone, E.G., Monti, M., Marsicano, C.A., de la Fuente, M.S., Naipauer, M., Armstrong, R., Mancuso,
5247 A.C., 2014. A new Late Triassic age for the Puesto Viejo Group (San Rafael depocenter,
5248 Argentina): SHRIMP U–Pb zircon dating and biostratigraphic correlations across southern
5249 Gondwana. *J. South Am. Earth Sci.* 56, 186–199.
- 5250 Owen, C.L., Bracken-Grissom, H., Stern, D., Crandall, K.A., 2015. A synthetic phylogeny of freshwater
5251 crayfish: insights for conservation. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 20140009.
- 5252 Pálffy, J., Smith, P.L., Mortensen, J.K., 2000. A U–Pb and ⁴⁰Ar/³⁹Ar time scale for the Jurassic. *Can. J.*
5253 *Earth Sci.* 37, 923–944.
- 5254 Pálffy, J., Smith, P.L., Mortensen, J.K., 2002. Dating the end-Triassic and Early Jurassic mass
5255 extinctions, correlative large igneous provinces, and isotopic events. *Spec. Pap.-Geol. Soc.*
5256 *Am.* 523–532.
- 5257 Palmer, A.R., 1954. The faunas of the Riley Formation in central Texas. *J. Paleontol.* 709–786.
- 5258 Palopoli, M.F., Minot, S., Pei, D., Satterly, A., Endrizzi, J., 2014. Complete mitochondrial genomes of
5259 the human follicle mites *Demodex brevis* and *D. folliculorum*: novel gene arrangement,
5260 truncated tRNA genes, and ancient divergence between species. *BMC Genomics* 15, 1124.
- 5261 Parham, J.F., Donoghue, P.C.J., Bell, C.J., Calway, T.D., Head, J.J., Holroyd, P.A., Inoue, J.G., Irmis,
5262 R.B., Joyce, W.G., Ksepka, D.T., Patane, J.S.L., Smith, N.D., Tarver, J.E., van Tuinen, M.,
5263 Yang, Z., Angielczyk, K.D., Greenwood, J.M., Hipsley, C.A., Jacobs, L., Makovicky, P.J., Müller,
5264 J., Smith, K.T., Theodor, J.M., Warnock, R.C.M., Benton, M.J., 2012. Best Practices for
5265 Justifying Fossil Calibrations. *Syst. Biol.* 61, 346–359.
- 5266 Parry, S.F., Noble, S.R., Crowley, Q.G., Wellman, C.H., 2011. A high-precision U–Pb age constraint on
5267 the Rhynie Chert Konservat-Lagerstätte: time scale and other implications. *J. Geol. Soc.* 168,
5268 863–872.
- 5269 Parry, S.F., Noble, S.R., Crowley, Q.G., Wellman, C.H., 2013. Reply to Discussion on “A high-precision
5270 U–Pb age constraint on the Rhynie Chert Konservat-Lagerstätte: time scale and other
5271 implications” *Journal*, 168, 863–872. *J. Geol. Soc.* 170, 703–706.

- 5272 Peñalver, E., Delclòs, X., 2010. Spanish amber, in: Penney, D. (Ed.), Biodiversity of Fossils in Amber
5273 from the Major World Deposits. pp. 236–270.
- 5274 Peng, N., Liu, Y., Kuang, H., Jiang, X., Xu, H., 2012. Stratigraphy and Geochronology of Vertebrate
5275 Fossil-Bearing Jurassic Strata from Linglongta, Jianchang County, Western Liaoning,
5276 Northeastern China. *Acta Geol. Sin.* 86, 1326–1339.
- 5277 Peng, S., 2003. Chronostratigraphic subdivision of the Cambrian of China. *Geol. Acta* 1, 135-144.
- 5278 Peng, S., 2009. The newly-developed Cambrian biostratigraphic succession and chronostratigraphic
5279 scheme for South China. *Chin. Sci. Bull.* 54, 4161–4170.
- 5280 Peng, S., Babcock, L.E., 2008. Cambrian Period, in: *The Concise Geologic Time Scale*. Cambridge
5281 University Press, Cambridge, pp. 37–46.
- 5282 Peng, S., Babcock, L.E., Cooper, R.A., 2012. The Cambrian Period, in: *The Geologic Time Scale*.
5283 Elsevier, pp. 437–488.
- 5284 Pepato, A.R., da Rocha, C.E., Dunlop, J.A., 2010. Phylogenetic position of the acariform mites:
5285 sensitivity to homology assessment under total evidence. *BMC Evol. Biol.* 10, 235.
- 5286 Pepato, A.R., Klimov, P.B., 2015. Origin and higher-level diversification of acariform mites – evidence
5287 from nuclear ribosomal genes, extensive taxon sampling, and secondary structure alignment.
5288 *BMC Evol. Biol.* 15.
- 5289 Pérez-Losada, M., Harp, M., Høeg, J.T., Aчитuv, Y., Jones, D., Watanabe, H., Crandall, K.A., 2008.
5290 The tempo and mode of barnacle evolution. *Mol. Phylogenet. Evol.* 46, 328–346.
- 5291 Pérez-Losada, M., Høeg, J.T., Crandall, K.A., 2009a. Remarkable convergent evolution in specialized
5292 parasitic Thecostraca (Crustacea). *BMC Biol.* 7, 15.
- 5293 Pérez-Losada, M., Høeg, J.T., Crandall, K.A., 2009b. Stalked and acorn barnacles (Thoracica), in:
5294 Hedges, B.S., Kumar, S. (Eds.), *The Timetree of Life*. Oxford University Press, Oxford, pp. 298-
5295 301.

- 5296 Pérez-Losada, M., Høeg, J.T., Simon-Blecher, N., Achituv, Y., Jones, D., Crandall, K.A., 2014.
5297 Molecular phylogeny, systematics and morphological evolution of the acorn barnacles
5298 (Thoracica: Sessilia: Balanomorpha). *Mol. Phylogenet. Evol.* 81, 147–158.
- 5299 Perrier, V., Charbonnier, S., 2014. The Montceau-les-Mines Lagerstätte (Late Carboniferous, France).
5300 *Comptes Rendus Palevol* 13, 353–367.
- 5301 Peters, R.S., Meusemann, K., Petersen, M., Mayer, C., Wilbrandt, J., Ziesmann, T., Donath, A., Kjer,
5302 K.M., Aspöck, U., Aspöck, H., Aberer, A., Stamatakis, A., Friedrich, F., Hunefeld, F. Niehuis, O.,
5303 Beutel, R.G., Misof, B., 2014. The evolutionary history of holometabolous insects inferred from
5304 transcriptome-based phylogeny and comprehensive morphological data. *BMC Evol. Biol.* 14,
5305 52.
- 5306 Petrunina, A.S., Neretina, T.V., Mugue, N.S., Kolbasov, G.A., 2014. Tantulocarida versus Thecostraca:
5307 inside or outside? First attempts to resolve phylogenetic position of Tantulocarida using gene
5308 sequences. *J. Zool. Syst. Evol. Res.* 52, 100–108.
- 5309 Petrunkevitch, A., 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. Yale
5310 University Press, New Haven.
- 5311 Petrunkevitch, A., 1949. A study of the structure classification and relationships of the Palaeozoic
5312 Arachnida based on the collections of the British Museum. *Transactions of the Connecticut*
5313 *Academy of Arts and Sciences* 37, 69–315.
- 5314 Plotnick, R.E., 1999. Habitat of Llandoveryan-Lockhovian eurypterids, in: Boucot, A.J., Lawson, J.D.
5315 (Eds.), *Paleocommunities - a Case Study from the Silurian and Lower Devonian*. Cambridge
5316 University Press, Cambridge, pp. 106–136.
- 5317 Pocock, R.I., 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain.
5318 Palaeontographical Society, London.
- 5319 Poinar, G., 2015. Rickettsial-like cells in the Cretaceous tick, *Cornupalpatum burmanicum* (Ixodida:
5320 Ixodidae). *Cretac. Res.* 52, 623–627.

- 5321 Poinar, G., Brown, A.E., 2003. A new genus of hard ticks in Cretaceous Burmese amber (Acari:
5322 Ixodida: Ixodidae). *Syst. Parasitol.* 54, 199–205.
- 5323 Pointon, M.A., Chew, D.M., Ovtcharova, M., Sevastopulo, G.D., Crowley, Q.G., 2012. New high-
5324 precision U–Pb dates from western European Carboniferous tuffs; implications for time scale
5325 calibration, the periodicity of late Carboniferous cycles and stratigraphical correlation. *J. Geol.*
5326 *Soc. Lond.* 169, 713–721.
- 5327 Polly, P.D., Ksepka, D.T., Parham, J.F., 2015. Announcing the Fossil Calibration Series and Database.
5328 *Palaeontol. Electron.* 18, 1–5.
- 5329 Ponomarenko, A.G., 1977. Suborder Adephaga, Polyphaga Incertae Sedis, Infraorder Staphyliniformia,
5330 in *Mezozoiskie zhestkokryiye [Mesozoic Coleoptera]*. *Akad. Nauk SSSR Tr. Paleontol. Instituta*
5331 161, 17–119.
- 5332 Pons, D., Berthou, P.Y., Campos, D. de A., 1990. Quelques observations sur la palynologie de l’Aptien
5333 Supérieur et de l’Albien du bassin d’Araripe (NE du Brésil). *Atas Do* 1, 241–252.
- 5334 Poore, G.C.B., 2005. Peracarida: monophyly, relationships and evolutionary success. *Nauplius* 13, 1–
5335 27.
- 5336 Pritykina, L.N., 1981. Noviy Triasoviye Strekozy Sredney Azii [New Triassic dragonflies from Central
5337 Asia]. *Trudy Paleontologicheskogo Instituta* 183, 5–42.
- 5338 Prokop, J., Krzeminski, W., Krzeminska, E., Hörschemeyer, T., Ilger, J.-M., Brauckmann, C.,
5339 Grandcolas, P., Nel, A., 2014. Late Palaeozoic Paoliida is the sister group of Dictyoptera
5340 (Insecta: Neoptera). *J. Syst. Palaeontol.* 12, 601–622.
- 5341 Prokop, J., Krzemiński, W., Krzemińska, E., Wojciechowski, D., 2012. Paoliida, a Putative Stem-Group
5342 of Winged Insects: Morphology of New Taxa from the Upper Carboniferous of Poland. *Acta*
5343 *Palaeontol. Pol.* 57, 161–173.
- 5344 Prokop, J., Nel, A., 2007. An enigmatic Palaeozoic stem-group: Paoliida, designation of new taxa from
5345 the Upper Carboniferous of the Czech Republic (Insecta: Paoliidae, Katerinkidae fam. n.). *Afr.*
5346 *Invertebr.* 48, 77–86.

- 5347 Prokop, J., Nel, A., 2009. Systematic position of *Triplosoba*, hitherto the oldest mayfly, from Upper
5348 Carboniferous of Commeny in Central France (Insecta: Palaeodictyoptera). Syst. Entomol.
5349 34, 610-615.
- 5350 Prokop, J., Nel, A., Hoch, I., 2005. Discovery of the oldest known Pterygota in the Lower
5351 Carboniferous of the Upper Silesian Basin in the Czech Republic (Insecta: Archaeorthoptera).
5352 Geobios 38, 383–387.
- 5353 Prokop, J., Nel, A., Tenny, A., 2010. On the phylogenetic position of the palaeopteran
5354 Syntonopteroidea (Insecta: Ephemeroptera), with a new species from the Upper Carboniferous
5355 of England. Org. Divers. Evol. 10, 331–340.
- 5356 Prokop, J., Rodrigues Fernandes, F., Lapeyrie, J., Nel, A., 2015. Discovery of the first lacewings
5357 (Neuroptera: Permithonidae) from the Guadalupian of the Lodève Basin (Southern France).
5358 Geobios 48, 263–270.
- 5359 Purdy, D.J., Cranfield, L.C., 2013. Ipswich Basin, in: Jell, P.A. (Ed.), Geology of Queensland.
5360 Geological Survey of Queensland, Brisbane, pp. 391-396.
- 5361 Raasch, G.O., 1951. Revision of Croixian dikelocephalids. III. Acad. Sci. Trans. 44, 137–151.
- 5362 Racheboeuf, P.R., Vannier, J., Anderson, L.I., 2002. A New Three-Dimensionally Preserved
5363 Xiphosuran Chelicerate from the Montceau-Les-Mines Lagerstätte (Carboniferous, France).
5364 Palaeontology 45, 125–147.
- 5365 Rainford, J.L., Hofreiter, M., Nicholson, D.B., Mayhew, P.J., 2014. Phylogenetic Distribution of Extant
5366 Richness Suggests Metamorphosis Is a Key Innovation Driving Diversification in Insects. PLoS
5367 ONE 9, e109085.
- 5368 Rasnitsyn, A.P., 1964. New Triassic Hymenoptera of the Middle Asia. Paleontol. Zhurnal 1, 88–96.
- 5369 Rasnitsyn, A.P., Quicke, D.L.J., 2002. History of Insects. Kluwer Academic Publishers, Dordrecht;
5370 Boston.
- 5371 Rees, D.J., Noever, C., Høeg, J.T., Ommundsen, A., Glenner, H., 2014. On the Origin of a Novel
5372 Parasitic-Feeding Mode within Suspension-Feeding Barnacles. Curr. Biol. 24, 1429–1434.

- 5373 Regier, J.C., Mitter, C., Zwick, A., Bazinet, A.L., Cummings, M.P., Kawahara, A.Y., Sohn, J.-C., Zwickl,
5374 D.J., Cho, S., Davis, D.R., Baixeras, J., Parr, C., Weller, S., Lees, D.C., Mitter, K.T., 2013. A
5375 large-scale, higher-level, molecular phylogenetic study of the insect order Lepidoptera (moths
5376 and butterflies). PLoS ONE 8, e58568.
- 5377 Regier, J.C., Shultz, J.W., Kambic, R.E., 2005. Pancrustacean phylogeny: hexapods are terrestrial
5378 crustaceans and maxillopods are not monophyletic. Proc. R. Soc. B Biol. Sci. 272, 395–401.
- 5379 Regier, J.C., Shultz, J.W., Zwick, A., Hussey, A., Ball, B., Wetzler, R., Martin, J.W., Cunningham, C.W.,
5380 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding
5381 sequences. Nature 463, 1079–1083.
- 5382 Rehm, P., Borner, J., Meusemann, K., von Reumont, B.M., Simon, S., Hadrys, H., Misof, B.,
5383 Burmester, T., 2011. Dating the arthropod tree based on large-scale transcriptome data. Mol.
5384 Phylogenet. Evol. 61, 880–887.
- 5385 Rehm, P., Meusemann, K., Borner, J., Misof, B., Burmester, T., 2014. Phylogenetic position of
5386 Myriapoda revealed by 454 transcriptome sequencing. Mol. Phylogenet. Evol. 77, 25–33.
- 5387 Reiss, Z., Almogi-Labin, A., Lewy, Z., Moshkovitz, S., 1986. Biostratigraphic datums in the Senonian of
5388 Israel. Proc. K. Ned. Akad. Van Wet. Ser. B Palaeontol. Geol. Phys. Chem. Anthropol. 89, 95–
5389 104.
- 5390 Remy, J.M., Avnimelech, M., 1955. *Eryon yehoachi* nov. sp. et *Cenomanocarcinus* cf. *vanstraeleni*
5391 Stenzel Crustacés décapodes du Crétacé supérieur de l'état de l'Israë. Bull. Société
5392 Géologique Fr. 5, 311–314.
- 5393 Ren, D., Labandeira, C.C., Santiago-Blay, J.A., Rasnitsyn, A.P., Shih, C., Bashkuev, A., Logan, M.A.V.,
5394 Hotton, C.L., Dilcher, D.L., 2009. A Probable Pollination Mode Before Angiosperms: Eurasian,
5395 Long-Proboscis Scorpionflies. Science 326, 840–846.
- 5396 Ren, D., Nel, A., Prokop, J., 2008. New early griffenfly, *Sinomeganeura huangheensis* from the Late
5397 Carboniferous of northern China (Meganisoptera: Meganeuridae). Insect Syst. Evol. 39, 223–
5398 229.

- 5399 Richards, B.C., 2013. Current status of the International Carboniferous time scale. Carbonif.-Permian
5400 Transit. NM Mus. Nat. Hist. Sci Bull 60, 348–353.
- 5401 Richardson, J.B., Bonamo, P.M., McGregor, D.C., 1993. The spores of *Leclercqia* and the dispersed
5402 spore morphon *Acinosporites lindlarensis* Riegel: a case of gradualistic evolution. Bull. Nat.
5403 Hist. Mus. Geol. Ser. 49, 121–155.
- 5404 Richter, S., Olesen, J., Wheeler, W.C., 2007. Phylogeny of Branchiopoda (Crustacea) based on a
5405 combined analysis of morphological data and six molecular loci. Cladistics 23, 301–336.
- 5406 Richter, S., Scholtz, G., 2001. Phylogenetic analysis of the Malacostraca (Crustacea). J. Zool. Syst.
5407 Evol. Res. 39, 113–136.
- 5408 Riek, E.F., 1976. New Upper Permian insects from Natal, South Africa. Ann. Natal Mus. 22, 755–789.
- 5409 Riek, E.F., Kukalová-Peck, J., 1984. A new interpretation of dragonfly wing venation based upon Early
5410 Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states
5411 in pterygote wings. Can. J. Zool. 62, 1150–1166.
- 5412 Rogers, D.C., 2013. Anostraca catalogus (Crustacea: Branchiopoda). Raffles Bull Zool 61, 525–546.
- 5413 Rogers, R.R., Swisher III, C.C., Sereno, P.C., Monetta, A.M., Forster, C.A., Martínez, R.N., 1993. The
5414 Ischigualasto Tetrapod assemblage (Late Triassic, Argentina) and $^{40}\text{Ar}/^{39}\text{Ar}$ dating of dinosaur
5415 origins. Science 260, 794–797.
- 5416 Ronquist, F., Klopstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D.L., Rasnitsyn, A.P., 2012. A
5417 Total-Evidence Approach to Dating with Fossils, Applied to the Early Radiation of the
5418 Hymenoptera. Syst. Biol. 61, 973–999.
- 5419 Ross, A.J., Cook, E., 1995. The stratigraphy and palaeontology of the Upper Weald Clay (Barremian)
5420 at Smokejacks Brickworks, Ockley, Surrey, England. Cretac. Res. 16, 705–716.
- 5421 Ross, A.J., York, P.V., 2003. A catalogue of the type and figured specimens of Hexapoda from the
5422 Rhynie chert (early Devonian) at The Natural History Museum, London, UK. Trans. R. Soc.
5423 Edinb. Earth Sci. 94.

- 5424 Rota-Stabelli, O., Campbell, L., Brinkmann, H., Edgecombe, G.D., Longhorn, S.J., Peterson, K.J.,
5425 Pisani, D., Philippe, H., Telford, M.J., 2011. A congruent solution to arthropod phylogeny:
5426 phylogenomics, microRNAs and morphology support monophyletic Mandibulata. *Proc. R. Soc.*
5427 *B Biol. Sci.* 278, 298–306.
- 5428 Rota-Stabelli, O., Daley, A.C., Pisani, D., 2013a. Molecular timetrees reveal a Cambrian colonization of
5429 land and a new scenario for ecdysozoan evolution. *Curr. Biol.* 23, 392–398.
- 5430 Rota-Stabelli, O., Lartillot, N., Philippe, H., Pisani, D., 2013b. Serine codon-usage bias in deep
5431 phylogenomics: Pancrustacean relationships as a case study. *Syst. Biol.* 62, 121–133.
- 5432 Rudkin, D.M., Cuggy, M.B., Young, G.A., Thompson, D.P., 2013. An Ordovician pycnogonid (sea
5433 spider) with serially subdivided 'head' region. *J. Paleontol.* 87, 395-405.
- 5434 Rudkin, D.M., Young, G.A., Nowlan, G.S., 2008. The Oldest Horseshoe Crab: A New Xiphosurid from
5435 Late Ordovician Konservat-Lagerstätten Deposits, Manitoba, Canada: The Oldest Horseshoe
5436 Crab. *Palaeontology* 51, 1–9.
- 5437 Sánchez-García, A., Peñalver, E., Pérez-de la Fuente, R., Delclòs, X., 2015. A rich and diverse
5438 tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-
5439 producing forests in North Iberia: palaeobiological implications. *J. Syst. Palaeontol.* 13, 645–
5440 676.
- 5441 Sanders, H.L., 1963. Significance of the Cephalocarida, in: Whittington, H.B., Rolfe, W.D.I. (Eds.),
5442 *Phylogeny and Evolution of Crustacea*. Museum of Comparative Zoology, Cambridge, MA, pp.
5443 163–175.
- 5444 Sanders, K.L., Lee, M.S.Y., 2010. Arthropod molecular divergence times and the Cambrian origin of
5445 pentastomids. *Syst. Biodivers.* 8, 63–74.

5446 Sanggaard, K.W., Bechsgaard, J.S., Fang, X., Duan, J., Dyrland, T.F., Gupta, V., Jiang, X., Cheng, L.,
 5447 Fan, D., Feng, Y., Han, L., Huang, Z., Wu, Z., Liao, L., Settepani, V., Thøgersen, I.B.,
 5448 Vanthournout, B., Wang, T., Zhu, Y., Funch, P., Enghild, J.J., Schauser, L., Andersen, S.U.,
 5449 Villesen, P., Schierup, M.H., Bilde, T., Wang, J., 2014. Spider genomes provide insight into
 5450 composition and evolution of venom and silk. *Nat. Commun.* 5, 3765.

5451 Sano, M., Nishibe, Y., Tanaka, Y., Nishida, S., 2015. Temporally sustained dietary niche partitioning in
 5452 two mesopelagic copepod species and their mouthpart morphology. *Mar. Ecol. Prog. Ser.* 518,
 5453 51–67.

5454 Sasaki, G., Ishiwata, K., Machida, R., Miyata, T., Su, Z.-H., 2013. Molecular phylogenetic analyses
 5455 support the monophyly of Hexapoda and suggest the paraphyly of Entognatha. *BMC Evol.*
 5456 *Biol.* 13, 236.

5457 Sawin, R.S., Franseen, E.K., West, R.R., Ludvigson, G.A., Watney, W.L., 2008. Clarification and
 5458 changes in Permian stratigraphic nomenclature in Kansas. Kansas Geological Survey.

5459 Schachat, S.R., Brown, R.L., 2015. Color Pattern on the Forewing of *Micropterix* (Lepidoptera:
 5460 Micropterigidae): Insights into the Evolution of Wing Pattern and Wing Venation in Moths. *PLoS*
 5461 *ONE* 10, e0139972.

5462 Schachat, S.R., Brown, R.L., 2016. Forewing color pattern in Micropterigidae (Insecta: Lepidoptera):
 5463 homologies between contrast boundaries, and a revised hypothesis for the origin of symmetry
 5464 systems. *BMC Evol. Biol.* 16, 116.

5465 Schawaller, W., Shear, W.A., Bonamo, P.M., 1991. The first Paleozoic pseudoscorpions (Arachnida,
 5466 Pseudoscorpionida). *Am. Mus. Novit.* 3009, 1-17.

5467 Schneider, J.W., Körner, F., Roscher, M., Kroner, U., 2006. Permian climate development in the
 5468 northern peri-Tethys area — The Lodève basin, French Massif Central, compared in a
 5469 European and global context. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 240, 161–183.

5470 Scholtz, G., 2000. Evolution of the nauplius stage in malacostracan crustaceans. *J. Zool. Syst. Evol.*
 5471 *Res.* 38, 175–187.

- 5472 Schram, F.R., 1970. Isopod from the Pennsylvanian of Illinois. *Science* 169, 854–855.
- 5473 Schram, F.R., 1975. A Pennsylvanian Lepadomorph Barnacle from the Mazon Creek Area, Illinois. *J.*
5474 *Paleontol.* 49, 928–930.
- 5475 Schram, F.R., 1984. Fossil Syncarida. *Trans. San Diego Soc. Nat. Hist.* 20, 189–246.
- 5476 Schram, F.R., 1986. *Crustacea*. Oxford University Press, New York.
- 5477 Schram, F.R., 2014. Family level classification within Thylacocephala, with comments on their
5478 evolution and possible relationships. *Crustaceana* 87, 340–363.
- 5479
- 5480 Schram, F.R., Dixon, C.J., 2004. Decapod phylogeny: addition of fossil evidence to a robust
5481 morphological cladistic data set. *Bull. Mizunami Foss. Mus.* 31, 1–19.
- 5482 Schram, F.R., Feldmann, R.M., Copeland, M.J., 1978. The Late Devonian Palaeopalaemonidae and
5483 the earliest decapod crustaceans. *J. Paleontol.* 1375–1387.
- 5484 Schram, F.R., Hof, C.H., 1998. Fossils and the interrelationships of major crustacean groups, in:
5485 Edgecombe, G.D. (Ed.), *Arthropod Fossils and Phylogeny*. Columbia University Press, New
5486 York, pp. 233–302.
- 5487 Schram, F.R., Hof, C.H., Steeman, F.A., 1999. Thylacocephala (Arthropoda: Crustacea?) from the
5488 Cretaceous of Lebanon and implications for thylacocephalan systematics. *Palaeontology* 42,
5489 769–797.
- 5490 Schram, F.R., Koenemann, S., 2004. Are the crustaceans monophyletic?, in: Cracraft, J., Donoghue,
5491 M.J. (Eds.), *Assembling the Tree of Life*. Oxford University Press, New York. pp. 319–329.
- 5492 Schram, F.R., Newman, W.A., 1980. *Verruca withersi* n. sp. (Crustacea: Cirripedia) from the middle of
5493 the Cretaceous of Colombia. *J. Paleontol.* 229–233.
- 5494 Schwarz, A., Cabezas-Cruz, A., Kopecký, J., Valdés, J.J., 2014. Understanding the evolutionary
5495 structural variability and target specificity of tick salivary Kunitz peptides using next generation
5496 transcriptome data. *BMC Evol. Biol.* 14, 1.

- 5497 Schweigert, G., Dietl, G., 1997. Ein fossiler Hundertfüßler (Chilopoda, Geophilida) aus dem
5498 Nusplinger Plattenkalk (Oberjura, Südwestdeutschland). Stuttg. Beitrage Naturkunde B Geol.
5499 Palaontologie 254, 1–111.
- 5500 Schwentner, M., Clavier, S., Fritsch, M., Olesen, J., Padhye, S., Timms, B.V., Richter, S., 2013.
5501 *Cyclestheria hislopi* (Crustacea: Branchiopoda): A group of morphologically cryptic species with
5502 origins in the Cretaceous. Mol. Phylogenet. Evol. 66, 800–810.
- 5503 Schwentner, M., Timms, B.V., Bastrop, R., Richter, S., 2009. Phylogeny of Spinicaudata
5504 (Branchiopoda, Crustacea) based on three molecular markers – An Australian origin for
5505 *Limnadopsis*. Mol. Phylogenet. Evol. 53, 716–725.
- 5506 Scourfield, D.J., 1926. On a New Type of Crustacean from the Old Red Sandstone (Rhynie Chert Bed,
5507 Aberdeenshire)-*Lepidocaris rhyniensis*, gen. et sp. nov. Philos. Trans. R. Soc. Lond. Ser. B
5508 Contain. Pap. Biol. Character 214, 153–187.
- 5509 Scourfield, D.J., 1940a. Two New and Nearly Complete Specimens of Young Stages of the Devonian
5510 Fossil Crustacean *Lepidocaris rhyniensis*. Proc. Linn. Soc. London 152, 290–298.
- 5511 Scourfield, D.J., 1940b. The oldest known fossil insect. Nature 3682, 799–801.
- 5512 Scudder, S.H., 1885. Palaeodictyoptera; Or the Affinities and Classification of Paleozoic Hexapoda.
5513 Mem. Boston Soc. Nat. Hist. 3, 319–351.
- 5514 Scudder, S.H., 1890a. Illustrations of the Carboniferous Arachnida of North America, of the orders
5515 Anthracomarti and Pedipalpi. Mem. Boston Soc. Nat. Hist. 4, 443–456.
- 5516 Scudder, S.H., 1890b. New Carboniferous Myriapoda from Illinois. Mem. Boston Soc. Nat. Hist. 4,
5517 417–442.
- 5518 Secrétan, S., Riou, B., 1983. Un groupe énigmatique de crustacés, ses représentants du Callovien de
5519 La Voulte- sur- Rhône. Ann. Paléontol. 69, 59–97.
- 5520 Secrétan, S., Riou, B., 1986. Les Mysidacés (Crustacea, Peracarida) du Callovien de La Voulte- sur-
5521 Rhône. Ann. Paléontol. 72, 295–323.

- 5522 Selden, P.A., 1996. First fossil mesothele spider, from the Carboniferous of France. *Rev. Suisse Zool.*
5523 2, 585–96.
- 5524 Selden, P.A., 2000. *Palaeothele*, replacement name for the fossil mesothele spider *Eothele* Selden
5525 non Rowell. *Bull.-Br. Arachnol. Soc.* 11, 292–292.
- 5526 Selden, P.A., Huys, R., Stephenson, M.H., Heward, A.P., Taylor, P.N., 2010. Crustaceans from bitumen
5527 clast in Carboniferous glacial diamictite extend fossil record of copepods. *Nat. Commun.* 1, 1–
5528 6.
- 5529 Selden, P.A., Lamsdell, J.C., Qi, L., 2015. An unusual euchelicerate linking horseshoe crabs and
5530 eurypterids, from the Lower Devonian (Lochkovian) of Yunnan, China. *Zool. Scr.* 44, 645–652.
- 5531 Selden, P.A., Shcherbakov, D.E., Dunlop, J.A., Eskov, K.Y., 2014. Arachnids from the Carboniferous of
5532 Russia and Ukraine, and the Permian of Kazakhstan. *Paläontol. Z.* 88, 297–307.
- 5533 Selden, P.A., Shear, W.A., 1996. The first Mesozoic Solifugae (Arachnida), from the Cretaceous of
5534 Brazil, and a redescription of the Palaeozoic solifuge. *Palaeontology* 39, 583–604.
- 5535 Sellards, E.H., 1907. Types of Permian Insects Part II Plectoptera. *Am. J. Sci.* 23, 345–355.
- 5536 Servais, T., Lehnert, O., Li, J., Mullins, G.L., Munnecke, A., Nützel, A., Vecoli, M., 2008. The Ordovician
5537 Biodiversification: revolution in the oceanic trophic chain. *Lethaia* 41, 99–109.
- 5538 Servais, T., Owen, A.W., Harper, D.A.T., Kröger, B., Munnecke, A., 2010. The Great Ordovician
5539 Biodiversification Event (GOBE): The palaeoecological dimension. *Palaeogeogr.*
5540 *Palaeoclimatol. Palaeoecol.* 294, 99–119.
- 5541 Shabica, C.W., Hay, A., 1997. Richardson's guide to the fossil fauna of Mazon Creek. Northeastern
5542 Illinois University, Chicago.
- 5543 Sharma, P.P., Fernández, R., Esposito, L.A., González-Santillan, E., Monod, L., 2015. Phylogenomic
5544 resolution of scorpions reveals multilevel discordance with morphological phylogenetic signal.
5545 *Proc. R. Soc. B Biol. Sci.* 282, 20142953.

- 5546 Sharma, P.P., Kaluziak, S.T., Pérez-Porro, A.R., González, V.L., Hormiga, G., Wheeler, W.C., Giribet,
5547 G., 2014. Phylogenomic Interrogation of Arachnida Reveals Systemic Conflicts in Phylogenetic
5548 Signal. *Mol. Biol. Evol.* 31, 2963–2984.
- 5549 Sharov, A.G., 1961. Otryad Plecoptera (Order Plecoptera). *Paleozojskoe nasekomye Kuznetskovo*
5550 *bassejna* [Paleozoic insects from the Kuznetsk basin]. *Tr. Paleontol. Instituta Akad. Nauk*
5551 *SSSR* 85, 225–234.
- 5552 Shcherbakov, D.E., 1995. A new genus of the Paleozoic order Hypoperlida. *Russ. Entomol. J.* 3, 33–
5553 36.
- 5554 Shcherbakov, D.E., 2000. Permian faunas of Homoptera (Hemiptera) in relation to phytogeography
5555 and the Permo-Triassic crisis. *Paleontol. J.* 34, S251–S267.
- 5556 Shcherbakov, D.E., 2008. On Permian and Triassic insect faunas in relation to biogeography and the
5557 Permian-Triassic crisis. *Paleontol. J.* 42, 15–31.
- 5558 Shear, W.A., Bonamo, P.M., 1988. Devonobiomorpha, a new order of centipeds (Chilopoda) from the
5559 Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centiped orders. *Am.*
5560 *Mus. Novit.* 2927, 1-30.
- 5561 Shear, W.A., Jeram, A.J., Selden, P., 1998. Centiped legs (Arthropoda, Chilopoda, Scutigermorpha)
5562 from the Silurian and Devonian of Britain and the Devonian of North America. *Am. Mus. Novit.*
5563 3231, 1-16.
- 5564 Shelomi, M., Danchin, E.G.J., Heckel, D., Wipfler, B., Bradler, S., Zhou, X., Pauchet, Y., 2016.
5565 Horizontal gene transfer of pectinases from bacteria preceded the diversification of stick and
5566 leaf insects. *Sci. Rep.* 6, 26388.
- 5567 Shen, X., Tian, M., Yan, B., Chu, K., 2015. Phylomitogenomics of Malacostraca (Arthropoda:
5568 Crustacea). *Acta Oceanol. Sin.* 34, 84–92.
- 5569 Shen, Y.-B., 1978. Leaid conchostracans from the Middle Devonian of South China with notes on their
5570 origin, classification and evolution. *Papers for the International Symposium on the Devonian*
5571 *System.* 1-15.

- 5572 Shen, Y.-B., 1983. Restudy of Devonian leaiid conchostracans from Hunan and Guangdong provinces.
5573 Bull. Nanjing Inst. Geol. Palaeontol. Acad. Sin. 6, 185–207.
- 5574 Shen, Y.-B., 1994. A new conchostracan genus (*Loxomegaglyptidae*) from Lower Carboniferous of
5575 Britain. Acta Palaeontol. Sin. 33, 156–165.
- 5576 Shen, Y.-B., Huang, D., 2008. Extant clam shrimp egg morphology: taxonomy and comparison with
5577 other fossil branchiopod eggs. J. Crustac. Biol. 28, 352–360.
- 5578 Shen, Y.-B., Schram, F.R., 2014. Soft-body preservation in the leaiid clam shrimp (Branchiopoda,
5579 Diplostraca) and its palaeoecological implications. Crustaceana 87, 1338–1350.
- 5580 Shen, Y.-B., Taylor, R.S., Schram, F.R., 1998. A new spelaeogriphacean (Crustacea: Peracarida) from
5581 the Upper Jurassic of China. Contrib. Zool. 68, 19–35.
- 5582 Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age
5583 constraint on Burmese amber based on U–Pb dating of zircons. Cretac. Res. 37, 155–163.
- 5584 Shmakov, A.S., 2008. The Jurassic thrips *Liassothrips crassipes* (Martynov, 1927) and its taxonomic
5585 position in the order Thysanoptera (Insecta). Paleontol. J. 42, 47–52.
- 5586 Shmakov, A.S., 2009. The oldest members of the families Aeolothripidae and Thripidae (Insecta:
5587 Thysanoptera) from the Lower Cretaceous of Transbaikalia. Paleontol. J. 43, 428–432.
- 5588 Shultz, J.W., 2007. A phylogenetic analysis of the arachnid orders based on morphological characters.
5589 Zool. J. Linn. Soc. 150, 221–265.
- 5590 Siddall, M.E., Whiting, M.F., 1999. Long-branch abstractions. Cladistics 15, 9–24.
- 5591 Simon, S., Narechania, A., DeSalle, R., Hadrys, H., 2012. Insect Phylogenomics: Exploring the Source
5592 of Incongruence Using New Transcriptomic Data. Genome Biol. Evol. 4, 1295–1309.
- 5593 Simon, S., Strauss, S., von Haeseler, A., Hadrys, H., 2009. A Phylogenomic Approach to Resolve the
5594 Basal Pterygote Divergence. Mol. Biol. Evol. 26, 2719–2730.
- 5595 Sinitisa, S.M., Starukhina, L.P., 1986. New data and problems of stratigraphy and paleontology of
5596 Upper Mesozoic of Trans-Baikal region. New Data Trans-Baikal Geol. 46–51.

- 5597 Sinitshenkova, N.D., 1987. Historical development of stoneflies. Tr Paleontol Inst Akad Nauk SSSR
5598 221, 1–143.
- 5599 Sinitshenkova, N.D., 2005. The oldest known record of an imago of Nemouridae (Insecta: Perlida =
5600 Plecoptera) in the late Mesozoic of eastern Transbaikalia. Paleontol. J. 39, 38–40.
- 5601 Sinitshenkova, N.D., Marchal-Papier, F., Grauvogel-Stamm, L., Gall, J.-C., 2005. The Ephemeroidea
5602 (Insecta) from the Grès à Voltzia (early Middle Triassic) of the Vosges (NE France). Paläontol.
5603 Z. 79, 377–397.
- 5604 Siveter, D.J., 2008. The Silurian Herefordshire Konservat-Lagerstätte: a unique window on the
5605 evolution of life. Proc. Shropsh. Geol. Soc. 13, 58–61.
- 5606 Siveter, D.J., Briggs, D.E.G., Siveter, D.J., Sutton, M.D., Joomun, S.C., 2013. A Silurian myodocope
5607 with preserved soft-parts: cautioning the interpretation of the shell-based ostracod record.
5608 Proc. R. Soc. B Biol. Sci. 280, 20122664.
- 5609 Siveter, D.J., Sutton, M.D., Briggs, D.E., Siveter, D.J., 2004. A Silurian sea spider. Nature 431, 978–
5610 980.
- 5611 Siveter, D.J., Tanaka, G., Farrell, Ú.C., Martin, M.J., Siveter, D.J., Briggs, D.E.G., 2014. Exceptionally
5612 Preserved 450-Million-Year-Old Ordovician Ostracods with Brood Care. Curr. Biol. 24, 801–
5613 806.
- 5614 Smith, M.R., Ortega-Hernández, J., 2014. *Hallucigenia*'s onychophoran-like claws and the case for
5615 Tactopoda. Nature 514, 363–366.
- 5616 Sohn, J.-C., Labandeira, C.C., Davis, D.R., 2015. The fossil record and taphonomy of butterflies and
5617 moths (Insecta, Lepidoptera): implications for evolutionary diversity and divergence-time
5618 estimates. BMC Evol. Biol. 15, 12.
- 5619 Sohn, J.-C., Labandeira, C.C., Davis, D.R., Mitter, C., 2012. An annotated catalog of fossil and
5620 subfossil Lepidoptera (Insecta: Holometabola) of the world. Zootaxa 3286, 1–132.

- 5621 Sologlad, M.E., Fet, V., Kovařík, F., 2005. The systematic position of the scorpion genera
5622 *Heteroscorpion* Birula, 1903 and *Urodacus* Peters, 1861 (Scorpiones: Scorpionoidea).
5623 *Euscorpius* 2005, 1–37.
- 5624 Song, F., Li, H., Jiang, P., Zhou, X., Liu, J., Sun, C., Vogler, A.P., Cai, W., 2016. Capturing the
5625 phylogeny of Holometabola with mitochondrial genome data and Bayesian site-heterogeneous
5626 mixture models. *Genome Biol. Evol.* 8, 1411–1426.
- 5627 Song, H., Amédégno, C., Cigliano, M.M., Desutter-Grandcolas, L., Heads, S.W., Huang, Y., Otte, D.,
5628 Whiting, M.F., 2015. 300 million years of diversification: elucidating the patterns of orthopteran
5629 evolution based on comprehensive taxon and gene sampling. *Cladistics* 31, 621–651.
- 5630 Soriano, C., Gratshev, V.G., Delclòs, X., 2006. New Early Cretaceous weevils (Insecta, Coleoptera,
5631 Curculionoidea) from El Montsec, Spain. *Cretac. Res.* 27, 555–564.
- 5632 Sowerby, J.C., 1836. Descriptive notes respecting the shells figured in Plates XI–XXIII Appendix A:
5633 335–348, in: Fitton, W.H. (Ed.), *Observations on Some of the Strata between the Chalk and the*
5634 *Oxford Oolite in the South-East of England*, Transactions of the Geological Society of London.
5635 pp. 103–389.
- 5636 Spalletti, L.A., Fanning, M., Rapela, C.W., 2009. Dating the Triassic continental rift in the southern
5637 Andes: the Potrerillos Formation, Cuyo basin, Argentina. *Geol. Acta* 6, 267–283.
- 5638 Spears, T., Abele, L.G., 2000. Branchiopod Monophyly and Interordinal Phylogeny Inferred from 18s
5639 Ribosomal DNA. *J. Crustac. Biol.* 20, 1–24.
- 5640 Spears, T., DeBry, R.W., Abele, L.G., Chodyla, K., 2005. Peracarid monophyly and interordinal
5641 phylogeny inferred from nuclear small-subunit ribosomal DNA sequences (Crustacea:
5642 Malacostraca: Peracarida). *Proc. Biol. Soc. Wash.* 118, 117–157.
- 5643 Sroka, P., Staniczek, A.H., Bechly, G., 2015. Revision of the giant pterygote insect *Bojophlebia prokopi*
5644 Kukalová-Peck, 1985 (Hydropalaeoptera: Bojophlebiidae) from the Carboniferous of the Czech
5645 Republic, with the first cladistic analysis of fossil palaeopterous insects. *J. Syst. Palaeontol.* 13,
5646 963–982.

- 5647 Staniczek, A., Bechly, G., Godunko, R., 2011. Coxoplectoptera, a new fossil order of Palaeoptera
5648 (Arthropoda: Insecta), with comments on the phylogeny of the stem group of mayflies
5649 (Ephemeroptera). *Insect Syst. Evol.* 42, 101–138.
- 5650 Starr, H.W., Hegna, T.A., McMenamin, M.A.S., 2016 (in press). Epilogue to the tale of the Triassic
5651 amphipod: *Rosagammarus* McMenamin, Zapata and Hussey, 2013 is a decapod tail (Luning
5652 Formation, Nevada, USA). *J. Crustac. Biol.*
- 5653 Starrett, J., Hedin, M., Ayoub, N., Hayashi, C.Y., 2013. Hemocyanin gene family evolution in spiders
5654 (Araneae), with implications for phylogenetic relationships and divergence times in the
5655 infraorder Mygalomorphae. *Gene* 524, 175–186.
- 5656 Stenderup, J.T., Olesen, J., Glenner, H., 2006. Molecular phylogeny of the Branchiopoda (Crustacea)–
5657 Multiple approaches suggest a “diplostracan” ancestry of the Notostraca. *Mol. Phylogenet.*
5658 *Evol.* 41, 182–194.
- 5659 Stewart, W.D., 1991. Stratigraphy and sedimentology of the Chancellor succession (Middle and Upper
5660 Cambrian) southeastern Canadian Rocky Mountains. (PhD). University of Ottawa, Ottawa,
5661 Canada.
- 5662 Strausfeld, N.J., Andrew, D.R., 2011. A new view of insect–crustacean relationships I. Inferences from
5663 neural cladistics and comparative neuroanatomy. *Arthropod Struct. Dev.* 40, 276–288.
- 5664 Sturm, H., 1998. Erstnachweis fischchenartiger Insekten (*Zygentoma*, Insecta) für das Mesozoikum
5665 (Untere Kreide, Brasilien). *Sencken. Lethaea* 78, 135–140.
- 5666 Sturm, H., Poinar, G.O., 1998. *Cretaceomachilis libanensis*, the Oldest Known Bristle-tail of the Family
5667 Meinertellidae (Machiloidea, Archaeognatha, Insecta) from the Lebanese Amber. *Dtsch.*
5668 *Entomol. Z.* 45, 43–48.
- 5669 Sukatsheva, I.D., Beattie, R., Mostovski, M.B., 2007. *Permomerope natalensis* sp. n. from the
5670 Lopingian of South Africa, and a redescription of the type species of *Permomerope*
5671 (Trichoptera: Protomeropidae). *Afr. Invertebr.* 48, 245–251.

- 5672 Sukatsheva, I.D., Vassilenko, D.V., 2011. Caddisflies from Chernovskie Kopi (Jurassic/Cretaceous of
5673 Transbaikalia). *Zoosymposia* 5, 434–438.
- 5674 Sun, X.-Y., Xia, X., Yang, Q., 2015 (in press). Dating the origin of the major lineages of Branchiopoda.
5675 *Palaeoworld*.
- 5676 Sutton, M.D., Briggs, D.E.G., Siveter, D.J., Siveter, D.J., Orr, P.J., 2002. The arthropod *Offacolus kingi*
5677 (Chelicerata) from the Silurian of Herefordshire, England: computer based morphological
5678 reconstructions and phylogenetic affinities. *Proc. R. Soc. B Biol. Sci.* 269, 1195–1203.
- 5679 Svenson, G.J., Whiting, M.F., 2009. Reconstructing the origins of praying mantises (Dictyoptera,
5680 Mantodea): the roles of Gondwanan vicariance and morphological convergence. *Cladistics* 25,
5681 468–514.
- 5682 Tasch, P., 1987. Fossil Conchostraca of the Southern Hemisphere and continental drift. *Geol. Soc.*
5683 *Am. Mem.* 165, 1–282.
- 5684 Tasch, P., 1962. Vertical extension of mid-continent Leonardian insect occurrences. *Science* 135, 378–
5685 379.
- 5686 Taylor, J.F., Repetski, J.E., Loch, J.D., Leslie, S.A., 2012. Biostratigraphy and chronostratigraphy of
5687 the Cambrian–Ordovician great American carbonate bank, in: Derby, J.R., Fritz, R.D.,
5688 Longacre, S.A., Morgan, W.A., Sternbach, C.A. (Eds.), *The Great American Carbonate Bank:
5689 The Geology and Economic Resources of the Cambrian – Ordovician Sauk Megasequence of
5690 Laurentia*, AAPG Memoir. pp. 15–35.
- 5691 Taylor, R.S., Schram, F.R., Shen, Y.-B., 2001. A new upper Middle Triassic shrimp (Crustacea:
5692 Lophogastrida) from Guizhou, China, with discussion regarding other fossil “mysidaceans”. *J.*
5693 *Paleontol.* 75, 310–318.
- 5694 Taylor, R.S., Shen, Y.-B., Schram, F.R., 1998. New pygocephalomorph crustaceans from the Permian of
5695 China and their phylogenetic relationships. *Palaeontology* 41, 815–834.
- 5696 Terry, M.D., Whiting, M.F., 2005. Mantophasmatodea and phylogeny of the lower neopterous insects.
5697 *Cladistics* 21, 240–257.

- 5698 Tetlie, O.E., Dunlop, J.A., 2008. *Geralinura carbonaria* (Arachnida; Uropygi) from Mazon Creek,
5699 Illinois, USA, and the Origin of Subchelate Pedipalps in Whip Scorpions. J. Paleontol. 82, 299–
5700 312.
- 5701 Thomas, J.A., Trueman, J.W.H., Rambaut, A., Welch, J.J., 2013. Relaxed Phylogenetics and the
5702 Palaeoptera Problem: Resolving Deep Ancestral Splits in the Insect Phylogeny. Syst. Biol. 62,
5703 285–297.
- 5704 Thorell, T., Lindström, G., 1885. On a Silurian scorpion from Gotland. Kungl Sven Vetenskaps 21, 1–
5705 33.
- 5706 Tillyard, R.J., 1918. Mesozoic insects of Queensland. No. 3. Odonata and Protodonata. Proc. Linn.
5707 Soc. New South Wales 43, 417–436.
- 5708 Tillyard, R.J., 1922. Some new Permian insects from Belmont, NSW in the collection of Mr. John
5709 Mitchell. Proc. Linn. Soc. New South Wales. pp. 279–292.
- 5710 Tillyard, R.J., 1926. Kansas Permian insects; Part 7, The order Mecoptera. Am. J. Sci. 133–164.
- 5711 Tillyard, R.J., 1928. Some remarks on the Devonian fossil insects from the Rhynie chert beds, Old
5712 Red Sandstone. Trans. R. Entomol. Soc. Lond. 76, 65–71.
- 5713 Tillyard, R.J., 1932. Kansas Permian insects; Part 15, The order Plectoptera. Am. J. Sci. 97–134.
- 5714 Timm, L., Bracken-Grissom, H.D., 2015. The forest for the trees: evaluating molecular phylogenies
5715 with an emphasis on higher-level Decapoda. J. Crustac. Biol. 35, 577–592.
- 5716 Tong, K.J., Duchêne, S., Ho, S.Y., Lo, N., 2015. Comment on “Phylogenomics resolves the timing and
5717 pattern of insect evolution.” Science 349, 487.
- 5718 Trussova, E.K., 1971. On the first finding of the Mesozoic species of order Anostraca (Crustacea).
5719 Paleontol. Zhurnal 4, 68–73.
- 5720 Trussova, E.K., 1975. On the taxonomic state of Anostraca, Crustacea from the lower Cretaceous of
5721 the Eastern Transbaikial. Paleontol. Sb. 12, 60–66.

- 5722 Tsang, L.M., Schubart, C.D., Ahyong, S.T., Lai, J.C.Y., Au, E.Y.C., Chan, T.-Y., Ng, P.K.L., Chu, K.H.,
5723 2014. Evolutionary History of True Crabs (Crustacea: Decapoda: Brachyura) and the Origin of
5724 Freshwater Crabs. *Mol. Biol. Evol.* 31, 1173–1187.
- 5725 Vakhrameev, V.A., Kotova, I.Z., 1977. Ancient angiosperms and accompanying plants from the Lower
5726 Cretaceous of Transbaikalia. *Palaeontol. J.* 11, 487–495.
- 5727 Valencio, D.A., Mendia, J.E., Vilas, J.F., 1975. Paleomagnetism and K-Ar ages of Triassic igneous
5728 rocks from the Ischigualasto-Ischichuca Basin and Puesto Viejo Formation, Argentina. *Earth*
5729 *Planet. Sci. Lett.* 26, 319–330.
- 5730 van Nieukerken, E.J., Kaila, L., Kitching, I.J., Kristensen, N.P., Lees, D.J., Minet, J., Mitter, J.,
5731 Mutanen, M., Regier, J.C., Simonsen, T.J., Wahlberg, N., Yen, S.-H., Zahiri, R., Adamski, D.,
5732 Baixeras, J., Bartsch, D., Bengtsson, B.Å., Brown, J.W., Bucheli, R.S., Davis, D.R., De Prins,
5733 J., De Prins, W., Epstein, M.E., Gentili-Poole, P., Gielis, C., Hättenschwiler, P., Hausmann, A.,
5734 Holloway, J.P., Kallies, A., Karsholt, O., Kawahara, A., Koster, S.J.C., Kozlov, M.V., Lafontaine,
5735 J.D., Lamas, G., Landry, J.-F., Lee, S., Nuss, M., Park, K.-T., Penz, C., Rota, J., Schmidt, B.C.,
5736 Schintlmeister, A., Sohn, J.C., Solis, M.A., Tarmann, G., Warren, A.D., Weller, S., Yakovlev, Y.,
5737 Zolotuhin, V.V., Zwick, A., 2011. Order Lepidoptera Linnaeus, 1758. *Zootaxa* 3148, 212–221.
- 5738 Vannier, J., Chen, J.-Y., Huang, D.-Y., Charbonnier, S., Wang, X.-Q., 2006. The Early Cambrian origin
5739 of thylacocephalan arthropods. *Acta Palaeontol. Pol.* 51, 201–214.
- 5740 Vannier, J., Schoenemann, B., Gillot, T., Charbonnier, S., Clarkson, E., 2016. Exceptional preservation
5741 of eye structure in arthropod visual predators from the Middle Jurassic. *Nat. Commun.* 7,
5742 10320.
- 5743 Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., Hariri, K. el, Briggs, D.E.G.,
5744 2010. Ordovician faunas of Burgess Shale type. *Nature* 465, 215–218.
- 5745 Van Straelen, V., 1923. Les Mysidacés du Callovien de La Voulte- sur- Rhône (Ardèche). *Bull. Société*
5746 *Géologique Fr.* 23, 431–439.

- 5747 Vía Boada, L., Villalta, J.F., 1966. *Heterolimulus gadeai* nov. gen., nov. sp., representante de una
5748 nueva familia de Limulacea en el Triásico español. Acta Geológica Hispánica 1, 9–11.
- 5749 von Reumont, B.M., Jenner, R.A., Wills, M.A., Dell’Ampio, E., Pass, G., Ebersberger, I., Meyer, B.,
5750 Koenemann, S., Iliffe, T.M., Stamatakis, A., Niehuis, O., Meusemann, K., Misof, B., 2012.
5751 Pancrustacean Phylogeny in the Light of New Phylogenomic Data: Support for Remipedia as
5752 the Possible Sister Group of Hexapoda. Mol. Biol. Evol. 29, 1031–1045.
- 5753 Vonk, R., Schram, F.R., 2007. Three new tanaid species (Crustacea, Peracarida, Tanaidacea) from the
5754 Lower Cretaceous Alava amber in northern Spain. J. Paleontol. 81, 1502-1509.
- 5755 Vršanský, P., Aristov, D., 2014. Termites (Isoptera) from the Jurassic/Cretaceous boundary: Evidence
5756 for the longevity of their earliest genera. Eur. J. Entomol. 111, 137–141.
- 5757 Waddington, J., Rudkin, D.M., Dunlop, J.A., 2015. A new mid-Silurian aquatic scorpion--one step
5758 closer to land? Biol. Lett. 11, 20140815.
- 5759 Wahlberg, N., Wheat, C.W., Peña, C., 2013. Timing and Patterns in the Taxonomic Diversification of
5760 Lepidoptera (Butterflies and Moths). PLoS ONE 8, e80875.
- 5761 Walcott, C.D., 1911. Middle Cambrian Merostomata. Smithson. Misc. Collect. 57, 17–40.
- 5762 Walossek, D., 1993. The upper Cambrian *Rehbachella* and the phylogeny of Branchiopoda and
5763 Crustacea. Lethaia 26, 318–318.
- 5764 Walossek, D., Müller, K.J., 1994. Pentastomid parasites from the Lower Palaeozoic of Sweden. Trans.
5765 R. Soc. Edinb. Earth Sci. 85, 1–37.
- 5766 Walossek, D., Müller, K.J., 1998. Cambrian “Orsten”-type arthropods and the phylogeny of Crustacea,
5767 in: Arthropod Relationships. Springer, pp. 139–153.
- 5768 Waloszek, D., Dunlop, J.A., 2002. A larval sea spider (Arthropoda: Pycnogonida) from the Upper
5769 Cambrian “Orsten” of Sweden, and the phylogenetic position of pycnogonids. Palaeontology
5770 45, 421–446.
- 5771 Wang, B., Zhang, H., 2010. Earliest evidence of fishflies (Megaloptera: Corydalidae): an exquisitely
5772 preserved larva from the Middle Jurassic of China. J. Paleontol. 84, 774-780.

- 5773 Wang, M., Béthoux, O., Bradler, S., Jacques, F.M.B., Cui, Y., Ren, D., 2014. Under Cover at Pre-
5774 Angiosperm Times: A Cloaked Phasmatodean Insect from the Early Cretaceous Jehol Biota.
5775 PLoS ONE 9, e91290.
- 5776 Wang, X., Wang, Y., Zhang, F., Zhang, J., Zhou, Z.-H., Jin, F., Hu, Y.-M., Gu, G., Hai-Chun, Z., 2000.
5777 Vertebrate biostratigraphy of the lower cretaceous Yixian formation in Lingyuan, western
5778 Liaoning and its neighboring southern Nei Mongol (inner Mongolia), China. *Vertebr. Palasiat.*
5779 38, 95–101.
- 5780 Wang, X., Zhou, Z., He, H., Fan, J., Wang, Y., Zhang, J., Wang, Y., Zhang, F., 2005. Stratigraphy and
5781 age of the Daohugou Bed in Ningcheng, Inner Mongolia. *Chin. Sci. Bull.* 50, 2369.
- 5782 Wang, Y., Liu, X., Winterton, S.L., Yang, D., 2012. The First Mitochondrial Genome for the Fishfly
5783 Subfamily Chauliodinae and Implications for the Higher Phylogeny of Megaloptera. *PLoS ONE*
5784 7, e47302.
- 5785 Ware, J.L., Grimaldi, D.A., Engel, M.S., 2010. The effects of fossil placement and calibration on
5786 divergence times and rates: An example from the termites (Insecta: Isoptera). *Arthropod Struct.*
5787 *Dev.* 39, 204–219.
- 5788 Ware, J.L., Litman, J., Klass, K.-D., Spearman, L.A., 2008. Relationships among the major lineages of
5789 Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. *Syst. Entomol.* 33,
5790 429–450.
- 5791 Warnock, R.C.M., Parham, J.F., Joyce, W.G., Lyson, T.R., Donoghue, P.C.J., 2015. Calibration
5792 uncertainty in molecular dating analyses: there is no substitute for the prior evaluation of time
5793 priors. *Proc. R. Soc. B Biol. Sci.* 282, 20141013.
- 5794 Warnock, R.C.M., Yang, Z., Donoghue, P.C.J., 2012. Exploring uncertainty in the calibration of the
5795 molecular clock. *Biol. Lett.* 8, 156–159.
- 5796 Waters, C.N., Davies, S.J., 2006. Carboniferous: extensional basins, advancing deltas and coal
5797 swamps. *Geol. Engl. Wales* 173–223.

- 5798 Waters, C.N., Glover, B.W., Powell, J.H., 1994. Structural synthesis of S Staffordshire, UK:
5799 Implications for the Variscan evolution of the Pennine Basin. J. Geol. Soc. Lond. 151, 697–713.
- 5800 Weber, B., Zhu, M., 2003. Arthropod trace fossils from the Zhujiqing Formation (Meishucunian,
5801 Yunnan) and their palaeobiological implications. Prog. Nat. Sci. 13, 795–800.
- 5802 Wedmann, S., Makarkin, V.N., 2007. A new genus of Mantispidae (Insecta: Neuroptera) from the
5803 Eocene of Germany, with a review of the fossil record and palaeobiogeography of the family.
5804 Zool. J. Linn. Soc. 149, 701–716.
- 5805 Weekers, P.H., Murugan, G., Vanfleteren, J.R., Belk, D., Dumont, H.J., 2002. Phylogenetic analysis of
5806 anostracans (Branchiopoda: Anostraca) inferred from nuclear 18S ribosomal DNA (18S rDNA)
5807 sequences. Mol. Phylogenet. Evol. 25, 535–544.
- 5808 Wellman, C.H., 1993. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven
5809 Group, Scotland. J. Micropalaeontology 12, 47–66.
- 5810 Whalley, P., 1978. New taxa of fossil and recent Micropterigidae with a discussion of their evolution
5811 and a comment on the evolution of Lepidoptera (Insecta). Ann. Transvaal Mus. 31, 71–86.
- 5812 Whalley, P.E., 1985. The systematics and palaeogeography of the Lower Jurassic insects of Dorset,
5813 England. Bull. Br. Mus. Nat. Hist. Geol. 39, 107–189.
- 5814 Whalley, P., 1986. A review of the current fossil evidence of Lepidoptera in the Mesozoic. Biol. J. Linn.
5815 Soc. 28, 253–271.
- 5816 Whalley, P., Jarzembowski, E.A., 1981. A new assessment of *Rhyniella*, the earliest known insect,
5817 from the Devonian of Rhynie, Scotland. Nature 291, 317.
- 5818 Wheat, C.W., Wahlberg, N., 2013. Phylogenomic Insights into the Cambrian Explosion, the
5819 Colonization of Land and the Evolution of Flight in Arthropoda. Syst. Biol. 62, 93–109.
- 5820 Wheeler, W.C., Whiting, M., Wheeler, Q.D., Carpenter, J.M., 2001. The Phylogeny of the Extant
5821 Hexapod Orders. Cladistics 17, 113–169.
- 5822 Whitfield, R.P., 1880. Notice of new forms of fossil crustaceans from the Upper Devonian rocks of
5823 Ohio, with descriptions of new genera and species. Am. J. Sci. 109, 33–42.

- 5824 Whitfield, R.P., 1885. An American Silurian scorpion. *Science* 6, 183–184.
- 5825 Whiting, M.F., 2002. Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and
5826 Siphonaptera. *Zool. Scr.* 31, 93–104.
- 5827 Whiting, M.F., Carpenter, J.C., Wheeler, Q.D., Wheeler, W.C., 1997. The Strepsiptera problem:
5828 Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA
5829 sequences and morphology. *Syst. Biol.* 46, 1–68.
- 5830 Whittington, H.B., 1981. Rare arthropods from the Burgess Shale, Middle Cambrian, British Columbia.
5831 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 329–357.
- 5832 Wiegmann, B.M., Trautwein, M.D., Kim, J.-W., Cassel, B.K., Bertone, M.A., Winterton, S.L., Yeates,
5833 D.K., 2009. Single-copy nuclear genes resolve the phylogeny of the holometabolous insects.
5834 *BMC Biol.* 7, 34.
- 5835 Wiegmann, B.M., Trautwein, M.D., Winkler, I.S., Barr, N.B., Kim, J.-W., Lambkin, C., Bertone, M.A.,
5836 Cassel, B.K., Bayless, K.M., Heimberg, A.M., Wheeler, B.M., Peterson, K.J., Pape, T., Sinclair,
5837 B.J., Skevington, J.H., Blagoderov, V., Caravas, J., Kutty, S.N., Schmidt-Ott, U., Kampmeier,
5838 G.E., Thompson, F.C., Grimaldi, D.A., Beckenbach, A.T., Courtney, G.W., Friedrich, M., Meier,
5839 R., Yeates, D.K., 2011. Episodic radiations in the fly tree of life. *Proc. Natl. Acad. Sci.* 108,
5840 5690–5695.
- 5841 Wiens, J.J., Lapoint, R.T., Whiteman, N.K., 2015. Herbivory increases diversification across insect
5842 clades. *Nat. Commun.* 6, 8370.
- 5843 Wilkinson, R.D., Steiper, M.E., Soligo, C., Martin, R.D., Yang, Z., Tavaré, S., 2011. Dating primate
5844 divergences through an integrated analysis of palaeontological and molecular data. *Syst. Biol.*
5845 60, 16–31.
- 5846 Williams, M., Siveter, D.J., Salas, M.J., Vannier, J., Popov, L.E., Ghobadi Pour, M., 2008. The earliest
5847 ostracods: the geological evidence. *Lethaia* 88, 11–21.
- 5848 Wills, M.A., 2001. How good is the fossil record of arthropods? An assessment using the stratigraphic
5849 congruence of cladograms. *Geol. J.* 36, 187–210.

- 5850 Wills, M.A., Briggs, D.E., Fortey, R.A., Wilkinson, M., Sneath, P.H., 1998. An arthropod phylogeny
5851 based on fossil and recent taxa, in: Edgecombe, G.D. (Ed.), *Arthropod Fossils and Phylogeny*.
5852 Columbia University Press, New York, pp. 33–105.
- 5853 Wills, M.A., Jenner, R.A., Dhubhghaill, C.N., 2009. Eumalacostracan evolution: conflict between three
5854 sources of data. *Arthropod Syst. Phylogeny* 67, 71–90.
- 5855 Wilson, G.D.F., 2009. The phylogenetic position of the Isopoda in the Peracarida (Crustacea:
5856 Malacostraca). *Arthropod Syst. Phylogeny* 67, 159–198.
- 5857 Wilson, G.D.F., 2012. Fossils in the phylogeny of isopod crustaceans (Arthropoda). Presented at the
5858 2012 GSA Annual Meeting, Charlotte, NC.
- 5859 Wilson, H.M., 2001. First Mesozoic scutigeromorph centipede, from the Lower Cretaceous of Brazil.
5860 *Palaeontology* 44, 489–495.
- 5861 Wilson, H.M., 2006. Juliformian Millipedes from the Lower Devonian of Euramerica: Implications for
5862 the Timing of Millipede Cladogenesis in the Paleozoic. *J. Paleontol.* 80, 638–649.
- 5863 Wilson, H.M., Anderson, L.I., 2004. Morphology and Taxonomy of Paleozoic Millipedes (Diplopoda:
5864 Chilognatha: Archipolypoda) from Scotland. *J. Paleontol.* 78, 169–184.
- 5865 Wilson, H.M., Martill, D.M., 2001. A new japygid dipluran from the Lower Cretaceous of Brazil.
5866 *Palaeontology* 44, 1025–1031.
- 5867 Wilson, J.S., von Dohlen, C.D., Forister, M.L., Pitts, J.P., 2013. Family-Level Divergences in the
5868 Stinging Wasps (Hymenoptera: Aculeata), with Correlations to Angiosperm Diversification.
5869 *Evol. Biol.* 40, 101–107.
- 5870 Wingstrand, K.G., 1972. Comparative spermatology of a pentastomid, *Raillietiella hemidactyli*, and a
5871 branchiuran crustacean, *Argulus foliaceus*, with a discussion of pentastomid relationships. Det
5872 K. Dan. Vidensk. Selsk. Biol. Skr. 19, 1–72.
- 5873 Winterton, S.L., Hardy, N.B., Wiegmann, B.M., 2010. On wings of lace: phylogeny and Bayesian
5874 divergence time estimates of Neuropterida (Insecta) based on morphological and molecular
5875 data. *Syst. Entomol.* 35, 349–378.

- 5876 Wipfler, B., Bai, M., Schoville, S., Dallai, R., Uchifune, T., Machida, R., Cui, Y., Beutel, R.G., 2014. Ice
5877 Crawlers (Grylloblattodea)—the history of the investigation of a highly unusual group of insects.
5878 J. Insect Biodivers. 2, 1–25.
- 5879 Wipfler, B., Machida, R., Müller, B., Beutel, R.G., 2011. On the head morphology of Grylloblattodea
5880 (Insecta) and the systematic position of the order, with a new nomenclature for the head
5881 muscles of Dicondylia. Syst. Entomol. 36, 241–266.
- 5882 Wirkner, C.S., Richter, S., 2010. Evolutionary morphology of the circulatory system in Peracarida
5883 (Malacostraca; Crustacea). Cladistics 26, 143–167.
- 5884 Wissler, L., Gadau, J., Simola, D.F., Helmkampf, M., Bornberg-Bauer, E., 2013. Mechanisms and
5885 Dynamics of Orphan Gene Emergence in Insect Genomes. Genome Biol. Evol. 5, 439–455.
- 5886 Withers, T.H., 1914. Some Cretaceous and Tertiary cirripedes referred to *Pollicipes*. Annals and
5887 Magazine of Natural History, Series 8, 14, 167–206.
- 5888 Withers, T.H., 1935. Catalogue of fossil Cirripedia in the Department of Geology. Vol II. Cretaceous.
5889 Trustees of the British Museum (Natural History), London.
- 5890 Wolfe, J.M., Hegna, T.A., 2014. Testing the phylogenetic position of Cambrian pancrustacean larval
5891 fossils by coding ontogenetic stages. Cladistics 30, 366–390.
- 5892 Womack, T., Slater, B.J., Stevens, L.G., Anderson, L.I., Hilton, J., 2012. First cladoceran fossils from
5893 the Carboniferous: Palaeoenvironmental and evolutionary implications. Palaeogeogr.
5894 Palaeoclimatol. Palaeoecol. 344–345, 39–48.
- 5895 Wood, H.M., Matzke, N.J., Gillespie, R.G., Griswold, C.E., 2013. Treating Fossils as Terminal Taxa in
5896 Divergence Time Estimation Reveals Ancient Vicariance Patterns in the Palpimanoid Spiders.
5897 Syst. Biol. 62, 264–284.
- 5898 Wu, H., Huang, D., 2012. A New Species of *Liadotaulius* (Insecta: Trichoptera) from the Middle
5899 Jurassic of Daohugou, Inner Mongolia. Acta Geol. Sin. 86, 320–324.
- 5900 Xie, X., Wang, Y., Shen, H., 2004. Facies Analysis and Sedimentary Environment Reconstruction of
5901 the Late Carboniferous in Zhongwei, Ningxia. Acta Sedimentol. Sin. 22, 19–28.

- 5902 Xiong, Y., Gao, Y., Yin, W., Luan, Y., 2008. Molecular phylogeny of Collembola inferred from ribosomal
5903 RNA genes. *Mol. Phylogenet. Evol.* 49, 728–735.
- 5904 Xu, X., Liu, F., Cheng, R.-C., Chen, J., Xu, X., Zhang, Z., Ono, H., Pham, D.S., Norma-Rashid, Y.,
5905 Arnedo, M.A., Kuntner, M., Li, D., 2015. Extant primitively segmented spiders have recently
5906 diversified from an ancient lineage. *Proc. R. Soc. B Biol. Sci.* 282, 20142486.
- 5907 Yang, F., 1987. Early Late Carboniferous ammonoids from Zhongwei, Ningxia Autonomous Region,
5908 China. *Geoscience* 1, 157–172.
- 5909 Yang, J.-S., Lu, B., Chen, D.-F., Yu, Y.-Q., Yang, F., Nagasawa, H., Tsuchida, S., Fujiwara, Y., Yang,
5910 W.-J., 2013. When Did Decapods Invade Hydrothermal Vents? Clues from the Western Pacific
5911 and Indian Oceans. *Mol. Biol. Evol.* 30, 305–309.
- 5912 Yang, S., Tian, S., Zheng, Z., 1988. Namurian conodonts from Xiaoyuchuan, Ningxia. *Prof. Pap.*
5913 *Stratigr. Palaeontol.* 22, 23–30.
- 5914 Yang, Z., Rannala, B., 2006. Bayesian estimation of species divergence times under a molecular clock
5915 using multiple fossil calibrations with soft bounds. *Mol. Biol. Evol.* 23, 212–226.
- 5916 Yoshizawa, K., 2011. Monophyletic Polyneoptera recovered by wing base structure. *Syst. Entomol.* 36,
5917 377–394.
- 5918 Yoshizawa, K., Johnson, K.P., 2003. Phylogenetic position of Phthiraptera (Insecta: Paraneoptera) and
5919 elevated rate of evolution in mitochondrial 12S and 16S rDNA. *Mol. Phylogenet. Evol.* 29, 102–
5920 114.
- 5921 Yoshizawa, K., Saigusa, T., 2001. Phylogenetic analysis of paraneopteran orders (Insecta: Neoptera)
5922 based on forewing base structure, with comments on monophyly of Auchenorrhyncha
5923 (Hemiptera). *Syst. Entomol.* 26, 1–13.
- 5924 Yuan, J., Zhang, X., Liu, C., Sun, X., Sivaramasamy, E., Li, F., Xiang, J., 2016. Comparative genomics
5925 analysis of decapod shrimps in the Pancrustacea clade. *Biochem. Syst. Ecol.* 64, 111–121.
- 5926 Yuan, X., Chen, Z., Xiao, S., Zhou, C., Hua, H., 2011. An early Ediacaran assemblage of macroscopic
5927 and morphologically differentiated eukaryotes. *Nature* 470, 390–393.

- 5928 Yuan, X., Xiao, S., Yin, L., Knoll, A.H., Zhou, C., Mu, X., 2002. Doushantuo fossils: life on the eve of
5929 animal radiation. China University of Science and Technology Press, Hefei, China.
- 5930 Zambito, J.J., Benison, K.C., Foster, T., Soreghan, G.S., Kane, M., Soreghan, M., 2012.
5931 Lithostratigraphy of the Permian Red Beds and Evaporites in the Rebecca K. Bounds Core,
5932 Greeley County, Kansas. Kans. Geol. Surv. Open-File Rep. 2012, 45.
- 5933 Zhang, C., Stadler, T., Klopstein, S., Heath, T.A., Ronquist, F., 2016. Total-Evidence Dating under the
5934 Fossilized Birth–Death Process. Syst. Biol. 65, 228–249.
- 5935 Zhang, J.-F., 2015. Archisargoid flies (Diptera, Brachycera, Archisargidae and Kovalevisargidae) from
5936 the Jurassic Daohugou biota of China, and the related biostratigraphical correlation and
5937 geological age. J. Syst. Palaeontol. 13, 857–881.
- 5938 Zhang, J.-F., Kluge, N.J., 2007. Jurassic larvae of mayflies (Ephemeroptera) from the Daohugou
5939 formation in Inner Mongolia, China. Orient. Insects 41, 351–366.
- 5940 Zhang, X., Han, J., Shu, D., 2002. New occurrence of the Burgess Shale arthropod *Sidneyia* in the
5941 Early Cambrian Chengjiang Lagerstätte (South China), and revision of the arthropod *Urokodia*.
5942 Alcheringa 26, 1–8.
- 5943 Zhang, X., Maas, A., Haug, J.T., Siveter, D.J., Waloszek, D., 2010. A Eucrustacean Metanauplius from
5944 the Lower Cambrian. Curr. Biol. 20, 1075–1079.
- 5945 Zhang, X., Siveter, D.J., Waloszek, D., Maas, A., 2007. An epipodite-bearing crown-group crustacean
5946 from the Lower Cambrian. Nature 449, 595–598.
- 5947 Zhang, Z., Schneider, J.W., Hong, Y., 2013. The most ancient roach (Blattodea): a new genus and
5948 species from the earliest Late Carboniferous (Namurian) of China, with a discussion of the
5949 phylomorphogeny of early blattids. J. Syst. Palaeontol. 11, 27–40.
- 5950 Zhao, C., Liu, X., Yang, D., 2014. Wing Base Structural Data Support the Sister Relationship of
5951 Megaloptera and Neuroptera (Insecta: Neuropterida). PLoS ONE 9, e114695.

- 5952 Zherikhin, V.V., Mostovski, M.B., Vršanský, P., Blagoderov, V., Lukashevich, E.D., 1998. The unique
5953 Lower Cretaceous locality Baissa and other contemporaneous fossil insect sites in North and
5954 West Transbaikalia, in: Proceedings of the First International Palaeoentomological Conference.
5955 Moscow.
- 5956 Zhou, D., Zhang, D., Ding, G., Shi, L., Hou, Q., Ye, Y., Xu, Y., Zhou, H., Xiong, C., Li, S., Yu, S., Hong,
5957 S., Yu, X., Zou, P., Chen, C., Chang, X., Wang, W., Lv, Y., Sun, Y., Ma, L., Shen, B., Zhu, C.,
5958 2014. Genome sequence of *Anopheles sinensis* provides insight into genetics basis of
5959 mosquito competence for malaria parasites. BMC Genomics 15, 42.
- 5960 Zhou, Z., 2006. Evolutionary radiation of the Jehol Biota: chronological and ecological perspectives.
5961 Geol. J. 41, 377–393.
- 5962 Zhu, Q., Hastriter, M.W., Whiting, M.F., Dittmar, K., 2015. Fleas (Siphonaptera) are Cretaceous, and
5963 evolved with Theria. Mol. Phylogenet. Evol. 90, 129–139.
- 5964 Zrzavý, J., Hypsa, V., Vlaskova, M., 1998. Arthropod phylogeny: taxonomic congruence, total evidence
5965 and conditional combination approaches to morphological and molecular data sets, in: Fortey,
5966 R.A., Thomas, R.H. (Eds.), Arthropod Relationships, The Systematics Association Special
5967 Volume Series. Chapman & Hall, London.
- 5968 Zrzavý, J., Štys, P., 1997. The basic body plan of arthropods: insights from evolutionary morphology
5969 and developmental biology. J. Evol. Biol. 10, 353–367.
- 5970 Zwick, A., Regier, J.C., Zwickl, D.J., 2012. Resolving Discrepancy between Nucleotides and Amino
5971 Acids in Deep-Level Arthropod Phylogenomics: Differentiating Serine Codons in 21-Amino-
5972 Acid Models. PLoS ONE 7, e47450.
- 5973 Zwick, P., 2000. Phylogenetic System and Zoogeography of the Plecoptera. Annu. Rev. Entomol. 45,
5974 700–746.
5975

5976 **FIGURE CAPTIONS**

5977

5978 **Fig. 1.** Calibration diagram for Ecdysozoa (nodes 2-5, 22-23, 34, 41). Altocrust. = Altocrustacea.

5979 Numbers in this and all other calibration diagrams are ages in Ma.

5980

5981 **Fig. 2.** Major fossil calibrations for (A) nodes 2-3: *Rusophycus* trace fossils, GSC 85983, scale bar

5982 20mm, image credit M. Coyne; (B-C) nodes 4, 22, 34, 41: *Yicaris dianensis*, YKLP 10840, scale bars

5983 100µm, images credit X. Zhang; (B) whole specimen; (C) detail of epipodites; (D) node 5:

5984 *Wisangocaris barbarahardya*, SAM P43679a, scale bar 5mm; (E) nodes 23-25, 27: *Cowiedesmus*

5985 *eroticopodus*, AMS F.64845, scale bar 2mm, image credit Y. Zhen; (F) nodes 64-65: *Rhyniella*

5986 *praecursor*, BMNH In.38228, scale bar 200µm, image credit NHMUK.

5987

5988 **Fig. 3.** Calibration diagram for non-arachnid Chelicerata (nodes 6-8).

5989

5990 **Fig. 4.** Calibration diagram for non-tetrapulmonate Arachnida (nodes 9-16). Pseudos. =

5991 Pseudoscorpiones.

5992

5993 **Fig. 5.** Chelicerate fossil calibrations for (A) node 6: *Haliestes dasos*, OUM C.29571, scale bar 500µm,

5994 image credit D. Siveter, M. Sutton, D. Briggs & D. Siveter; (B) node 7: *Chasmataspis*-like resting

5995 traces, MBA 1084, scale bar 20mm, image credit J. Dunlop; (C) node 13: *Protofeaella peetersae*,

5996 NHMII3115, scale bar 500µm, image credit H. Henderickx; (D) node 10: *Eophalangium sheari*, PBM

5997 3503, scale bar 1mm, image credit J. Dunlop; (E) node 14: *Electrokoenenia yaksha*, NIGP 163263,

5998 scale bar 500µm, image credit M. Engel; (F) node 15: *Cratosolpuga wunderlichi*, SMNK 1268PAL,

5999 scale bar 5mm, image credit P. Selden; (G) node 9: *Eramoscorpius brucensis*, holotype ROM 5324,

6000 scale bar 10mm, image credit D. Rudkin & J. Waddington; (H) node 9: *Palaeophonon loudonensis*,

6001 NMS 1897.122.196, scale bar 20mm, image credit: J. Lamsdell; (I-J) node 12: *Cornupalpatum*

6002 *burmanicum*, scale bars 100 µm, image credit G. Poinar; (I) Holotype A-10-160; (J) Paratype A-10-261;
6003 (K) node 11: *Protacarus crani*, BMNH In.24665, scale bar 100µm, image credit NHMUK.

6004

6005 **Fig. 6.** Calibration diagram for Tetrapulmonata (nodes 17-21).

6006

6007 **Fig. 7.** Tetrapulmonata fossil calibrations for (A) nodes 17-19: *Parageralinura naufraga*, LWL Ar.K.1,
6008 scale bar 5mm, image credit C. Brauckmann; (B) node 20: *Graeophonus anglicus*, BMNH In 31233,
6009 scale bar 5mm, image credit J. Dunlop; (C, D) node 21: *Palaeothele montceauensis*, images credit P.
6010 Selden; (C) Holotype MNHN 51961, scale bar 2mm; (D) Reconstructed specimen BMNH In.62050,
6011 scale bar 0.2mm; (E) node 21: *Arthrolycosa* sp., PIN 5431/9, scale bar 1mm, image credit P. Selden.

6012

6013 **Fig. 8.** Calibration diagram for Myriapoda (nodes 24-33). Chilogn. = Chilognatha, Scutigerom. =
6014 Scutigeromorpha, Geophilom. = Geophilomorpha.

6015

6016 **Fig. 9.** Myriapod fossil calibrations for (A-B) node 26: *Electroxenus jezzinensis*, MNHN JS 231/1, scale
6017 bar 0.5mm, image credit D. Azar; (C-E) node 28: *Crussolum* sp., images credit L. Anderson; (C)
6018 Forcipular segment, slide AUGD 12308, scale bar 0.5mm; (D) Prefemur of a trunk leg, slide AUGD
6019 12307, scale bar 0.2mm; (E) Tibia of a trunk leg, slide AUGD 12307, scale bar 0.2mm; (F) node 29:
6020 *Fulmenocursor tenax*, SMNS 64275, scale bar 5mm, image credit G. Bechly; (G-H) node 30:
6021 *Devonobius delta*, scale bars 0.1mm, images credit W. Shear; (G) Head and anterior part of trunk,
6022 AMNH slide 411-15-AR18; (H) Forcipular segment, AMNH slide 4329-AR4; (I) nodes 31-32:
6023 *Mazoscolopendra richardsoni*, FMNH PE29002, scale bar 5mm, image credit J. Wittry; (J-K) node 33:
6024 *Kachinophilus pereirai*, AMNH Bu-Ba41a; (J) Head and anterior part of trunk, scale bar 0.3 mm; (K)
6025 Posterior body segments, scale bar 0.1mm.

6026

6027 **Fig. 10.** Calibration diagram for Oligostraca (nodes 35-40).

6028

6029 **Fig. 11.** Oligostraca fossil calibrations for (A) nodes 35-36: *Boeckelericambria pelturae*, UB W116,
6030 scale bar 50µm, image credit D. Waloszek; (B) nodes 37, 39-40: *Luprisca incuba*, YPM IP 307300,
6031 scale bar 500µm, image credit D. Siveter, G. Tanaka, U. Farrell, M. Martin, D. Siveter & D. Briggs; (C-
6032 E) node 38: *Cytherellina submagna*, ZPAL O.60/001, images credit E. Olempska; (C) steinkern left
6033 lateral view, scale bar 200 µm; (D) soft anatomy of posterior region, scale bar 100µm; (E) walking legs
6034 and presumed furca, scale bar 50µm.

6035

6036 **Fig. 12.** Calibration diagram for Copepoda and Thecostraca (nodes 42-47).

6037

6038 **Fig. 13.** Calibration diagram for Malacostraca (nodes 48-56). Verunip. = Verunipeltata, Tanaid =
6039 Tanaidacea.

6040

6041 **Fig. 14.** Multicrustacea fossil calibrations for (A) node 42: *Arenosicaris inflata*, PRI 10130, scale bar
6042 10mm, image credit J. Collette; (B) node 43: *Kabatarina pattersoni*, NHMUK 63466, scale bar 100µm,
6043 image credit G. Boxshall; (C-D) node 44: *Rhamphoverritor reduncus*, OUM C.29587, scale bars
6044 500µm, image credit D. Briggs, M. Sutton, D. Siveter & D. Siveter; (C) lateral views with (left) and
6045 without (right) head shield; (D) transverse section before serial grinding; (E) nodes 45-46: *Illilepas*
6046 *damrowi*, FMNH P32055, scale bar 5mm, image credit J. Wittry; (F-G) node 48: *Cinerocaris magnifica*,
6047 images credit D. Briggs, M. Sutton, S. Siveter & D. Siveter; (F) OUM C.29566, reconstruction in lateral
6048 view with (top) and without (bottom) head shield, scale bar 2mm; (G) holotype C.29565, sub-
6049 transverse section, scale bar 1mm; (H-I) nodes 49, 55-56: *Palaeopalaemon newberryi*, KSU 3484,
6050 scale bars 5mm, image credit W. Jones; (H) left view; (I) right view; (J) nodes 52-53: *Hesslerella*
6051 *shermani*, FMNH PE 16527, latex cast whitened with ammonium chloride, scale bar image credit T.
6052 Hegna; (K) node 50: *Anaspidites antiquus*, AMS F64765, scale bar 5mm, image credit S. Ah Yong; (L-
6053 M) node 54: *Alavatanaais carabe*, scale bars 500 µm, images credit A. Sánchez-García; (L) holotype

6054 MCNA 9537; (M) MCNA 13888 lateral view.

6055

6056 **Fig. 15.** Calibration diagram for Allotriocarida (nodes 57-63).

6057

6058 **Fig. 16.** Allotriocarida fossil calibrations for (A) node 57: *Rehbachella kinnekullensis*, UB 611, scale
6059 bar 200µm, image credit D. Waloszek; (B) node 58: *Lepidocaris rhyniensis*, NHMUK In. 24493, scale
6060 bar 200µm, image credit NHMUK; (C) node 60: *Chenops yixianensis*, CNU-CAL-HP-2009001, scale
6061 bar 10mm, image credit T. Hegna; (D) node 61: *Leaia chinensis*, NIGP 51786, scale bar 1mm, image
6062 credit Y. Shen; (E) node 62: *Dundgobiestheria mandalgobiensis*, ED-A-14-1, scale bar 1 mm, image
6063 credit G. Li; (F) node 63: *Smirnovidaphnia smirnovi*, PIN 1873/100, scale bar 200 µm, image credit A.
6064 Kotov.

6065

6066 **Fig. 17.** Calibration diagram for non-neopteran Hexapoda (nodes 64-73). Microc. = Microcoryphia,
6067 Zygent. = Zygentoma, Euplect. = Euplectoptera.

6068

6069 **Fig. 18.** Hexapoda fossil calibrations for (A) node 70: *Delitzschala bitterfeldensis*, BGR X 9216, scale
6070 bar 2mm, image credit C. Brauckmann; (B) node 68: *Cretaceomachilis libanensis*, Milki No. 194/35,
6071 scale bar 500µm, image credit G. Poinar; (C) node 69: *Burmalepisma cretacicum*, B-TH-1, scale bar
6072 500µm, image credit G. Poinar; (D) node 67: *Rhyniognatha hirsti*, BMNH IN. 38234, scale bar 200µm,
6073 image credit NHMUK; (E) node 72: *Triassonurus doliiformis*, Louis Grauvogel collection No. 9304,
6074 scale bar 10mm, image credit L. Grauvogel-Stamm.

6075

6076 **Fig. 19.** Calibration diagram for Polyneoptera (nodes 75-83). Dermap. = Dermaptera, Notop. =
6077 Notoptera, Phasm. = Phasmatodea.

6078

6079 **Fig. 20.** Polyneoptera fossil calibrations for (A) node 75: *Qilianiblatella namurensis*, CNU-NX1-303,

6080 scale bar 5mm, image credit D. Ren; (B) node 77: *Palaeotaeniopteryx elegans*, PIN 1197/333, scale
6081 bar 1mm, image credit N. Sinitshenkova; (C) node 78: *Raphogla rubra*, Ld LAP 415 B, scale bar 5
6082 mm, image credit S. Fouché; (D) node 80: *Cretophasmomima melanogramma*, CNU-PHA-
6083 NN2012002, scale bar 10mm, image credit D. Ren; (E) node 76: *Rhadinolabis phoenicica*, Azar
6084 collection 1013, scale bar 500µm, image credit M. Engel;; (F) node 81: *Echinosomiscus primoticus*,
6085 NIGP 163536, scale bar 2mm, image credit M. Engel; (G) node 79: *Juramantophasma sinica*, NIGP
6086 142171, scale bar 10mm, image credit D. Huang.

6087

6088 **Fig. 21.** Calibration diagram for Condylgnatha and Psocodea (nodes 74, 84-88).

6089

6090 **Fig. 22.** Condylgnatha fossil calibrations for (A) nodes 85, 87: *Aviorrhyncha magnifica*, holotype
6091 MNHN Avion No. 2, scale bar 1mm, image credit A. Nel; (B) node 86: *Fusithrips crassipes*, PIN
6092 3064/8547, scale bar 200µm, image credit A. Rasnitsyn.

6093

6094 **Fig. 23.** Calibration diagram for Hymenoptera, Neuropterida, and Coleopterida (nodes 89-96).

6095 Hymenopt. = Hymenoptera, Mec. = Mecopterida, Megalopt. = Megaloptera.

6096

6097 **Fig. 24.** Calibration diagram for Mecopterida (nodes 97-103). Mecopt. = Mecoptera.

6098

6099 **Fig. 25.** Holometabola fossil calibrations for (A) node 90: *Triassoxyela foveolata*, PIN 2070/1, scale bar
6100 1mm, image credit A. Rasnitsyn; (B) node 92: *Elmothone martynovae*, MCZ 5585, scale bar 2mm,
6101 image credit Museum of Comparative Zoology, Harvard University (©President and Fellows of Harvard
6102 College); (C) node 93: *Eochauliodes striolatus*, CNU-MEG-NN2011004 P/C, scale bar 5mm, image
6103 credit D. Ren; (D) node 96: *Triadogyrus sternalis*, PIN 3320/13, scale bar 2mm, image credit A.
6104 Rasnitsyn; (E) node 97: *Permopanorpa inaequalis*, YPM IP 005058, scale bar 1mm, image credit J.
6105 Utrup; (F) node 98: *Archaeolepis mane*, BMNH In. 59397, scale bar 2mm, image credit NHMUK; (G)

- 6106 node 99: *Liadotaulius maior*, LGA 1995, scale bar 2mm, image credit J. Ansorge; (H) node 100:
- 6107 *Parasabatinca aftimacrai*, holotype, scale bar 2mm, image credit D. Azar; (I) node 101:
- 6108 *Pseudonannochorista willmanni*, PIN 966/21, scale bar 1mm, image credit A. Bashkuev; (J) node 103:
- 6109 *Grauvogelia arzvilleriana*, Louis Grauvogel collection No. 5514, scale bar 1mm, image credit L.
- 6110 Grauvogel-Stamm.

1. Introduction

Accurate and precise systematic placement and dating of fossils underpins most efforts to infer a chronology for the Tree of Life. Arthropods, as a whole or in part, have received considerable focus owing to their incredible morphological disparity, species richness, and (relative to much of the Tree of Life) excellent fossil record. A growing number of recent studies have constructed timetrees for arthropods as a whole or for major groups therein (e.g. Bellec and Rabet, 2016; Bond et al., 2014; Bracken-Grissom et al., 2014, 2013; Djernæs et al., 2015; Fernández et al., 2016, 2014; Fernández and Giribet, 2015; Garrison et al., 2016; Garwood et al., 2014; Giribet and Edgecombe, 2013; Herrera et al., 2015; Klopstein et al., 2015; Legendre et al., 2015; Malm et al., 2013; McKenna et al., 2015; Misof et al., 2014; Oakley et al., 2013; Rehm et al., 2011; Schwentner et al., 2013; Song et al., 2015; Sun et al., 2015; Thomas et al., 2013; Tsang et al., 2014; Wahlberg et al., 2013; Wiegmann et al., 2011; Wood et al., 2013; Xu et al., 2015; Zhu et al., 2015). These studies vary in how well they have adhered to best practices for selecting calibration fossils, as many previous calibrations assume that fossil taxonomy accurately reflects phylogeny. Compounding the issue is the expansion of divergence time studies for a variety of comparative questions far beyond systematics and biogeography, including habitat shifts (Letsch et al., 2016; Lins et al., 2012; Rota-Stabelli et al., 2013a; Yang et al., 2013), genome evolution (Cao et al., 2013; Schwarz et al., 2014; Starrett et al., 2013; Wissler et al., 2013; Yuan et al., 2016), origins of novel characters and behaviours (Rainford et al., 2014; Sanggaard et al., 2014; Wheat and Wahlberg, 2013), evolution of parasites and disease (Ibarra-Cerdeña et al., 2014; Palopoli et al., 2014; Rees et al., 2014; Zhou et al., 2014), rate of diversification and its relationship to morphology and ecology (Lee et al., 2013; Wiens et al., 2015), coevolution (Kaltenpoth et al., 2014; Shelomi et al., 2016; Wilson et al., 2013), conservation (Owen et al., 2015), and the use of arthropods as a model for methodological development (O'Reilly et al., 2015; Ronquist et al., 2012; Warnock et al., 2012; Zhang et al., 2016).

Recent consensus on best practices for selecting calibration fossils comes with several

27 requirements. There must be references to specific fossil specimen(s), phylogenetic or morphological
28 evidence justifying placement of the fossil, and stratigraphic and/or radiometric dating information for
29 the fossil (Parham et al., 2012). The importance of accurate phylogenetic knowledge of calibration
30 fossils is underscored by recent controversies in dating the evolution of insects, where arguments
31 hinge on the classification of particular 'roachoid' fossils on the stem lineage of Dictyoptera, with
32 resulting differences on the order of 100 Myr (Kjer et al., 2015; Tong et al., 2015). With the explosion of
33 taxonomic sampling in molecular phylogenies due to improvements in sequencing technology,
34 improving the coverage of fossil calibrations is equally important. Recommendations include, for
35 example, including as many as one fossil per ten extant taxa for precise ages, with a varied
36 distribution across lineages and clade depth (Bracken-Grissom et al., 2014). As a response, we have
37 compiled an atlas of 80 rigorously scrutinized calibration fossils for 102 key nodes in arthropod
38 phylogeny. These represent four basal ecdysozoan and arthropod clades, 17 chelicerates, 12
39 myriapods, 30 non-hexapod pancrustaceans, and 39 hexapod clades.

40 Where possible, we favour clade topologies resulting from a phylogenetic analysis of the
41 largest total dataset. If phylogenomic analysis of genomes or transcriptomes has been performed but
42 conflicts with morphology, a strongly supported molecular result is presented (e.g. putative clades
43 such as Oligostraca that do not yet have identified morphological autapomorphies). If, however,
44 molecular phylogenies have been constructed with few genes (e.g. clades such as Peracarida) or with
45 highly conflicting results (e.g. Arachnida), morphological results are given greater weight. Where
46 relevant, we discuss clade names with respect to NCBI's GenBank taxonomy (as recommended by
47 the Fossil Calibrations Database: Polly et al., 2015), as this review is intended to be used by molecular
48 biologists who are interested in dating the evolution of arthropod groups.

49 As there are >1.2 million species of arthropods, our calibrations are limited to fossils from the
50 Palaeozoic and Mesozoic. Many extant clades have their oldest fossils in Cenozoic ambers such as
51 the Eocene Baltic amber but are predicted to be vastly older based on fossils of allied taxa (e.g.
52 Symphyla and Pauropoda relative to Chilopoda and Diplopoda).

While acknowledging the complexity of estimating an age prior for a fossil species known from multiple deposits, we use the oldest (e.g. section 28.3) and/or best known (e.g. section 51.3) horizons to provide minimum age constraints with the narrowest and most accurate age interval. Where there is substantial variation in age estimates for a fossil species, this issue is noted in the text. To accommodate the possibility of older fossils not yet discovered, we provide generous soft maxima (Holland and Phillips, 2009). Accordingly, when conducting divergence time analyses, prior distributions accounting for the large probability tail (e.g. gamma or lognormal) of an older undiscovered fossil may be appropriate. All fossil calibrations described herein are listed with their age information in Table A.1, formatted for adding age constraints in BEAST or PhyloBayes.

2. Crown Ecdysozoa

This clade comprises Euarthropoda, Onychophora (velvet worms), Tardigrada (water bears), Nematoidea (itself comprising Nematoda and Nematomorpha), and Scalidophora (itself comprising Kinorhyncha, Loricifera, and Priapulida), their last common ancestor and all of its descendants (**Fig. 1**). Monophyly has been demonstrated on the basis of coding and non-coding molecular data (Campbell et al., 2011).

2.1. Fossil specimens

Rusophycus trace fossils in Member 2 of the Chapel Island Formation of the southwestern Burin Peninsula of southeastern Newfoundland, defining the base of the *R. avalonensis* Biozone. Arbitrarily, we fix this calibration on a specimen (**Fig. 2a**) from this unit figured by Narbonne et al. (1987: Fig. 6l; GSC 85983), as in Benton et al. (2015).

2.2. Phylogenetic justification

79

80 *Rusophycus* trace fossils are widely accepted to have been produced by arthropod-grade
81 organisms, showing bilateral symmetry and evidence of segmented limbs used in their construction,
82 the latter an apomorphy of Euarthropoda (Budd and Jensen, 2000).

83

84 2.3. Age justification

85

86 *Rusophycus* occurs well below the first animal body fossils in Cambrian sections around the
87 world (Crimes, 1987; Crimes and Jiang, 1986; Goldring and Jensen, 1996; MacNaughton and
88 Narbonne, 1999; Weber and Zhu, 2003). In many of these regions, records of *Rusophycus* begin with
89 proximity to the base of the Cambrian. However, their ages are only well constrained in sections in
90 Newfoundland, Canada, and Yunnan, China. Of these, records of *Rusophycus* begin low in Member 2
91 of the Chapel Island Formation of the southwestern Burin Peninsula of southeastern Newfoundland,
92 defining the base of the *R. avalonensis* Biozone (Narbonne et al., 1987). The Biozone is itself dated
93 through correlations to a section in New Brunswick where the younger ash bed has been dated by U-
94 Pb series to 530.02 Ma \pm 1.2 Myr (Isachsen et al., 1994; Peng et al., 2012), thus providing for a
95 minimum constraint of 528.82 Ma.

96 A soft maximum constraint is based on that used by Benton et al. (2015), the maximum age
97 interpretation of the Lantian Biota (Yuan et al., 2011). This, together with the Doushantuo Biota (Yuan
98 et al., 2002), provides a series of Konservat-Lagerstätten preserving the biota in Orsten- and Burgess
99 Shale-like modes of fossilization. None of these Lagerstätten, least of all the Lantian, preserves
100 anything that could possibly be interpreted as even a total group eumetazoan and on this basis we
101 define our soft maximum constraint at 635.5 Ma \pm 0.6 Myr (Condon et al., 2005) and, thus, 636.1 Ma.

102

103 3. Crown Arthropoda

104

105 This clade comprises Euarthropoda and Onychophora (*sensu* Ortega-Hernández, 2016), their
106 last common ancestor and all of its descendants (**Fig. 1**). This clade has traditionally been called
107 Panarthropoda (Nielsen, 1995), however, this latter name is most often used to refer to a group
108 encompassing Arthropoda and Tardigrada, but we exclude tardigrades from our current grouping.
109 Monophyly of this clade has been established through phylogenetic analysis of both non-coding and
110 protein-coding gene datasets (Campbell et al., 2011), and morphological data sets (Legg et al., 2013),
111 although it has been challenged by other recent morphological analyses that endorsed a rival sister
112 group relationship between Euarthropoda and Tardigrada (e.g. Smith and Ortega-Hernández, 2014).
113 Note the name Arthropoda in GenBank refers to what we consider Euarthropoda; there is no GenBank
114 taxonomy ID for the clade comprising Euarthropoda and Onychophora.

115

116 3.1. *Fossil specimens*

117

118 As for 2.1.

119

120 3.2. *Phylogenetic justification*

121

122 As for 2.2.

123

124 3.3. *Age justification*

125

126 As for 2.3.

127

128 4. **Crown Euarthropoda**

129

130 This clade comprises Chelicerata, Myriapoda and Pancrustacea, their last common ancestor

131 and all of its descendants (**Fig. 1**). The monophyly of Euarthropoda, comprising the sister clades
132 Chelicerata and Mandibulata (itself comprising Myriapoda and Pancrustacea) has been established on
133 the basis of protein-coding and noncoding molecular data, as well as morphological data (Rota-Stabelli
134 et al., 2011). Note that in Benton et al. (2015) this node was named Arthropoda (likely with reference
135 to GenBank taxonomy). Here we follow the naming conventions outlined by Ortega-Hernández (2016).

136

137 4.1. Fossil specimens

138

139 *Yicaris dianensis* Zhang et al., 2007. YKLP 10840, holotype (**Fig. 2b,c**), consisting of an almost
140 complete articulated specimen (Zhang et al., 2007).

141

142 4.2. Phylogenetic justification

143

144 Several phylogenetic analyses of morphology (Edgecombe, 2010; Legg et al., 2013; Wolfe and
145 Hegna, 2014) and morphology plus molecules (Oakley et al., 2013) place *Y. dianensis* within the
146 crown group of Pancrustacea. Key characters include the presence of epipodites on the thoracic
147 limbs; paddle-shaped mandibular and maxillary exopods; and the protopodite of post-mandibular limbs
148 elongated as soft, setiferous endites. Any position supported within the crown group of Pancrustacea
149 is within crown Euarthropoda.

150

151 4.3. Age justification

152

153 *Y. dianensis* was recovered from the Yu'an-shan Formation at Xiaotan section, Yongshan,
154 Yunnan Province, attributed to the *Eoredlichia*–*Wutingaspis* Biozone (Zhang et al., 2007). Chinese
155 Cambrian stratigraphy has been revised substantially and the *Eoredlichia* – *Wutingaspis* Biozone is no
156 longer recognized (Peng, 2009, 2003). However, *Eoredlichia* is known to co-occur with *Hupeidiscus*,

157 which is diagnostic of the *Hupeidiscus-Sinodiscus* Biozone, which is formally recognised as the
158 second biozone of the Nangaoan Stage of the Qiandongian Series of the Cambrian of China (Peng
159 and Babcock, 2008). The Nangaoan is the proposed third stage of the Cambrian System for the
160 International Geologic Timescale (Peng et al., 2012). Thus, a minimum constraint can be established
161 on the age of the top of the Nangaoan, which has been dated to 514 Ma (Peng et al., 2012; Peng and
162 Babcock, 2008).

163 Soft maximum as for 2.3.

164

165 4.4. Discussion

166

167 There are older records of euarthropods than *Y. dianensis*, notably trilobites, but their
168 phylogenetic position within Arthropoda is contested (it is unclear whether trilobites are stem-
169 Euarthropoda, stem-Chelicerata or stem-Mandibulata). *Wujicaris muelleri* Zhang et al., 2010 has an
170 equal claim to being the earliest record of Arthropoda, but it is of equal age to the holotype of *Y.*
171 *dianensis*.

172

173 5. Crown Chelicerata

174

175 This clade comprises Pantopoda (sea spiders) and Euchelicerata, their last common ancestor
176 and all of its descendants (**Figs. 1, 3 and 4**). Monophyly of this clade has been established by
177 phylogenetic analysis of nuclear protein-coding genes (Regier et al., 2010), transcriptomes
178 (Meusemann et al., 2010; Rota-Stabelli et al., 2011), and morphology (Legg et al., 2013).

179

180 5.1. Fossil specimens

181

182 *Wisangocaris barbarahardyae* Jago, García-Bellido and Gehling, 2016. SAM P45427,

183 holotype, almost complete specimen (**Fig. 2d**).

184

185 5.2. *Phylogenetic justification*

186

187 Few recent phylogenetic studies have addressed the stem-lineage of Euchelicerata (notable
188 exceptions being Lamsdell, 2013; Legg, 2014; Legg et al., 2013). Including *W. barbarahardya* in the
189 dataset of Legg (2014), this species was resolved in most shortest cladograms as sister taxon to the
190 middle Cambrian *Sanctacaris* and *Sidneyia*, and in all shortest cladograms as more closely related to
191 Euchelicerata than Pantopoda, i.e. as crown group Chelicerata (Jago et al., 2016). This relationship is
192 supported by the shared presence of pediform cephalic exites, multi-partite trunk exites, and a trunk
193 composed of a posterior limb-less abdomen in both crown euchelicerates and the Cambrian taxa.

194

195 5.3. *Age justification*

196

197 *W. barbarahardya* was collected from the Emu Bay Shale on Kangaroo Island, South Australia.
198 Trilobite biostratigraphy correlates this unit with the upper part of the *Pararaia janeae* Zone in
199 mainland South Australia (Jell in Bengtson et al., 1990; Fig. 2 in Jago et al., 2012), equivalent to the
200 Canglangpuan Stage in South China and the late Botoman in Siberia (Gehling et al., 2011, Fig. 9).
201 This dates the Emu Bay Shale to Cambrian Series 2, Stage 4, providing a minimum constraint of 509
202 Ma.

203 Soft maximum as for 2.3.

204

205 5.4. *Discussion*

206

207

208 Until recently the oldest evidence of chelicerates in the fossil record were thought to be

209 represented by *Chasmataspis*-like trace fossils from the Furongian of Texas (Dunlop et al., 2004), and
210 a putative pycnogonid larva from the Furongian of Sweden (Waloszek and Dunlop, 2002). However, in
211 a number of recent phylogenetic analyses (e.g. Legg, 2014; Legg et al., 2013), a number of taxa from
212 the middle Cambrian Burgess Shale Formation, namely *Sanctacaris uncata* Briggs and Collins, 1988,
213 *Sarotrocercus oblita* Whittington, 1981, and *Sidneyia inexpectans* Walcott, 1911, have been resolved
214 as stem-lineage representatives of Euchelicerata. These relationships are preserved with the addition
215 of the older *W. barbarahardyae* to the dataset (Jago et al., 2016). Although another purported species
216 of *Sidneyia* (*S. sinica* Zhang et al., 2002) is known from the older Chengjiang biota, it lacks many
217 diagnostic features of this genus, and could therefore not be reliably used for calibration purposes. It
218 should also be noted that *Sidneyia* only resolved as a stem representative of Euchelicerata under
219 some iterations of the analysed data set of Legg (2014), specifically only when all characters were
220 weighted equally, and therefore its exact phylogenetic position is equivocal.

221

222 6. Crown Pantopoda

223

224 This clade comprises Ammotheidae, Austrodecidae, Callipallenidae, Colossendeidae,
225 Endeididae, Nymphonidae, Pallenopsidae, Phoxichilidiidae, Pycnogonidae and Rhynchothoracidae,
226 their last common ancestor and all of its descendants (**Fig. 3**). Phylogenetic analyses of protein-
227 coding genes (Arabi et al., 2010) or protein-coding genes combined with morphology (Arango and
228 Wheeler, 2007) indicate monophyly.

229

230 6.1. Fossil specimens

231

232 *Haliestes dasos* Siveter et al., 2004. OUM C.29571, holotype (**Fig. 5a**). As the reconstruction of
233 Herefordshire fossils requires serial grinding and photography of 20 µm sections (Sutton et al., 2002),
234 the holotype figured in Siveter et al. (2004) and herein was thus destroyed in preparation.

235 Morphological data for Herefordshire fossils are published as 3D models of the thin section
236 photographs.

237

238 6.2. *Phylogenetic justification*

239

240 Arango and Wheeler (2007) resolved *H. dasos* as sister to part of Ammonotheidae (nested within
241 clade of Ammonotheidae, Callipallenidae, Nymphonidae, Pallenopsidae, Phoxichilidiidae,
242 Rhynchothoracidae), i.e. as crown-group Pantopoda. *H. dasos* was classified separately from extant
243 pycnogonids (Pantopoda) as an Order Nectopantopoda by Bamber (2007), although without explicit
244 phylogenetic justification. It should be noted that *H. dasos* was included in the phylogenetic analysis of
245 Legg et al. (2013), and resolved as sister-taxon to *Palaeopantopus*, which in turn resolved as sister-
246 taxon to extant pycnogonids, however, just three extant exemplars were included in this study and as
247 this was not extensive enough to determine the exact position of these fossil taxa with respect to
248 crown-group exemplars, we continue to follow Arango and Wheeler (2007) in their placement.

249

250 6.3. *Age justification*

251

252 This fossil is preserved as a carbonate concretion from the volcanoclastic Herefordshire
253 Lagerstätte of Herefordshire, England, at the Sheinwoodian-Homerian stage boundary, within the
254 Early Silurian Wenlock Series (Siveter, 2008). As the Homerian begins at 430.5 Ma \pm 0.7 Myr, a
255 minimum age constraint for the Herefordshire can thus be placed at 429.8 Ma.

256 Soft maximum as for 2.3.

257

258 6.4. *Discussion*

259

260 Although *H. dasos* is the oldest assignable crown group pycnogonid, there is an older fossil,

261 *Cambropycnogon klausmuelleri* Waloszek and Dunlop, 2002, from the Cambrian Orsten biota
262 (minimally 497 Ma). *C. klausmuelleri*, however, is known only from larval stages, and does not share
263 specific apomorphies with any extant larva. Without such characters, it is not possible to adequately
264 confirm crown group affinity. Another fossil species, *Palaeomarachne granulata* Rudkin et al., 2013
265 from the Late Ordovician of Manitoba, is specifically noted as a stem pantopod due to its likely
266 plesiomorphic head tagmosis.

267

268 **7. Crown Euchelicerata**

269

270 This clade comprises Xiphosurida (horseshoe crabs) and Arachnida, their last common
271 ancestor and all of its descendants (**Fig. 3**). Monophyly is established on the basis of phylogenetic
272 analysis of transcriptomes (Rota-Stabelli et al., 2011; Sharma et al., 2014) and morphology (Legg et
273 al., 2013). Note that monophyly of Euchelicerata is challenged by a recent morphological phylogeny, a
274 result attributed to outgroup sampling (Garwood and Dunlop, 2014). Euchelicerata is not recognized in
275 GenBank taxonomy.

276

277 *7.1. Fossil specimens*

278

279 *Chasmataspis*-like resting trace fossils (MBA 1084), **Fig 5b**. Described and illustrated in
280 Dunlop et al. (2004, Figs. 9 and 10).

281

282 *7.2. Phylogenetic justification*

283

284 The assignment of the traces to Chasmataspida is based on impressions of plate-like
285 opisthosomal opercula, one of the characters used to define Euchelicerata (Dunlop et al., 2004)
286 Furthermore, recent phylogenetic analyses of morphology place chasmataspid body fossil species

287 within Euchelicerata, as sister group to eurypterids (Garwood and Dunlop, 2014; Legg et al., 2013) or
288 sister group to a clade composed of eurypterids and arachnids (Lamsdell, 2013; Lamsdell et al., 2015;
289 Selden et al., 2015).

290

291 7.3. Age justification

292

293 The *Chasmataspis*-like resting traces were found in the Cambrian Hickory Sandstone Member
294 of the Riley Formation, Texas (Dunlop et al., 2004). The top of the Hickory Sandstone preserves
295 trilobite representatives of the *Bolaspidella* Zone and the *Cedarina* Zone (Miller et al., 2012; Palmer,
296 1954). These trilobite biozones are assigned to the lowermost Marjumiid Biomere in the Marjuman
297 Stage of the Lincolnian Series (Miller et al., 2012). The early Marjuman itself is correlated to the
298 Drumian Stage of Cambrian Series 3 (Taylor et al., 2012). The end of the Drumian is dated to 500.5
299 Ma, providing a minimum age for *Chasmataspis*-like trace fossils.

300 Soft maximum as for 2.3.

301

302 8. Crown Xiphosurida

303

304 This clade comprises four extant species, all members of the family Limulidae: *Carcinoscorpius*
305 *rotundicauda*, *Limulus polyphemus*, *Tachypleus gigas* and *Tachypleus tridentatus*, their last common
306 ancestor and all of its descendants (**Fig. 3**). Monophyly is established by phylogenetic analyses of
307 housekeeping genes (Obst et al., 2012) and morphology (Lamsdell and McKenzie, 2015).

308

309 8.1. Fossil specimens

310

311 *Tachypleus gadeai* Vía Boada and de Villalta, 1966. MGSB 19195, holotype.

312

313 8.2. Phylogenetic justification

314

315 *Heterolimulus gadeai* Vía Boada and de Villalta, 1966 was reassigned to the extant genus
316 *Tachypleus* by Diedrich (2011), who cited the presence of lateral immobile opisthosomal spines as
317 evidence. This was validated by the phylogenetic analysis of Lamsdell and McKenzie (2015), who
318 resolved *T. gadeai* as sister-taxon to a clade composed of all other members of *Tachypleus*. This more
319 inclusive clade in turn resolved as sister-taxon to the extant genus *Carcinoscorpius*.

320

321 8.3. Age justification

322

323 *T. gadeai* was discovered in the Alcover unit of the Montral site, Tarragona province, Catalonia,
324 Spain (Vía Boada and de Villalta, 1966). Based on sequence stratigraphy, the Alcover dolomite unit is
325 dated to the late Muschelkalk, a European regional stage of the Triassic (Calvet and Tucker, 1995; Vía
326 Boada and de Villalta, 1966). The middle and late Muschelkalk correspond to the global Ladinian
327 stage (Calvet and Tucker, 1995). The upper boundary of the Ladinian is 237.0 Ma \pm 1 Myr (Ogg,
328 2012), thus, a minimum age of 236.0 Ma.

329 Soft maximum as for 2.3.

330

331 8.4. Discussion

332

333 We note that morphological phylogenetic analysis has suggested paraphyly of Xiphosura
334 (crown Xiphosurida plus several fossil genera), and resolved synziphosurines as basal euchelicerates
335 (Lamsdell, 2013). A subsequent morphological phylogeny resolved synziphosurines as polyphyletic
336 (Garwood and Dunlop, 2014). Some other morphological phylogenies resolve the traditional
337 monophyletic Xiphosura (Briggs et al., 2012; Legg et al., 2013).

338 Crown xiphosurid affinities of older fossils cannot be confirmed. For example, an undescribed

339 Early Ordovician fossil from Morocco (Van Roy et al., 2010) exhibits fused opisthosomal tergites, a
340 synapomorphy of Xiphosurida *sensu* Lamsdell (2013), but its position with respect to the crown has
341 not been tested in a phylogeny. The Late Ordovician *Lunataspis aurora* Rudkin et al., 2008 and the
342 Pennsylvanian genus *Euproops* are resolved on the stem group of Xiphosurida in a morphological
343 phylogeny (Lamsdell, 2013).

344 Morphological conservatism in the evolution of Xiphosura (as illustrated by a Jurassic member
345 assigned to a living genus) has led to use of the misnomer 'living fossil' for the clade, despite
346 continued molecular evolution throughout its history (Avisé et al., 1994; Obst et al., 2012). The more
347 appropriate term of 'stabilomorph' was proposed with the discovery of *Limulus darwini* (Kin and
348 Błażejowski, 2014); it refers to morphological stability over evolutionary history, at the genus level.
349 However, long branches unbroken by unsampled extinct species may have significantly
350 underestimated divergence times among crown Xiphosurida (Lamsdell and McKenzie, 2015), though
351 this assertion has not yet been tested with a divergence time analysis.

352

353 9. Crown Arachnida

354

355 This clade comprises Acariformes (acariform mites), Opiliones (harvestmen), Palpigradi
356 (microwhip scorpions), Parasitiformes (parasitiform mites, ticks), Pseudoscorpiones, Ricinulei (hooded
357 tickspiders), Schizomida, Scorpiones, Solifugae (camel spiders), and Tetrapulmonata, their last
358 common ancestor and all of its descendants (**Fig. 4**). Monophyly is established on the basis of
359 phylogenetic analysis of transcriptomes (Rota-Stabelli et al., 2013a), nuclear protein-coding genes
360 (Regier et al., 2010), strong support from morphology (Garwood and Dunlop, 2014; Legg et al., 2013;
361 Rota-Stabelli et al., 2011; Shultz, 2007), and combined morphological and molecular data (Giribet et
362 al., 2002; Lee et al., 2013). Some recent phylogenetic analyses of transcriptomes have failed to
363 resolve a monophyletic Arachnida; instead Xiphosurida is variably placed within the traditional
364 arachnids (Sharma et al., 2014; von Reumont et al., 2012).

365

366 9.1. Fossil specimens

367

368 *Palaeophonus loudonensis* Laurie, 1899. NMS 1897.122.196 (holotype), a dorsally preserved
369 specimen lacking walking legs and telson (**Fig. 5h**). For additional anatomical detail, we refer to
370 *Eramoscorpius brucensis* Waddington et al., 2015. ROM 53247, holotype (**Fig. 5g**).

371

372 9.2. Phylogenetic justification

373

374 The genus *Dolichophonus* Petrunkevitch, 1949, was erected for *P. loudonensis*, based on the
375 increased length of the prosoma compared to other palaeophonids, namely *P. nuncius* Thorell and
376 Lindström, 1885, and *P. caledonicus* Hunter, 1886. An examination (by D.A.L.) of the single known
377 specimen of *P. loudonensis* could not confirm this character because the specimen is very poorly
378 preserved, and the junction between the prosoma and mesosoma is not easily distinguished. We
379 retain the holotype within *Palaeophonus*. It is even possible that this specimen may belong to one of
380 the other currently recognised species of *Palaeophonus*, although more material would be required. *P.*
381 *loudonensis* was included in a phylogenetic analysis by Legg et al. (2013), in which it resolved
382 amongst total-group Scorpiones. Other Siluro-Devonian fossil scorpions such as *Proscorpius osborni*
383 Whitfield, 1885 and *Palaeoscorpius devonicus* Lehmann, 1944 have been placed in the stem group of
384 Orthosterni (crown-group Scorpiones) (e.g. Legg et al., 2013; Garwood and Dunlop, 2014), which are
385 therefore crown group members of Arachnida.

386

387 9.3. Age justification

388

389 *P. loudonensis* was recovered from the Gutterford Burn section of the “Eurypterid Bed”
390 (Reservoir Formation) in the Pentland Hills, Midlothian, Scotland (Kjellesvig-Waering, 1986), which

391 has been dated as Late Llandovery. The associated graptolite fauna suggests a late Llandovery
392 (Telychian) age for this formation, within the *Oktavites spiralis* Biozone (Bull and Loydell, 1995). A
393 spline-fit age for the upper boundary of the *O. spiralis* Biozone provides a minimum age constraint of
394 435.15 Ma (Melchin et al., 2012).

395 Soft maximum as for 2.3.

396

397 **10. Crown Opiliones**

398

399 This clade comprises Cyphophthalmi and Phalangida (itself comprising Laniatores, Dyspnoi
400 and Eupnoi), their last common ancestor and all of its descendants (**Fig. 4**). Monophyly has been
401 demonstrated by phylogenetic analysis of transcriptomes (Sharma et al., 2014), morphology (Garwood
402 et al., 2011), and combined morphology and molecules (Garwood et al., 2014; Giribet et al., 2002).

403

404 *10.1. Fossil specimens*

405

406 *Eophalangium sheari* Dunlop et al., 2003. PBM slide no. 3503, holotype (**Fig. 5d**), consisting of
407 a lateral thin section outlining nearly the entire female body (Dunlop et al., 2003).

408

409 *10.2. Phylogenetic justification*

410

411 In a phylogenetic analysis of morphology, *E. sheari* was placed in a polytomy with members of
412 Phalangida, to the exclusion of Cyphophthalmi (Garwood and Dunlop, 2014). In combined analysis of
413 molecules and morphology, *E. sheari* was resolved as a stem group Cyphophthalmi (Garwood et al.,
414 2014). Both positions, however, fall within the crown group of Opiliones.

415

416 *10.3. Age justification*

417

418 This fossil is known from the Early Devonian (Pragian) Rhynie Chert of Aberdeenshire,
419 Scotland. Spore assemblages of the Windyfield and stratigraphically underlying Rhynie Chert are
420 dated to the early but not earliest Pragian to early (earliest?) Emsian (polygonalis-emsian Spore
421 Assemblage Biozone) (Parry et al., 2011). Radiometric dating of the underlying Milton of Noth
422 Andesite at ca. 411 Ma (Parry et al., 2013, 2011) has been subject to a dispute over its temporal
423 relationship to hot spring activity associated with the cherts (Mark et al., 2013, 2011) and predates the
424 biostratigraphic dating of the Rhynie Chert relative to the global dating of the base of the Pragian
425 Stage. Therefore, a minimum age constraint may be defined at 405.0 Ma for the Rhynie Chert, using
426 the Pragian-Emsian boundary (407.6 Ma \pm 2.6 Myr) as a reference.

427 A soft maximum constraint comes from the oldest chelicerate *W. barbarhardyae* from the Emu
428 Bay Shale on Kangaroo Island, South Australia, which has been correlated based on trilobite
429 biostratigraphy to the upper part of the *Pararaia janeae* Zone in mainland South Australia (Jell in
430 Bengtson et al., 1990; Fig. 2 in Jago et al., 2012). As this is equivalent to the Canglangpuan Stage in
431 South China and the late Botoman in Siberia (Gehling et al., 2011, Fig. 9), the Emu Bay Shale can be
432 dated to Cambrian Series 2, Stage 4, providing a maximum age of ~514 Ma.

433

434 **11. Crown Acariformes**

435

436 This clade comprises Sarcoptiformes, Trombidiformes and 'Endeostigmata', their last common
437 ancestor and all of its descendants (**Fig. 4**). Monophyly is established by phylogenetic analysis of
438 nuclear ribosomal genes (Pepato and Klimov, 2015), morphology (Garwood and Dunlop, 2014), and
439 combined molecular and morphological data (Pepato et al., 2010).

440

441 *11.1. Fossil specimens*

442

443 *Protacarus crani* Hirst, 1923. BMNH In. 24665, holotype, preserving a nearly complete
444 individual in chert (**Fig. 5k**).

445

446 11.2. *Phylogenetic justification*

447

448 Originally described as a single species (Hirst, 1923), *P. crani* from the Rhynie Chert was
449 subsequently treated as five species belonging to five different genera (Dubinin, 1962). *P. crani* itself,
450 as exemplified by the holotype, was described as a member of Eupodidae, within Trombidiformes
451 (Hirst, 1923), or potentially more basal within the Acariformes (Bernini, 1986). While the specifics of its
452 classification may be debatable due to the lack of preserved diagnostic characters, the fan-like setae
453 observed dorsally in *P. crani* support a relationship with endeostigmatids within crown group
454 Acariformes (Bernini, 1986; Dunlop and Selden, 2009).

455

456 11.3. *Age justification*

457

458 As for 10.3.

459

460 11.4. *Discussion*

461

462 Bernini et al. (2002) figured a putative oribatid mite from terrestrial sediments dated to the Early
463 Ordovician of Sweden. However, its age and systematic placement were queried by Dunlop (2010, p.
464 134) and this species is not used for calibration herein.

465 Arguments that *P. crani* is a Recent contaminant (Crowson, 1985) have been countered by
466 Kühne and Schlüter (1985) and Greenslade (1988). Other species of fossil Acariformes have also
467 been described from the Rhynie Chert (all originally *P. crani*), including *Protospeleorchestes*
468 *pseudoprotacarus*, *Pseudoprotacarus scoticus*, *Palaeotydeus devonicus*, and *Paraprotocarus hirsti* (all

469 Dubinin, 1962).

470

471 **12. Crown Parasitiformes**

472

473 This clade comprises Opilioacariformes, Ixodida (hard and soft ticks), Holothyrida and
474 Mesostigmata, their last common ancestor and all of its descendants (**Fig. 4**). Monophyly is
475 established by phylogenetic analysis of nuclear ribosomal genes (Pepato and Klimov, 2015) and
476 morphology (Garwood and Dunlop, 2014).

477

478 *12.1. Fossil specimens*

479

480 *Cornupalpatum burmanicum* Poinar and Brown, 2003. Holotype larva (accession number A-10-
481 260; **Fig. 5i**) and paratype (accession number A-10-261; **Fig. 5j**) deposited in the Poinar amber
482 collection maintained at Oregon State University, later to be deposited at the California Academy of
483 Sciences (Poinar, 2015; Poinar and Brown, 2003).

484

485 *12.2. Phylogenetic justification*

486

487 Morphological characters such as the subcircular body with a marginal groove, free coxae,
488 ventral anal opening, the presence of a capitulum and Haller's organ, absence of an anal groove, and
489 elongate four-segmented palpi are all suggestive of Parasitiformes affinity for *C. burmanicum* (Poinar
490 and Brown, 2003). A particularly diagnostic character, suggesting placement within at least total-group
491 Ixodida (and thus crown Parasitiformes), is the presence of claws on palpal segment 3 in the larva
492 (Poinar and Brown, 2003). Putative morphologies similar to bacterial pathogens exclusive to modern
493 Ixodida were recently described from the paratype (Poinar, 2015).

494

495 12.3. Age justification

496

497 This fossil is sourced from amber mines in the Hukawng Valley of Kachin State, northern
498 Myanmar (formerly Burma). The depositional age of Burmese amber was estimated from U-Pb dating
499 of zircons from the volcanoclastic matrix surrounding the amber (Shi et al., 2012). Shi et al. (2012)
500 argue the amber is not older than its associated sediments, as burial and preservation would have to
501 be rapid for survival of organic material, so the amber was probably formed at, but not earlier than the
502 U-Pb date: at 98.79 Ma \pm 0.62 Myr. Therefore, a minimum age for any fossil from Burmese amber
503 deposits is 98.17 Ma.

504 Soft maximum as for 10.3.

505

506 13. Crown Pseudoscorpiones

507

508 This clade comprises Feaelloidea, Chthonioidea, Neobisiodea, Garypoidea, Sternophoroidea
509 and Cheliferoidea, their last common ancestor and all of its descendants (**Fig. 4**). While relationships
510 between superfamilies remain unclear, monophyly of Pseudoscorpiones was demonstrated with wide
511 taxon sampling and three genes (Muriene et al., 2008). More limited taxon sampling supports
512 monophyly with morphology (Garwood and Dunlop, 2014) and morphology combined with ribosomal
513 genes (Pepato et al., 2010).

514

515 13.1. Fossil specimens

516

517 *Protofeaella peetersae* Henderickx in Henderickx and Boone, 2016. NHM II 3115, holotype,
518 near complete specimen preserved in amber (**Fig. 5c**).

519

520 13.2. Phylogenetic justification

521

522 Although *P. peetersae* has not been included in a formal phylogenetic analysis, it was assigned
523 to the extant family Feaellidae by Henderickx and Boone (2016:8), based on its narrow cephalothorax,
524 granulated abdomen, and presence of small pedipalps with narrow coxa and small hands. Whilst
525 these features are certainly found in both *P. peetersae* and feaellids, other features, such as slender
526 pedipalp fingers, and the overall shape of the cephalic shield are more like those of pseudogarypids
527 (Harvey, 1992). Both the feaellid and pseudogarypids belong to the superfamily Feaelloidea (*sensu*
528 Harvey, 1992), and thus it is still likely *P. peetersae* belongs within the pseudoscorpion crown-group.

529

530 13.3. Age justification

531

532 As for 12.3.

533

534

535 13.4. Discussion

536

537 *Dracochela deprehendor* Schawaller et al., 1991 from the Middle Devonian of Gilboa, New
538 York State, was originally interpreted as a crown-group pseudoscorpion but was reassigned to the
539 pseudoscorpion stem group (Judson, 2012). Preliminary morphological phylogenetic analyses by one
540 of us (D.A.L.), however, suggest that *D. deprehendor* may be within the crown group. If so, this would
541 drastically extend the range of crown Pseudoscorpiones by over 280 Myr (to a minimum age of 382.7
542 Ma; Richardson et al., 1993).

543 Note that other Cretaceous pseudoscorpions have been preserved in amber (older from
544 Lebanon and Spain; younger from France, New Jersey and Alberta), but these have yet to be fully
545 described or examined for their systematic positions (Judson, 2009). If the Lebanese or Spanish
546 fossils were found to be members of the crown group, they could extend the range of

547 Pseudoscorpiones by up to 27 Myr.

548

549 **14. Crown Palpigradi**

550

551 This clade comprises the families Eukoeneniidae and Prokoeneniidae, their last common
552 ancestor and all of its descendants (**Fig. 4**). Monophyly has been supported by a phylogenetic
553 analysis of two nuclear ribosomal and one mitochondrial gene (Giribet et al., 2014).

554

555 *14.1. Fossil specimens*

556

557 *Electrokoenenia yaksha* Engel et al., 2016b. NIGP 163253, holotype in amber (**Fig. 5e**).

558

559 *14.2. Phylogenetic justification*

560

561 *E. yaksha* was classified within the extant family Eukoeneniidae (Engel et al., 2016b). This was
562 justified with morphological characters, in particular the rounded lateral “arms” to the frontal organ of
563 the propeltidium, as seen in the extant genus *Leptokoenenia* (Engel et al., 2016b). Thus *E. yaksha* is
564 within the crown group of Palpigradi.

565

566 *14.3. Age justification*

567

568 As for 12.3.

569

570 **15. Crown Solifugae**

571

572 This clade comprises Ammotrechidae, Ceromidae, Daesiidae, Eremobatidae, Galeodidae,

573 Gylippidae, Hexisopodidae, Karschiidae, Melanoblossidae, Mummuciidae, Rhagodidae and
574 Solpugidae, their last common ancestor and all of its descendants (**Fig. 4**). No phylogenetic analysis
575 has yet included all families, but limited taxon sampling has shown monophyly with morphology
576 (Garwood and Dunlop, 2014; Shultz, 2007) and morphology combined with nuclear genes (Giribet et
577 al., 2002; Pepato et al., 2010). Extensive morphological work on the homology of cheliceral characters
578 was recently published by Bird et al. (2015).

579

580 15.1. Fossil specimens

581

582 *Cratosolpuga wunderlichi* Selden and Shear, 1996 (Sol. 1 in the private Wunderlich collection,
583 Straubenhardt, Germany), holotype. An additional specimen (SMNK 1268 PAL; **Fig. 5f**), not a
584 paratype, is also deposited.

585

586 15.2. Phylogenetic justification

587

588 *C. wunderlichi* was assigned to the extant family Ceromidae on the basis of shape of the
589 cheliceral flagellum, shape of the propeltidium, eye tubercle, and leg spination (Selden and Shear,
590 1996). Only a single tarsal segment is present on the legs (Selden and Shear, 1996). A position in
591 total-group Ceromidae would therefore be within crown-group Solifugae.

592

593 15.3. Age justification

594

595 This fossil was recovered from the Nova Olinda Member of the Crato Formation in the Araripe
596 Basin, northeastern Brazil. This unit is generally agreed to be around the Aptian/Albian border (Martill
597 et al., 2007). Batten (2007) suggests that if assemblages in the upper layers are consistent across the
598 lower layers, a late Aptian date should be considered. The Crato formation has been dated using

599 palynomorphs (Pons et al., 1990) to the Aptian, though an accurate date for the Nova Olinda Member
600 is not available. The upper boundary of the Aptian, at 113.0 Ma \pm 0.4 Myr, gives a minimum date of
601 112.6 Ma.

602 Soft maximum as for 10.3.

603

604 15.4. Discussion

605

606 The Pennsylvanian *Protosolpuga carbonaria* Petrunkevitch, 1913, the only older possible fossil
607 solifuge, was discounted from the crown group of Solifugae in the same paper as described *C.*
608 *wunderlichi* (Selden and Shear, 1996). It is too poorly preserved to assign to the crown group without
609 additional phylogenetic justification.

610

611 16. Crown Scorpiones

612

613 This clade comprises Buthida and Iurida, their last common ancestor and all of its descendants
614 (**Fig. 4**). The composition of Buthida and Iurida are as detailed in Sharma et al. (2015). Monophyly has
615 been supported by phylogenetic analysis of transcriptomes (Sharma et al., 2015, 2014), morphology
616 (Garwood and Dunlop, 2014; Shultz, 2007), and combined ribosomal sequences and morphology
617 (Pepato et al., 2010).

618

619 16.1. Fossil specimens

620

621 *Protoischnurus axelrodurum* Carvalho and Lourenço, 2001. MN-7601-I, holotype, a male. We
622 also refer to the specimen SMNS 65534, which preserves phylogenetically relevant details of the
623 pedipalps (Fig. 3c in Menon, 2007).

624

625 16.2. *Phylogenetic justification*

626

627 Menon (2007) placed *P. axelrodurum* in the extant family Hemiscorpiidae, based on, amongst
628 other things, an inverse Y-shape on sulcus on the cephalic shield, the placement of Est trichobothria
629 on the pedipalp chela, and the placement of carinae V2 and V3 in the pedipalp chela, all of which are
630 diagnostic of the hemiscorpidid subfamily Hormurinae (Soleglad et al., 2005). Hemiscorpiidae is
631 classified within Iurida (Sharma et al., 2015), and is thus crown group Scorpiones.

632

633 16.3. *Age justification*

634

635 As for 15.3.

636

637 16.4. *Discussion*

638

639 A number of fossil taxa have been placed within crown group scorpion families, including
640 *Protobuthus elegans* Lourenço and Gall, 2004, from the Early Triassic Buntsanstein of France. It was
641 assigned to the superfamily Buthoidea, however, a subsequent study (Baptista et al., 2006),
642 considered this taxon and *Archaeobuthus* from the Early Cretaceous of Lebanon, outside the crown-
643 group based on trichobothrial arrangement.

644 *Araripescorpius ligabuei* Campos, 1986 is coeval to *P. axelrodurum*, and from the same locality.
645 Menon (2007) placed *A. ligabuei* in the extant family Chactidae based on general habitus and
646 trichobothrial pattern. Therefore it is also a member of the crown group of Scorpiones, albeit a less
647 well-preserved species.

648

649 17. **Crown Tetrapulmonata**

650

651 This clade comprises Pedipalpi and Araneae (spiders), their last common ancestor and all of its
652 descendants (**Fig. 6**). Monophyly is supported by phylogenetic analysis of transcriptomes (Sharma et
653 al., 2014), nuclear protein-coding genes (Regier et al., 2010), and morphology (Garwood and Dunlop,
654 2014; Legg et al., 2013; Shultz, 2007). This clade is not recognized in GenBank taxonomy.

655

656 17.1. Fossil specimens

657

658 *Parageralinura naufraga* (Tetlie and Dunlop, 2008), LWL Ar.K.1 (**Fig. 7a**). Counterpart in the
659 private collection of W. Elze, Ennepetal, Germany.

660

661 17.2. Phylogenetic justification

662

663 Tetlie and Dunlop (2008) interpreted Coal Measures uropygids to comprise a plesion on the
664 stem of the extant Thelyphonidae, the sole extant family of Thelyphonida. A subchelate pedipalp is
665 considered apomorphic of the crown group but is lacking in *Geralinura* and *P. naufraga*. This identifies
666 them as crown Uropygi, and thus, Tetrapulmonata.

667

668 17.3. Age justification

669

670 Of the uropygid fossils, the oldest are *P. naufraga* (formerly *Prothelyphonus naufragus*) from
671 deposits of "Ziegelei-Grube," Hagen-Vorhalle, Nordrhein-Westphalia, Germany (Brauckmann and
672 Koch, 1983; Tetlie and Dunlop, 2008). The fossil-bearing deposits are assigned to the Namurian B
673 (Marsdenian) based on the *Bilinguites metabilinguis* R2c1 subzone of ammonoid stratigraphy
674 (Brauckmann et al., 1994; Tetlie and Dunlop, 2008). The (late) Namurian-(early) Westphalian
675 boundary is defined by the earliest occurrence of the goniatite *Gastrioceras subcrenatum* (Waters and
676 Davies, 2006), but lacks a precise isotopic date. Pointon et al. (2012) estimated an age of c. 319.9 Ma

677 for the base of the Westphalian (top of the Namurian, only slightly younger than the Marsdenian)
678 based on Milankovitch cycles of sedimentation, giving a minimum age for *P. naufraga*.

679 Soft maximum as for 10.3.

680

681 **18. Crown Pedipalpi**

682

683 This clade comprises Amblypygi (tailless whip scorpions) and Uropygi, their last common
684 ancestor and all of its descendants (**Fig. 6**). Monophyly is supported by phylogenetic analysis of
685 transcriptomes (Sharma et al., 2014), nuclear protein-coding genes (Regier et al., 2010), and
686 morphology (Garwood and Dunlop, 2014; Legg et al., 2013; Shultz, 2007). This clade is not
687 recognized in GenBank taxonomy.

688

689 *18.1. Fossil specimens*

690

691 As for 17.1.

692

693 *18.2. Phylogenetic justification*

694

695 As for 17.2.

696

697 *18.3. Age justification*

698

699 As for 17.3.

700

701 **19. Crown Uropygi**

702

703 This clade comprises Thelyphonida (whip scorpions) and Schizomida, their last common
704 ancestor and all of its descendants (**Fig. 6**). Monophyly is supported by phylogenetic analysis of
705 nuclear protein-coding genes (Regier et al., 2010), and morphology (Garwood and Dunlop, 2014;
706 Legg et al., 2013; Shultz, 2007).

707

708 *19.1. Fossil specimens*

709

710 As for 17.1.

711

712 *19.2. Phylogenetic justification*

713

714 As for 17.2.

715

716 *19.3. Age justification*

717

718 As for 17.3.

719

720 **20. Crown Amblypygi**

721

722 This clade comprises Paracharontidae, Charinidae, Charontidae, Phrynichidae and Phrynidae,
723 their last common ancestor and all of its descendants (**Fig. 6**). Monophyly of Amblypygi has not been
724 fully investigated with phylogenetic analysis; however, monophyly has been shown for at least some
725 families with morphological data (Garwood and Dunlop, 2014; Shultz, 2007) and morphology
726 combined with nuclear genes (Pepato et al., 2010).

727

728 *20.1. Fossil specimens*

729

730 *Graeophonus anglicus* Pocock, 2011. BMNH In. 31233, holotype (**Fig. 7b**). Figured in Dunlop
731 et al. (2007: Fig. 1 a,b).

732

733 20.2. Phylogenetic justification

734

735 *G. anglicus* was redescribed by Dunlop et al. (2007) as a member of the Amblypygi crown
736 group. This was based on several morphological character comparisons to living members, such as
737 the pedipalp femur with dorsal spination similar to *Paracharon* (the monotypic extant species of the
738 family Paracharontidae). *G. anglicus*, unlike *Paracharon*, has a pear-shaped ocular tubercle,
739 suggesting it was not blind. *G. anglicus* is inferred to be on the stem lineage of Paracharontidae, and
740 thus, crown group Amblypygi (Dunlop et al., 2007).

741

742 20.3. Age justification

743

744 The genus *Graeophonus* was originally described from the Sydney Basin, Cape Breton
745 Carboniferous Coal Measures, Nova Scotia, Canada, which corresponds to Westphalian in age
746 (Dunlop et al., 2007; Giles et al., 2002; Scudder, 1890a). Further studies are needed on the Canadian
747 material, so the minimum age was taken from the oldest European specimen (which is roughly the
748 same age as the Cape Breton specimen) from the British Middle Coal Measures (Coseley,
749 Staffordshire), which is Westphalian B (or Duckmantian) at the youngest (Waters et al., 1994; Waters
750 and Davies, 2006). U-Pb dating of zircons constrains the upper boundary of the Duckmantian to
751 313.78 Ma \pm 0.08 Myr (Pointon et al., 2012), so a minimum age for *G. anglicus* is 313.70 Ma.

752 Soft maximum as for 10.3.

753

754 21. Crown Araneae

755

756 This clade comprises Mesothelae, Mygalomorphae (tarantulas, funnel-web spiders) and
757 Araneomorphae (most spiders), their last common ancestor and all of its descendants (**Fig. 6**).
758 Monophyly is established by phylogenetic analysis of transcriptomes (Fernández et al., 2014a;
759 Garrison et al., 2016) and morphology (Garwood and Dunlop, 2014; Legg et al., 2013; Shultz, 2007).

760

761 21.1. Fossil specimens

762

763 *Palaeothele montceauensis* Selden, 2000. Muséum d'Histoire naturelle, Autun: 51961
764 (holotype; **Fig. 7c**), and BMNH 62050, second specimen (not a paratype, **Fig. 7d**; Selden, 1996). We
765 also compare to *Arthrolycosa* sp. B Selden et al. 2014. PIN 5431/9 (**Fig. 7e**).

766

767 21.2. Phylogenetic justification

768

769 The deep, narrow sternum of *P. montceauensis* (formerly *Eothele montceauensis* Selden,
770 1996) is shared by extant members of Mesothelae (Selden, 1996). Several other characters that are
771 symplesiomorphic within Araneae, such as spinnerets, suggest a position within crown Araneae, and
772 perhaps on the stem lineage of Mesothelae (Selden, 1996).

773

774 21.3. Age justification

775

776 *P. montceauensis* was found in the Montceau Lagerstätte, Montceau-les-Mines, Massif
777 Central, France. The nodule-rich layer is just above the first seam in the Great Seams Formation (late
778 Stephanian) (Perrier and Charbonnier, 2014). The age within the Stephanian has been assigned to
779 Stephanian B, with some biostratigraphic evidence for Stephanian C (Racheboeuf et al., 2002). The
780 Stephanian B/C is a European stage of the Pennsylvanian, straddling the boundary of the globally

781 used Kasimovian and Gzhelian (Richards, 2013). The upper boundary of the Gzhelian is 298.9 Ma \pm
782 0.15 Myr, hence the minimum age of the Montceau Lagerstätte is 298.75 Ma.

783 Soft maximum as for 10.3.

784

785 21.4 Discussion

786

787 A possible older spider, *Arthrolycosa* sp. B Selden et al., 2014, is known from the
788 Krasnodonsky Horizon of Rostov Province, Russia (Duckmantian, ~313 Ma). It shares characters with
789 extant Mesothelae, such as the position and morphology of the eye tubercles, but lacks spinnerets, so
790 the inference is largely based on better-known *Arthrolycosa* from other localities (Selden et al., 2014).
791 Because phylogenetic evidence for crown group membership is largely indirect, we maintain *P.*
792 *montceauensis* as the oldest well-supported Araneae.

793

794 22. Crown Mandibulata

795

796 This clade comprises Myriapoda and Pancrustacea, their last common ancestor and all of its
797 descendants (**Fig. 1**). Monophyly has been independently demonstrated based on protein-coding
798 genes and microRNAs, as well as morphological data (Rota-Stabelli et al., 2011).

799

800 22.1. Fossil specimens

801

802 As for 4.1.

803

804 22.2. Phylogenetic justification

805

806 As for 4.2.

807

808 22.3. *Age justification*

809

810 As for 4.3.

811

812 22.4. *Discussion*

813

814 *Wujicaris muelleri* Zhang et al., 2010 has an equal claim to being the earliest record of
815 Mandibulata, but it is of equal age to the holotype of *Y. dianensis*.

816

817 **23. Crown Myriapoda**

818

819 This is the clade comprising Chilopoda (centipedes) and Progoneata, their last common
820 ancestor and all of its descendants (**Fig. 1**). Monophyly has been demonstrated by morphology
821 (Edgecombe, 2004; Legg et al., 2013; Rota-Stabelli et al., 2011), nuclear protein-coding genes (Regier
822 et al., 2010; Zwick et al., 2012), transcriptomes (Rehm et al., 2014), and combined analysis of
823 molecules and morphology (Lee et al., 2013).

824

825 23.1. *Fossil specimens*

826

827 *Cowiedesmus eroticopodus* Wilson and Anderson, 2004. AMS F.64845, holotype (**Fig. 2e**).

828

829 23.2. *Phylogenetic justification*

830

831 Membership of *C. eroticopodus* in Diplopoda is indicated by its strict diplosegmentation,
832 whereas its cuticular mineralization supports membership in the subgroup Chilognatha, and its

833 modified legs on trunk segment 8 support membership in Helminthomorpha. *C. eroticopodus* is
834 resolved as total-group Helminthomorpha in the morphological cladistic analysis of Fernández et al.
835 (2016) and is accordingly a member of the crown-groups of Chilognatha, Diplopoda, Progoneata and
836 Myriapoda.

837

838 23.3. Age justification

839

840 The earliest myriapods in the body fossil record are three species of Diplopoda from the
841 *Dictyocaris* Member of the Cowie Formation at Cowie Harbour, near Stonehaven, Aberdeenshire,
842 Scotland, one of which is *C. eroticopodus* (Wilson and Anderson, 2004). Based on associated spores,
843 the Cowie Formation taxa are late Wenlock to early Ludlow in age (Marshall, 1991; Wellman, 1993)
844 and the Early Ludlow upper boundary (Gorstian-Ludfordian boundary) is 425.6 Ma \pm 0.9 Myr, so the
845 minimum age for Myriapoda is 424.7 Ma.

846 Soft maximum as for 2.3.

847

848 23.4. Discussion

849

850 *Albadesmus almondi* and *Pneumodesmus newmani* (both described by Wilson and Anderson,
851 2004) have an equal claim to being the oldest myriapod, sourced from the same locality and unit as *C.*
852 *eroticopodus*. The latter was selected because it has been explicitly coded in a morphological cladistic
853 analysis (Fernández et al., 2016). We have not used trace fossil evidence suggestive of Ordovician
854 diplopods (Wilson, 2006) for dating.

855

856 24. Crown Progoneata

857

858 This clade comprises Diplopoda (millipedes), Pauropoda and Symphyla, their last common

859 ancestor and all of its descendants (**Fig. 8**). Monophyly is supported by phylogenetic analysis of
860 nuclear protein-coding genes (Regier et al., 2010; Zwick et al., 2012), whole mitochondrial genomes
861 (Brewer et al., 2013), and morphology (Edgecombe, 2004; Legg et al., 2013). Two recent molecular
862 phylogenies reject monophyly of Progoneata in favour of a putative clade of Chilopoda and Diplopoda:
863 one based on three protein-coding genes (Miyazawa et al., 2014) and one on transcriptomes (Rehm
864 et al., 2014). This clade is not recognized in GenBank taxonomy.

865

866 *24.1. Fossil specimens*

867

868 As for 23.1.

869

870 *24.2. Phylogenetic justification*

871

872 As for 23.2.

873

874 *24.3. Age justification*

875

876 As for 23.3.

877

878 *24.4. Discussion*

879

880 As for 23.4.

881

882 **25. Crown Diplopoda**

883

884 This clade comprises Penicillata (bristly millipedes) and Chilognatha, their last common

885 ancestor and all of its descendants (**Fig. 8**). Monophyly is supported by morphological analyses
886 (Blanke and Wesener, 2014), nuclear protein-encoding genes (Regier et al., 2010), and
887 transcriptomes (Fernández et al., 2016; Rehm et al., 2014).

888

889 *25.1. Fossil specimens*

890

891 As for 23.1.

892

893 *25.2. Phylogenetic justification*

894

895 As for 23.2.

896

897 *25.3. Age justification*

898

899 As for 23.3.

900

901 *25.4. Discussion*

902

903 As for 23.4.

904

905 **26. Crown Penicillata**

906

907 This clade comprises Polyxenoidea and Synxenoidea, their last common ancestor and all of its
908 descendants (**Fig. 8**). Monophyly has been defended based on the shared presence of serrate setae
909 arranged in lateral and caudal tufts (Enghoff, 1984).

910

911 26.1. *Fossil specimens*

912

913 *Electroxenus jezzinensis* Nguyen Duy-Jacquemin and Azar, 2004 (Acra collection, provisionally
914 deposited at MNHN: JS 231/1), holotype (**Fig. 9a,b**), adult in amber (Nguyen Duy-Jacquemin and
915 Azar, 2004, Fig. 1A, B).

916

917 26.2. *Phylogenetic justification*

918

919 Cretaceous amber penicillates are readily assigned to two of the three extant families,
920 Polyxenidae and Synxenidae (Nguyen Duy-Jacquemin and Azar, 2004; classification of Penicillata
921 following Short in Enghoff et al., 2015). *E. jezzinensis* preserves diagnostic characters of Polyxenidae
922 such as lateral extensions of the gnathochilarial palps. Membership in an extant family indicates status
923 as crown Penicillata.

924

925 26.3. *Age justification*

926

927 *E. jezzinensis* was discovered in amber from the Jouar Ess-Souss locality, in the Jezzine area,
928 South Lebanon (Azar et al., 2010). Previous work suggested a Neocomian (Valanginian-Hauterivian)
929 age for the Jezzine area (Azar et al., 2010). However, Lebanese stratigraphy has recently been
930 revised; the Jouar Ess-Souss locality is now recognized as part of the lowermost interval of the Grès
931 du Liban (Maksoud et al., 2016). The lower interval lies below a shale layer bearing the echinoid fossil
932 *Heteraster oblongus*, and below a pisolitic interval bearing charyophyte fossils (Maksoud et al., 2016).
933 The charyophyte layer is associated to the *Cruciata-Paucibracteatus* Zone of Martín-Closas et al.
934 (2009) in the late Barremian-early Aptian, but this layer is also older than the Banc de Mrejatt subunit
935 within Lebanon, thus Jezzine amber is older than the Ba2 layer in Fig. 6 of Maksoud et al. (2016).
936 Jezzine amber is therefore no younger than early Barremian. The upper boundary of the early

937 Barremian is proposed to be the first appearance of the ammonite *Ancyloceras vandenheckii* (Ogg et
938 al., 2012). Cyclostratigraphy dates the *A. vandenheckii* Zone beginning at 129.41 Ma (Ogg et al.,
939 2012), providing a minimum age for Jezzine Lebanese amber fossils.

940 A soft maximum age is obtained from the oldest mandibulate, *Y. dianensis*, which was
941 recovered from the Yu'anshan Formation at Xiaotan section, Yongshan, Yunnan Province, attributed to
942 the *Eoredlichia*–*Wutingaspis* Biozone (Zhang et al., 2007). Chinese Cambrian stratigraphy has been
943 revised substantially and the *Eoredlichia* – *Wutingaspis* Biozone is no longer recognized (Peng, 2009,
944 2003). However, *Eoredlichia* is known to co-occur with *Hupeidiscus*, which is diagnostic of the
945 *Hupeidiscus*-*Sinodiscus* Biozone, which is formally recognised as the second biozone of the
946 Nangaoan Stage of the Qiandongian Series of the Cambrian of China (Peng and Babcock, 2008). The
947 Nangaoan is the proposed third stage of the Cambrian System for the International Geologic
948 Timescale (Peng et al., 2012). Thus, a soft maximum constraint can be established on the age of the
949 lower boundary of the Nangaoan, which has been dated to 521 Ma (Peng et al., 2012; Peng and
950 Babcock, 2008).

951

952 26.4. Discussion

953

954 Another species of Polyxenidae from Lebanese amber, *Libanoxenus hammanaensis* Nguyen
955 Duy-Jacquemin and Azar, 2004, is likewise known from a single specimen, from the Mdeiriji/Hammana
956 locality in Central Lebanon. Its age data are similar to those of the more completely known *E.*
957 *jezzinensis*, so the latter is used for calibration.

958

959 27. Crown Chilognatha

960

961 This clade comprises Pentazonia (pill millipedes) and Helminthomorpha (long-bodied
962 millipedes), their last common ancestor and all of its descendants (**Fig. 8**). Monophyly is supported by

963 morphological analyses (Blanke and Wesener, 2014), nuclear coding genes (Miyazawa et al., 2014),
964 and transcriptomes (Fernández et al., 2016). Chilognthan monophyly has rarely been opposed: some
965 analyses of nuclear protein coding genes by Regier et al. (2005) found weak support for an
966 unconventional grouping of Penicillata with Pentazonia, but others retrieved Chilognatha.

967

968 *27.1. Fossil specimens*

969

970 As for 23.1.

971

972 *27.2. Phylogenetic justification*

973

974 As for 23.2.

975

976 *27.3. Age justification*

977

978 Minimum as for 23.3. Soft maximum as for 26.3.

979

980 *27.4. Discussion*

981

982 As for 23.4.

983

984 **28. Crown Chilopoda**

985

986 This clade comprises Scutigermorpha (house centipedes) and Pleurostigmophora, their last
987 common ancestor and all of its descendants (**Fig. 8**). Monophyly is robustly supported by
988 morphological analyses (Edgecombe and Giribet, 2004; Muriene et al., 2010), nuclear protein-coding

989 genes (Miyazawa et al., 2014; Regier et al., 2010; Zwick et al., 2012), and transcriptomics (Fernández
990 et al., 2016; Rehm et al., 2014).

991

992 28.1. Fossil specimens

993

994 *Crussolum* sp. Jeram et al., 1990. DE 1.3.2/50 (Fig. 1N) and DE 3.1.1/88 (Fig. 1P; Jeram et al.,
995 1990). As mentioned below, we also refer to material from the Windyfield Chert (AUGD 12307-12308;
996 Anderson and Trewin, 2003) for morphological details (**Fig. 9c-e**).

997

998 28.2. Phylogenetic justification

999

1000 *Crussolum* was resolved as stem-group Scutigeromorpha in the morphological cladistic
1001 analysis of Fernández et al. (2016). Codings were a composite of material described as *Crussolum* sp.
1002 from the Windyfield Chert (Pragian) of the Dryden Flags Formation, Aberdeenshire, Scotland (figured
1003 by Anderson and Trewin, 2003), and the one formally named species of the genus, *C. crusseratum*
1004 (Shear et al., 1998), known from isolated and fragmentary legs from the Middle Devonian Gilboa
1005 locality, Schoharie County, New York State (Givetian).

1006

1007 28.3. Age justification

1008

1009 The oldest examples of *Crussolum* are isolated legs from Ludford Lane in England (Shear et
1010 al., 1998), which come from a horizon 0.15-0.20 m above the base of the Ludlow Bone Bed Member,
1011 in the Downtown Castle Sandstone Formation. The Ludlow Bone Bed Member is early Pridoli in age
1012 (Jeram et al., 1990), that stage having an upper boundary of 419.2 Ma \pm 3.2 Myr, providing a minimum
1013 age of 416.0 Ma. *Crussolum* as currently delimited crosses the Silurian-Devonian boundary.

1014 Soft maximum as for 2.3.

1015

1016 **29. Crown Scutigeromorpha**

1017

1018 This clade comprises Scutigeridae, Scutigerinidae and Psellioididae, their last common
1019 ancestor and all of its descendants (**Fig. 8**). Monophyly is robustly supported by morphological
1020 analyses (Edgecombe and Giribet, 2004), targeted gene sequencing (Murienne et al., 2010), and
1021 transcriptomics (Fernández et al., 2016).

1022

1023 *29.1. Fossil specimens*

1024

1025 *Fulmenocursor tenax* Wilson, 2001. SMNS 64275, holotype (**Fig. 9f**), nearly complete
1026 specimen (Wilson, 2001, Pl. 1, Fig. 2).

1027

1028 *29.2. Phylogenetic justification*

1029

1030 Wilson (2001) assigned *F. tenax* to the extant family Scutigeridae based on the proportions of
1031 its antennal articles and its styliiform male gonopods. Paired spine-bristles on the tibia of the second
1032 maxilla (synapomorphy of Psellioididae + Scutigeridae) are consistent with this interpretation
1033 (Edgecombe, 2011). These affinities place the genus in crown-group Scutigeromorpha.

1034

1035 *29.3. Age justification*

1036

1037 Minimum as for 15.3. Soft maximum as for 26.3.

1038

1039 *29.5 Discussion*

1040

1041 A total-group scutigeromorph from the Carboniferous Mazon Creek deposits, *Latzelia*
1042 *primordialis* Scudder, 1890b, cannot be reliably assigned to the scutigeromorph crown group
1043 (Edgecombe, 2011; J. T. Haug et al., 2014) and is accordingly not used for dating that clade.

1044

1045 **30. Crown Pleurostigmophora**

1046

1047 This clade comprises Craterostigmomorpha and Amalpighiata, their last common ancestor and
1048 all of its descendants (**Fig. 8**); membership is identical if the internal relationships of the clade are
1049 resolved as Lithobiomorpha + Phylactometria. Monophyly is supported by morphological analyses
1050 (Edgecombe and Giribet, 2004), nuclear ribosomal and mitochondrial genes, and their combination
1051 with morphology (Giribet and Edgecombe, 2006; Murienne et al., 2010), nuclear protein coding genes
1052 (Regier et al., 2010), and transcriptomics (Fernández et al., 2016, 2014b).

1053

1054 *30.1. Fossil specimens*

1055

1056 *Devonobius delta* Shear and Bonamo, 1988. AMNH slide 411-15-AR18, holotype (**Fig. 9g**),
1057 complete head with 15 or 16 trunk segments. We also refer to AMNH slide 4329-AR4 (**Fig. 9h**).

1058

1059 *30.2. Phylogenetic justification*

1060

1061 *D. delta* was resolved in a trichotomy with *Craterostigmus* and Epimorpha in the morphological
1062 cladistic analysis of (Edgecombe and Giribet, 2004, Fig. 9), and as sister group to extant
1063 Phylactometria when those data were combined with sequence data from four genes (Edgecombe
1064 and Giribet, 2004, Fig. 14). Published analyses agree on it being more closely related to Epimorpha
1065 than to Lithobiomorpha (Shear and Bonamo, 1988, Fig. 1; Murienne et al., 2010, Fig. 2; Fernández et
1066 al., 2016) and it is accordingly crown Pleurostigmophora.

1067

1068 30.3. *Age justification*

1069

1070 *D. delta* occurs in the Middle Devonian Gilboa locality, Schoharie County, New York State,
1071 USA. Fossils come from the upper part of the Panther Mountain Formation, dated to the Tioughniogan
1072 regional Stage, Givetian in the global time scale. Palynomorphs are consistent with a Givetian age
1073 (Richardson et al., 1993). Accordingly, minimum date for the end of the Givetian/base of the Frasnian
1074 is applied (382.7 Ma).

1075 Soft maximum as for 26.3.

1076

1077 31. Crown Amalpighiata

1078

1079 This clade comprises Lithobiomorpha (stone centipedes) and Epimorpha, their last common
1080 ancestor and all of its descendants (**Fig. 8**). Monophyly is supported by targeted gene sequencing
1081 (Regier et al., 2010) and transcriptomics (Fernández et al., 2016, 2014b).

1082

1083 31.1. *Fossil specimens*

1084

1085 *Mazoscolopendra richardsoni* Mundel, 1979. FMNH PE 22936, holotype, nearly complete
1086 specimen in siderite concretion (J. T. Haug et al., 2014; Mundel, 1979). We also refer to FMNH PE
1087 29002 (**Fig. 9i**).

1088

1089 31.2. *Phylogenetic justification*

1090

1091 *M. richardsoni* was coded by Fernández et al. (2016) for its morphological data based on
1092 descriptions and figures of Mundel (1979) and Haug et al. (J. T. Haug et al., 2014), and personal

1093 observation by G.D.E. of type and other material in the Field Museum. It was resolved as total-group
1094 Scolopendromorpha based on possession of autapomorphies of that order (e.g. single tergite on the
1095 forcipular/first leg-bearing segments, 21 pairs of trunk legs) but cannot be placed more precisely with
1096 regards to whether it is a stem- or crown-group scolopendromorph. Nonetheless, its membership in
1097 Scolopendromorpha assigns it to crown Amalpighiata. The same calibration would apply were the
1098 putative clade Phylactometria endorsed in lieu of Amalpighiata.

1099

1100 31.3. *Age justification*

1101

1102 Specimens are derived from the Francis Creek Shale Member of the Carbondale Formation,
1103 Mazon Creek, Illinois, of Westphalian D age (Baird et al., 1985; Shabica and Hay, 1997). The
1104 Westphalian D is equivalent to the latest Moscovian stage of the Pennsylvanian (Richards, 2013). As
1105 the upper boundary of the Moscovian is $307.0 \text{ Ma} \pm 0.1 \text{ Myr}$, this provides a minimum age of 306.9
1106 Ma.

1107 Soft maximum as for 26.3.

1108

1109 32. Crown Epimorpha

1110

1111 This clade comprises Scolopendromorpha and Geophilomorpha, their last common ancestor
1112 and all of its descendants (**Fig. 8**). Monophyly is supported by morphological analyses (Fernández et
1113 al., 2016; Murienne et al., 2010) and transcriptomics (Fernández et al., 2016, 2014b).

1114

1115 32.1. *Fossil specimens*

1116

1117 As for 31.1.

1118

1119 32.2. *Phylogenetic justification*

1120

1121 As for 31.2.

1122

1123 32.3. *Age justification*

1124

1125 As for 31.3.

1126

1127 **33. Crown Geophilomorpha**

1128

1129 This clade comprises Placodesmata and Adesmata, their last common ancestor and all of its
1130 descendants (**Fig. 8**). Monophyly is supported by morphological analyses, targetted sequencing, and
1131 combination of molecular and morphological data (Bonato et al., 2014a; Fernández et al., 2014b;
1132 Murienne et al., 2010) and transcriptomics (Fernández et al., 2016).

1133

1134 33.1. *Fossil specimens*

1135

1136 *Kachinophilus pereirai* Bonato et al., 2014b. AMNH Bu-Ba41a, holotype (**Fig. 9j,k**), complete
1137 adult male in amber (Bonato et al., 2014b, Fig. 1A-B, 2).

1138

1139 33.2. *Phylogenetic justification*

1140

1141 *K. pereirai* was originally assigned to the extant family Geophilidae based on a combination of
1142 characters that is unique to that family. More precisely it compares most closely to a subgroup within
1143 Geophilidae that has been classified as subfamilies Chilenophilinae or Pachymeriinae. *K. pereirai* was
1144 coded by Fernández et al. (2016) for its morphological data based on original observations on the type

1145 material. It was resolved as more closely related to extant Geophilidae (*sensu* Bonato et al., 2014a)
1146 than to members of any of the other sampled geophilomorph family, as predicted by its original
1147 classification. Thus it is unambiguously a member of crown Adesmata and accordingly crown
1148 Geophilomorpha.

1149

1150 33.3. *Age justification*

1151

1152 Minimum as for 12.3. Soft maximum as for 26.3.

1153

1154 33.4. *Discussion*

1155

1156 A total-group geophilomorph from the Late Jurassic of Germany, *Eogeophilus jurassicus*
1157 Schweigert and Dietl, 1997 (refigured by J. T. Haug et al., 2014), is too inadequately known to
1158 establish whether or not it is a member of the geophilomorph crown-group.

1159

1160 34. **Crown Pancrustacea**

1161

1162 This clade comprises Oligostraca, Multicrustacea, and Allotriocarida, their last common
1163 ancestor and all of its descendants (**Fig. 1**). The inclusion of Hexapoda in a paraphyletic ‘Crustacea’
1164 (and hence, erection of the clade Pancrustacea; Zrzavý and Štys, 1997) has been supported by
1165 numerous phylogenetic analyses, including those based on nuclear protein-coding genes (Regier et
1166 al., 2010, 2005), transcriptomes (Andrew, 2011; Meusemann et al., 2010; Rota-Stabelli et al., 2011;
1167 von Reumont et al., 2012), morphology (Legg et al., 2013; Schram and Koenemann, 2004; Strausfeld
1168 and Andrew, 2011) and combined morphological and molecular data (Oakley et al., 2013).

1169 This clade has also been named Tetraconata (Dohle, 2001) referring to the shared apomorphy
1170 of four cone cells within the compound eye; however this character is absent in many members of the

1171 clade, with multiple possible reconstructions of homology (Oakley, 2003; T. Oakley, pers. comm.).
1172 Terminology that does not rely on the homology of cone cell arrangement is thus preferred. More
1173 recently, an amended version of 'Crustacea' has been proposed (Haug and Haug, 2015) to avoid a
1174 different application of the 'Pan-' prefix (Lauterbach, 1989). While this concept of Crustacea is in our
1175 view valid, for this purpose we favour the original use of Pancrustacea referring to the crown group
1176 members only (Zrzavý and Štys, 1997). Haug and Haug (2015) argue that fossils such as
1177 Phosphatocopina would need to be included within Pancrustacea, however recent phylogenetic
1178 analyses show the sister group to crown Pancrustacea is in fact crown Myriapoda, with all other fossils
1179 outside (Legg et al., 2013). Pancrustacea is the clade name implemented in GenBank, and is the most
1180 commonly used name among molecular workers.

1181

1182 *34.1. Fossil specimens*

1183

1184 As for 4.1.

1185

1186 *34.2. Phylogenetic justification*

1187

1188 As for 4.2.

1189

1190 *34.3. Age justification*

1191

1192 As for 4.3.

1193

1194 *34.4. Discussion*

1195

1196 As for 22.4.

1197

1198 **35. Crown Oligostraca**

1199

1200 This clade comprises Ostracoda (seed shrimp), Branchiura (fish lice), Pentastomida (tongue
1201 worms), and Mystacocarida, their last common ancestor and all of its descendants (**Fig. 10**).
1202 Monophyly of this clade has been demonstrated with nuclear protein-coding genes (Regier et al.,
1203 2010; Zwick et al., 2012) and combined phylogenetic analysis of molecules and morphology (Lee et
1204 al., 2013; Oakley et al., 2013; Zrzavý et al., 1998). GenBank taxonomy does not recognize this clade.
1205 Instead GenBank prefers the Maxillopoda hypothesis (Branchiura, Pentastomida, Mystacocarida,
1206 Thecostraca and Copepoda), which has not been recovered in molecular analyses (Abele et al., 1992;
1207 Regier et al., 2005) despite support from morphology (Legg et al., 2013).

1208

1209 *35.1. Fossil specimens*

1210

1211 *Boeckelericambria pelturae* Walossek and Müller, 1994. UB W116, holotype, consisting of a
1212 complete larva (**Fig. 11a**).

1213

1214 *35.2. Phylogenetic justification*

1215

1216 *B. pelturae* is likely a stem group pentastomid, based especially on the diagnostic
1217 synapomorphy of a head with two pairs of grasping hooks (similar to the extant *Reighardia* larva;
1218 Walossek and Müller, 1994, Fig. 25a). This species is a member of the round headed (as opposed to
1219 hammer headed) morphotype (Walossek and Müller, 1994). It was resolved in the pentastomid stem-
1220 group in a cladistic analysis that sampled the extant genera by Almeida and Christoffersen (Almeida
1221 and Christoffersen, 1999). Its pentastomid identity is not dependent on whether pentastomids are
1222 interpreted as Ichthyostraca (Møller et al., 2008; Regier et al., 2010; Sanders and Lee, 2010) or early

1223 diverging euarthropods (e.g. Castellani et al., 2011). Because we accept crown pentastomids as sister
1224 group to crown branchiurans on the basis of strong support from molecular data, *B. pelturae* must
1225 therefore be within crown Oligostraca.

1226

1227 35.3. Age justification

1228

1229 The Orsten fossils come from the lowest zone of the late Cambrian Alum Shale, formally called
1230 the *Agnostus pisiformis* Zone or Zone 1, previously corresponding to the Uppermost Zone of the
1231 Middle Cambrian (Babcock et al., 2005). The *Agnostus pisiformis* Zone was recently redefined as the
1232 uppermost zone of the Guzhangian, at the upper boundary of Cambrian Series 3 (Nielsen et al.,
1233 2014). This age of the uppermost stage of the Cambrian Series 3 is 499 Ma \pm 2 Myr. Thus the
1234 minimum age applied to Oligostraca is 497 Ma.

1235 Soft maximum as for 2.3.

1236

1237 36. Crown Ichthyostraca

1238

1239 This clade comprises Branchiura and Pentastomida, their last common ancestor and all of its
1240 descendants (**Fig. 10**). It was first proposed based on sperm ultrastructure (Wingstrand, 1972).
1241 Subsequent analyses of morphology combined with protein-coding genes (Zrzavý et al., 1998) or with
1242 transcriptomes (Oakley et al., 2013), as well as molecular data on their own (Møller et al., 2008;
1243 Regier et al., 2010) have supported monophyly of this clade.

1244

1245 36.1. Fossil specimens

1246

1247 As for 35.1.

1248

1249 36.2. *Phylogenetic justification*

1250

1251 As for 35.2.

1252

1253 36.3. *Age justification*

1254

1255 As for 35.3.

1256

1257 **37. Crown Ostracoda**

1258

1259 This clade comprises Myodocopa, Podocopa (including Palaeocopida), their last common
1260 ancestor and all its descendants (**Fig. 10**). Monophyly of this clade has been demonstrated by
1261 phylogenetic analysis of a dataset including nuclear protein-coding genes, transcriptomes, and
1262 morphology (Oakley et al., 2013). Additional phylogenetic analyses of morphology alone (Legg et al.,
1263 2013; Wolfe and Hegna, 2014) also support monophyly.

1264

1265 37.1. *Fossil specimens*

1266

1267 *Luprisca incuba* Siveter et al., 2014. YPM IP 307300, holotype, consisting of a complete
1268 pyritized specimen in ventral aspect (**Fig. 11b**).

1269

1270 37.2. *Phylogenetic justification*

1271

1272 To date, *L. incuba* is yet to be included in an extensive phylogenetic analysis, but a number of
1273 features confirm both its placement within Myodocopida, and therefore Myodocopa. Specifically, the
1274 arrangement of setae on the antennula of *L. incuba* is currently only observed amongst extant

1275 myodocopid ostracods (Kornicker, 1981).

1276

1277 37.3. Age justification

1278

1279 The holotype of *L. incuba* was collected from siltstone of the Original Trilobite Bed, Walcott
1280 Quarry of Beecher's Trilobite Bed, in the Frankfort Shale of upstate New York (Siveter et al., 2014).
1281 Beecher's site within the Frankfort Shale is within the Lorraine Group, part of the regional Maysvillian
1282 Stage of the Cincinnati Series (Farrell et al., 2011, 2009). Globally, the Maysvillian (*Amplexograptus*
1283 *manitoulinensis* Graptolite Zone) corresponds to the early Katian Stage, from the base of the
1284 *Diplacanthograptus caudatus* Graptolite Zone to the base of the *Pleurograptus linearis* Graptolite Zone
1285 (Bergström et al., 2009). The upper boundary of the Katian is 445.2 Ma \pm 1.4 Myr, providing a
1286 minimum age of 443.8 Ma.

1287 As in Oakley et al. (2013), we suggest the maximum age of ostracods must be 509 Ma, the
1288 age of the Burgess Shale. Myodocope ostracods possess bivalved, calcified carapaces, which are
1289 preserved from many other Burgess Shale arthropods. There is no taphonomic reason why they would
1290 not have been preserved from ostracods. The Burgess Shale type locality is from Unit 3 of the Collins
1291 Quarry on Mount Stephen in the Canadian Rocky Mountains, British Columbia, which falls within the
1292 Kicking Horse Shale Member of the "thick" Stephen Formation (Aitkin, 1997; Caron et al., 2010;
1293 Stewart, 1991), also referred to as the Burgess Shale Formation (Fletcher and Collins, 2003, 1998).
1294 This unit yields trilobites from the *Polypheuraspis insignis* Subzone of the *Glossopleura* Zone (Fletcher
1295 and Collins, 1998), and is the oldest soft-bodied fossil excavation of the Burgess Shale sites. The age
1296 of the *Glossopleura* Zone corresponds to the Cambrian Series 3 Stage 5, giving a maximum constraint
1297 of 509 Ma.

1298

1299 37.4. Discussion

1300

1301 Older fossils, from the Tremadocian (~40 Myr older) have been reported from numerous
1302 localities across the current and Ordovician world: Argentina, Australia, China, Iran, Norway, Sweden,
1303 and the UK (Williams et al., 2008). However, all of these fossils are known solely from carapaces,
1304 which are known to be highly homoplastic (Siveter et al., 2013). The affinities of Tremadocian
1305 ostracods are therefore ambiguous. Other bivalved crustacean-like taxa from the Cambrian, such as
1306 bradoriids and phosphatocopines, are demonstrably not closely related to ostracods, or even
1307 Oligostraca, based on phylogenetic analyses (Hou et al., 2010; Legg et al., 2013; Oakley et al., 2013;
1308 Wolfe and Hegna, 2014).

1309

1310 **38. Crown Podocopa**

1311

1312 This clade comprises Palaeocopida, Podocopida and Platycopida, their last common ancestor
1313 and all of its descendants (**Fig. 10**). Monophyly has been demonstrated by phylogenetic analysis of
1314 morphology (Horne et al., 2005), and morphology combined with nuclear protein-coding genes and
1315 transcriptomes (Oakley et al., 2013). Although the sole living representative of Palaeocopida, *Manawa*
1316 *staceyi*, has to date only been represented by a single ribosomal sequence and morphology, bootstrap
1317 support for its position as a sister to the remaining Podocopa is strong (Oakley et al., 2013).

1318

1319 *38.1. Fossil specimens*

1320

1321 *Cytherellina submagna* Krandijevsky, 1963. For phylogenetically relevant details, we refer to
1322 ZPAL O.60/001 (**Fig. 11c-e**), preserving soft anatomy, and ZPAL O.60/002, preserving adductor
1323 muscle scars (Olempska et al., 2012).

1324

1325 *38.2. Phylogenetic justification*

1326

1327 *C. submagna* is very similar to modern podocopes, particularly sigilloideans and
1328 darwinuloideans, with which it shares a particular adductor muscle scar pattern, long terminal seta on
1329 the seventh limb pair, and a furca with large distal setae (Olempska et al., 2012).

1330

1331 38.3. Age justification

1332

1333 Specimens of *C. submagna* were recovered from two localities in Podolia, Ukraine: Kasperovcy
1334 village, left border of the river Seret (type locality), and from the right escarpment of the River Dniester
1335 near the village Ivanye Zlote (Olempska et al., 2012). The type locality, part of the Chortkov/Chortkiv
1336 Horizon, underlies the second locality, which is part of the Ivanye Horizon (Filipiak et al., 2012;
1337 Olempska et al., 2012). Thus we must use the Chortkiv age as a minimum constraint on the age of *C.*
1338 *submagna*, to provide the narrowest interval of clade divergence. The Chortkiv Horizon comfortably
1339 lies within the middle Lochkovian stage of the Early Devonian (Filipiak et al., 2012; Małkowski et al.,
1340 2009; Plotnick, 1999). Conodont biostratigraphy places the upper boundary of the Chortkiv Horizon at
1341 the end of the *Caudicriodus postwoschmidtii* Biozone, the oldest conodont Biozone within the
1342 Devonian (Drygant and Szaniawski, 2012). Spline fits on radiometric ages for the Devonian place the
1343 *C. postwoschmidtii* Biozone at 417.27 Ma with a duration of 1.89 Myr (Becker et al., 2012). Thus the
1344 end of the *C. postwoschmidtii* Biozone, and a minimum age for the first appearance of *C. submagna*, is
1345 415.38 Ma.

1346 Soft maximum as for 37.3.

1347

1348 38.4. Discussion

1349

1350 Although isolated ostracod carapace valves are incredibly abundant in the fossil record, the
1351 morphology of carapaces has been shown to have little systematic value (Siveter et al., 2013). For this
1352 reason we have selected a taxon with soft-tissue preservation, of which *C. submagna* is the oldest

1353 recognized example, although other species of *Cytherellina* are known from older deposits including
1354 the later Silurian of Ludlow, England, with only the carapaces preserved (Olempska et al., 2012).
1355 These older species cannot be ruled out as myodocopes or stem members of any of Podocopa,
1356 Myodocopa, or even Ostracoda, as they lack diagnostic soft parts.

1357

1358 **39. Crown Myodocopa**

1359

1360 This clade comprises Myodocopida and Halocyprida, their last common ancestor and all of its
1361 descendants (**Fig. 10**). Monophyly has been demonstrated by phylogenetic analysis of morphology
1362 (Horne et al., 2005), and morphology combined with nuclear protein-coding genes and transcriptomes
1363 (Oakley et al., 2013).

1364

1365 *39.1. Fossil specimens*

1366

1367 As for 37.1.

1368

1369 *39.2. Phylogenetic justification*

1370

1371 As for 37.2.

1372

1373 *39.3. Age justification*

1374

1375 As for 37.3.

1376

1377 **40. Crown Myodocopida**

1378

1379 This clade comprises Cylindroleberidoidea, Cypridinoidea and Sarsielloidea, their last common
1380 ancestor and all of its descendants (**Fig. 10**). Monophyly has been demonstrated by phylogenetic
1381 analysis of morphology (Horne et al., 2005), and morphology combined with nuclear protein-coding
1382 genes and transcriptomes (Oakley et al., 2013).

1383

1384 *40.1. Fossil specimens*

1385

1386 As for 37.1.

1387

1388 *40.2. Phylogenetic justification*

1389

1390 As for 37.2.

1391

1392 *40.3. Age justification*

1393

1394 As for 37.3.

1395

1396 **41. Crown Altocrustacea**

1397

1398 This clade comprises Multicrustacea and Allotriocarida, their last common ancestor and all of
1399 its descendants (**Fig. 1**). Monophyly has been supported by phylogenetic analysis of nuclear protein-
1400 coding genes (Regier et al., 2010; Zwick et al., 2012), transcriptomes (von Reumont et al., 2012), and
1401 combined analysis of morphology and nuclear protein-coding genes (Lee et al., 2013) or morphology
1402 and transcriptomes (Oakley et al., 2013). However, this clade has been challenged as paraphyletic
1403 (containing Oligostraca) by Rota-Stabelli et al. (2013b), and has not been supported by morphological
1404 data alone. It is not recognized in GenBank taxonomy.

1405

1406 *41.1. Fossil specimens*

1407

1408 As for 4.1.

1409

1410 *41.2. Phylogenetic justification*

1411

1412 As for 4.2.

1413

1414 *41.3. Age justification*

1415

1416 As for 4.3.

1417

1418 *41.4. Discussion*

1419

1420 A series of disarticulated Small Carbonaceous Fossils (Harvey and Butterfield, 2008) from the
1421 early Cambrian Mount Cap Formation, Northwest Territories, Canada, have been cited as calibration
1422 fossils within Altocrustacea or even Allotriocarida (e.g. Rehm et al., 2011; Sun et al., 2015). These
1423 fossils were argued by Harvey (2008) to comprise part of the feeding apparatus of a single crustacean
1424 taxon. The Mount Cap arthropod fossils would have represented structures each specialized for
1425 precise feeding functions. The fossil species may have initially scraped food with saw-toothed and
1426 hooked setae, further processed particles with filter plates and other delicate setal associations, then
1427 macerated with mandibular molar surfaces and passed to the mouth with long fringing setae (Harvey
1428 and Butterfield, 2008). Estimates of the body size of the animal, based on regression of body length
1429 versus molar surface length (from extant crustaceans) suggest the Mount Cap arthropod was, in total,
1430 about the same size as an adult cladoceran or anostracan (Harvey and Butterfield, 2008). While direct

1431 synapomorphies linking the Mount Cap arthropod to crown group branchiopods are lacking, the
1432 evidence together suggests affinity along the stem lineage of Altocrustacea (Harvey, 2008, Fig. 5.6).

1433

1434 **42. Crown Multicrustacea**

1435

1436 This clade comprises Copepoda, Thecostraca (barnacles) and Malacostraca, their last
1437 common ancestor and all of its descendants (**Figs. 12 and 13**). Monophyly was first demonstrated by
1438 nuclear protein-coding genes (Regier et al., 2010) and supported by transcriptomes (von Reumont et
1439 al., 2012) and combined analysis of molecular and morphological data (Lee et al., 2013; Oakley et al.,
1440 2013). This clade has, however, not been recovered in any morphology-only phylogenetic analyses,
1441 presumably owing to widespread support for Malacostraca as sister to much of the rest of
1442 Pancrustacea (the Entomostraca hypothesis, e.g. Walossek and Müller, 1998). See Wolfe and Hegna
1443 (2014) for a morphological deconstruction of Entomostraca. Neither Multicrustacea nor Entomostraca
1444 is recognized in GenBank taxonomy.

1445

1446 *42.1. Fossil specimens*

1447

1448 *Arenosicaris inflata* Collette and Hagadorn, 2010a. PRI 10130), holotype from the Elk Mound
1449 Group (**Fig. 14a**), which is difficult to date (see 42.3). Therefore, we refer to a second specimen,
1450 UWGM 745.

1451

1452 *42.2. Phylogenetic justification*

1453

1454 *A. inflata* was identified within the Archaeostraca, the likely fossil sister group to extant
1455 Leptostraca (together comprising 'Phyllocarida') and included in the morphological cladistic analysis of
1456 Collette and Hagadorn (2010b). In that analysis, the exceptionally preserved fossils *Nahecaris stuerzi*

1457 Jaeckel, 1921 and *Cinerocaris magnifica* Briggs et al., 2004 were also included within Archaeostraca
1458 (Collette and Hagadorn, 2010b). A separate extensive combined molecular and morphological
1459 analysis placed *C. magnifica* within crown Malacostraca (as is traditionally assumed for members of
1460 Archaeostraca), while *N. stuarti* was equivocally stem Leptostraca or stem Malacostraca (Oakley et
1461 al., 2013), suggesting non-monophyly of Archaeostraca. *C. magnifica* was also crown Malacostraca in
1462 another morphological analysis that omitted *N. stuarti* (Legg et al., 2013). *A. inflata* is within the same
1463 archaeostracan clade as *N. stuarti* (Pephracaridina + Rhinocaridina) while *C. magnifica* is in a
1464 separate archaeostracan group (Echinocaridina; Collette and Hagadorn, 2010b). Given the uncertainty
1465 of crown affinities and potential monophyly of Archaeostraca, we conservatively assign *A. inflata* to
1466 crown-group Multicrustacea, but not Malacostraca.

1467

1468 42.3. Age justification

1469

1470 *A. inflata* is found in the Elk Mound Group (holotype) and in the Lodi Member of the St.
1471 Lawrence Formation, both in Wisconsin (Collette and Hagadorn, 2010a). Although the Elk Mound
1472 Group is the older of these, no biostratigraphically useful fossils co-occur with *A. inflata*, limiting the
1473 ability to determine the formation to which they belong (Collette and Hagadorn, 2010a). The St.
1474 Lawrence Formation is younger, containing *Saukia* Zone trilobites, which mark it as late Sunwaptan
1475 within the Furongian (Collette and Hagadorn, 2010a; Raasch, 1951). The Sunwaptan is the second
1476 latest stage of the Furongian, postdated by the Skullrockian (which extends into the Early Ordovician;
1477 Peng et al., 2012). The Sunwaptan-Skullrockian boundary is determined by the appearance of
1478 conodonts in the *Hirsutodontus hirsutus* Subzone of the *Cordylodus proavus* Zone (Peng et al., 2012).
1479 Based on the correlation diagram of Peng et al. (2012), the Sunwaptan-Skullrockian boundary is
1480 approximately 487 Ma, providing a minimum age estimate.

1481 Soft maximum as for 2.3.

1482

1483 43. Crown Copepoda

1484

1485 This clade comprises Calanoida, Cyclopoida, Gelyelloida, Harpacticoida (benthic copepods),
1486 Misophrioida, Mormonilloida, Platycopioidea and Siphonostomatoida (fish parasites), their last common
1487 ancestor and all of its descendants (**Fig. 12**). Members of Calanoida, Cyclopoida, and
1488 Siphonostomatoida were included in a large combined analysis of transcriptomes and morphology,
1489 forming a monophyletic group (Oakley et al., 2013). Phylogenetic analysis of morphology (Huys and
1490 Boxshall, 1991; Ho, 1994), mitochondrial genes (Minxiao et al., 2011), and ribosomal genes combined
1491 with morphology (Huys et al., 2007) suggest this sampling covers distant lineages of Copepoda,
1492 although omitting Platycopioidea, the presumed most basal order (Huys and Boxshall, 1991). Molecular
1493 data remain unavailable from Platycopioidea, although comparative morphological investigations
1494 support copepod monophyly (Dahms, 2004).

1495

1496 43.1. Fossil specimens

1497

1498 *Kabatarina pattersoni* Cressey and Boxshall, 1989. BMNH IN. 63466, holotype, preserving the
1499 cephalothorax, mouthparts, oral cone, and first and second thoracic limbs (**Fig. 14b**). This specimen
1500 likely represents an adult female, recovered from the gills of a fossil teleost fish (Cressey and
1501 Boxshall, 1989).

1502

1503 43.2. Phylogenetic justification

1504

1505 *K. pattersoni* has not been included in a formal phylogenetic analysis. Cressey and Boxshall
1506 (1989) detail one apomorphy shared by the fossil and recent members of the family Dichelesthidae,
1507 which is a medial groove delimiting the distal part of the maxillary claw. A number of other characters
1508 are shared more generally with copepods, such as the shape of the oral cone (typical for fish parasitic

1509 copepods), and biramous thoracic limbs with a 2-segmented protopod, joined by the intercoxal plate
1510 (Cressey and Boxshall, 1989). Dichelesthidae is a family belonging to the Siphonostomatoida. Even a
1511 position for *K. pattersoni* on the stem of Dichelesthidae or stem Siphonostomatoida would be within
1512 crown group Copepoda.

1513

1514 43.3. Age justification

1515

1516 *K. pattersoni* was found in the Cretaceous Santana Formation, Serra do Araripe, Ceará, Brazil
1517 (Cressey and Boxshall, 1989), which is mainly famous for concretions enclosing fossil fishes. The age
1518 of the Santana Formation is poorly constrained (as it lacks biostratigraphic index fossils and igneous
1519 rocks for radiometric dating); dates have been suggested that range from the Aptian to the Albian or
1520 Cenomanian (Martill, 2007). In order to ensure a minimum date, the upper boundary of the
1521 Cenomanian, which is 93.7 Ma (from 93.9 Ma \pm 0.2 Myr; Ogg et al., 2012), is used.

1522 Soft maximum as for 26.3.

1523

1524 43.4. Discussion

1525

1526 Despite their overwhelming abundance in modern aquatic ecosystems, copepods have a poor
1527 fossil record, likely due to their small size, unsclerotized cuticle, and planktonic ecology. Apart from *K.*
1528 *pattersoni*, putative copepod appendages have been reported from much older sediments in the
1529 Pennsylvanian (Selden et al., 2010) and even the Cambrian (Harvey et al., 2012; Harvey and Pedder,
1530 2013; These fossils each bear one to four characters found in crown copepods, from partial maxillae
1531 (Selden et al., 2010) and partial or complete mandibular gnathal edges (Harvey et al., 2012; Harvey
1532 and Pedder, 2013). Relationships between feeding habits and mandibular morphology have been
1533 observed in extant copepods (Michels and Schnack-Schiel, 2005), and variation may occur among
1534 closely related species (Sano et al., 2015). It is therefore extremely unlikely that mandibular characters

1535 have not experienced any homoplasy since the Cambrian.

1536 Nevertheless, divergence time analyses suggest Devonian-Carboniferous (calibrated with *K.*
1537 *pattersoni*; (Rota-Stabelli et al., 2013a), Carboniferous (calibrated with external fossils from other
1538 pancrustacean clades; Oakley et al., 2013), or Permian (external fossils; Wheat and Wahlberg, 2013)
1539 origins for crown Copepoda. These analyses do not conflict stratigraphically with a crown assignment
1540 for the Pennsylvanian fossils (Selden et al., 2010). Therefore we must caution that a Cretaceous age
1541 is likely a severe underestimate of crown copepod antiquity.

1542

1543 **44. Crown Thecostraca**

1544

1545 This clade comprises Facetotecta (y-larvae), Ascothoracida, and Cirripedia, their last common
1546 ancestor and all of its descendants (**Fig. 12**). Monophyly of Thecostraca has been demonstrated by
1547 separate analysis of nuclear housekeeping genes and morphology (Pérez-Losada et al., 2009a). All
1548 included clades have complex (sometimes only partially known) life histories, but particularly strong
1549 morphological support comes from a shared larval stage, the cyprid.

1550 More recently, the enigmatic parasitic Tantulocarida were added within Thecostraca based on
1551 analysis of a single ribosomal gene (Petrutina et al., 2014), however, other relationships within
1552 Pancrustacea differed significantly from those outlined herein. In light of the paucity of data other than
1553 ribosomal genes, we remain ambivalent about including Tantulocarida. As tantulocarids have no
1554 known fossil record, if further evidence supports their position within Thecostraca, this calibration may
1555 be modified to include them as well.

1556

1557 *44.1. Fossil specimens*

1558

1559 *Rhamphoverritor reduncus* Briggs et al., 2005. OUM C.29587, holotype (**Fig. 14c,d**),
1560 preserving a cyprid larva in a volcanoclastic concretion. As the reconstruction of Herefordshire fossils

1561 requires serial grinding and photography of 20 µm sections (Sutton et al., 2002), the holotype (figured
1562 in Briggs et al., 2005: Fig. 1) was thus destroyed in preparation. Morphological data for Herefordshire
1563 fossils are published as 3D models of the thin section photographs.

1564

1565 44.2. Phylogenetic justification

1566

1567 In a phylogenetic analysis of morphology, *R. reduncus* is the sister group of two species of
1568 Thoracica (both are members of Balanomorpha) (Legg et al., 2013). This is a position likely within the
1569 crown group of Thecostraca, however, no other thecostracans (such as Facetotecta and
1570 Ascothoracida) were included. Generally, the cyprid larval morphotype (with an elongated head shield,
1571 six swimming thoracopods, and robust modified antennules) is considered a synapomorphy of
1572 Thecostraca (Høeg et al., 2004). *R. reduncus* differs from cirripede cyprids as it lacks attachment
1573 discs, and its abdomen extends past the head shield; a differentiated abdomen is a condition of
1574 Ascothoracida (Briggs et al., 2005; Høeg et al., 2009a). Based on the presence of five shell plates in a
1575 juvenile specimen, Høeg et al. (2009b) suggested that *R. reduncus* may be placed on the cirripede
1576 stem lineage. In combination with the phylogenetic analysis of Legg et al. (2013), these apomorphies
1577 indicate that *R. reduncus* is very likely a member of crown group Thecostraca, and likely on the stem
1578 of Cirripedia.

1579

1580 44.3. Age justification

1581

1582 Minimum as for 6.3. Soft maximum as for 26.3.

1583

1584 45. Crown Cirripedia

1585

1586 This clade comprises Acrothoracica, Rhizocephala and Thoracica (barnacles), their last

1587 common ancestor and all of its descendants (**Fig. 12**). Monophyly has been demonstrated by separate
1588 phylogenetic analysis of nuclear housekeeping genes and morphology (Pérez-Losada et al., 2009a).

1589

1590 *45.1. Fossil specimens*

1591

1592 *Illilepas damrowi* Schram, 1986. FMNH P32055, holotype (**Fig. 14e**).

1593

1594 *45.2. Phylogenetic justification*

1595

1596 Schram (1975) described this fossil as *Praeilepas damrowi*, a congener of *P. jaworskii*
1597 Chernyshev, 1930. Restudy led to the transfer of this fossil to the new genus *Illilepas* under the
1598 combination *I. damrowi*, as the original description of a carina more closely resembled a tergum, and
1599 the original tergum was more likely an enlarged spine along the margin of the aperture, similar to that
1600 seen in Ibliformes (Thoracica) (Buckeridge and Newman, 2006; Schram, 1986). However, both
1601 molecular and morphological data place *Ibla* as the most basal clade of Thoracica (Pérez-Losada et
1602 al., 2009a, 2008), which, if *I. damrowi* is on the Ibliformes stem lineage, would still situate the fossil
1603 within the crown group of Cirripedia.

1604

1605 *45.3. Age justification*

1606

1607 As for 31.3.

1608

1609 *45.4. Discussion*

1610

1611 A possible Early Ordovician stalked barnacle (Pedunculata: Lepadomorpha?) was illustrated in
1612 Fig. 2c and S3h of Van Roy et al. (2010). It has not been formally described and its affinities are

1613 unclear.

1614 *P. jaworskii* is in some ways a more appropriate fossil calibration than *I. damrowi*. It is
1615 approximately coeval to *I. damrowi*, and was coded in a morphological phylogenetic analysis (Glenn
1616 et al., 1995), where it was placed within Thoracica (sister to all other Thoracica except *Ibla*). *P.*
1617 *jaworskii* has been used as a calibration fossil for Thoracica and Cirripedia (Pérez-Losada et al.,
1618 2009b, 2008; Rees et al., 2014). However, no specimen information was available in the original
1619 publication, nor was any significant stratigraphic data beyond Carboniferous of the Kusnetz Basin,
1620 Russia (Chernyshev, 1930). As the papers using *P. jaworskii* for calibration estimate its age at 306.5-
1621 311.7 Ma (e.g. Rees et al., 2014), substitution of the slightly younger *I. damrowi* will not significantly
1622 violate the minimum age.

1623

1624 **46. Crown Thoracica**

1625

1626 This clade comprises Ibliformes, 'Pedunculata' (goose barnacles) and Sessilia (acorn
1627 barnacles), their last common ancestor and all of its descendants (**Fig. 12**). Pedunculata is no longer
1628 supported as monophyletic (Buckeridge and Newman, 2006; Pérez-Losada et al., 2009a; Rees et al.,
1629 2014). Ibliformes is identified as the sister group of all other Thoracica (Pérez-Losada et al., 2009a).
1630 Monophyly has been established by phylogenetic analysis of nuclear housekeeping genes (Pérez-
1631 Losada et al., 2009a), although a morphological phylogenetic analysis in the same paper resolves all
1632 studied members of Rhizocephala and Thoracica together in a polytomy. This is because only larval
1633 characters can be scored for Rhizocephala, with missing data for all adult characters due to their
1634 parasitic lifestyle.

1635

1636 *46.1. Fossil specimens*

1637

1638 As for 45.1.

1639

1640 46.2. *Phylogenetic justification*

1641

1642 As for 45.2.

1643

1644 46.3. *Age justification*

1645

1646 As for 31.3.

1647

1648 46.4. *Discussion*

1649

1650 As for 45.4.

1651

1652 **47. Crown Sessilia**

1653

1654 This clade comprises Verrucomorpha and Balanomorpha, their last common ancestor and all
1655 of its descendants (**Fig. 12**). Monophyly is supported by phylogenetic analysis of nuclear protein-
1656 coding and ribosomal genes (Pérez-Losada et al., 2008; Rees et al., 2014).

1657

1658 47.1. *Fossil specimens*

1659

1660 *Brachylepas fallax* Withers, 1935. For calibration, we refer to the stratigraphically oldest
1661 specimen (SM 704275), which is undescribed (A. Gale, pers. comm.).

1662

1663 47.2. *Phylogenetic justification*

1664

1665 This species was originally described from disarticulated material by Darwin (1851) as
1666 *Pollicipes fallax*. Withers (1935, 1914) recognized it was a sessile, rather than pedunculate barnacle,
1667 and that it had similarities to the basal sessilian genus *Pycnolepas* in overall form and plate
1668 development. Synapomorphies shared by *B. fallax* and all crown Sessilia include: the absence of a
1669 peduncle, presence of an operculum, and absence of all lateral plates (Gale and Sørensen, 2015). *B.*
1670 *fallax* shares with crown Balanomorpha a low, hemiconical carina and rostrum (Gale and Sørensen,
1671 2015). On the basis of these characters, a recent cladogram depicts *B. fallax* as one of the most
1672 distant stem lineages of Balanomorpha, which is therefore a position within the crown group of
1673 Sessilia (Gale and Sørensen, 2015).

1674

1675 47.3. Age justification

1676

1677 The oldest known locality from which *B. fallax* has been recovered is Pit No. 125 (Brydone,
1678 1912), close to junction of Barnet Side Lande and King's Lane, Froxfield, Hampshire, England (A.
1679 Gale, pers. comm.). This locality bears fossils of *Holaster (Sternotaxis) planus*, and is thus part of the
1680 *S. planus* echinoid zone, which is the uppermost zone of the Turonian in English Chalk (Gale, 1996;
1681 Mortimore, 2011). The GSSP defining the global upper boundary of the Turonian remains debated
1682 (due to difficulty in identifying its index ammonite fossil, *Forresteria (Harleites) petrocoriensis* (Ogg et
1683 al., 2012). Currently, the upper boundary of the Turonian is dated to 89.8 Ma \pm 0.3 Myr, providing a
1684 minimum age of 89.5 Ma.

1685 Soft maximum as for 26.3.

1686

1687 47.4. Discussion

1688

1689 The Albian-Cenomanian *Verruca withersi* Schram and Newman, 1980 has been shown not to
1690 be a cirripede (Jagt and Buckeridge, 2005) and cannot be used as a minimum. *Proverruca* (coded at

the genus level) was included in a morphological phylogenetic analysis, where it was placed in a polytomy with the fossil *Eoverruca* and the crown family Verrucidae (Glenner et al., 1995), and subsequently used as a calibration fossil for divergence time analysis (Pérez-Losada et al., 2014, 2008). However, the placement of *Proverruca* was based on similarities to the extant genus *Neoverruca*, which was shown in molecular analyses to fall outside Sessilia entirely, instead within the Scalpelliformes (Pérez-Losada et al., 2008; Rees et al., 2014). More recent morphological phylogenetic analyses confirm the convergence between *Neoverruca* + *Proverruca* and crown Verrucomorpha (Gale, 2015; Gale and Sørensen, 2015).

The Albian *Pycnolepas rigida* Sowerby, 1836 was included in a morphological phylogenetic analysis, where it was placed on the stem lineage of Verrucomorpha (Gale, 2015). However, that analysis did not include members of Balanomorpha, so the topology did not explicitly exclude a position on the stem lineage of Sessilia. In fact, this species was referred to stem Sessilia (Gale, 2015, p. 770). Unlike crown group Sessilia, it retains the pedunculate character of a lateral plate, the tall upper latus (Gale, 2015).

Verruca tasmanica tasmanica (Buckeridge, 1983), a previously used calibration fossil at the base of Verrucomorpha (Herrera et al., 2015; Linse et al., 2013; Pérez-Losada et al., 2014, 2008; Rees et al., 2014), is known from the Santonian Gingin Chalk Formation of Dandaragan, Western Australia (as well as type material from younger Oligocene strata of Oamaru, New Zealand; Buckeridge, 1979). As it is both younger than *B. fallax* and has not been studied in a phylogenetic context, it is not used herein.

1711

1712 **48. Crown Malacostraca**

1713

This clade comprises Leptostraca and Eumalacostraca, their last common ancestor and all of its descendants (**Fig. 13**). Its monophyly is one of the least contested matters in arthropod phylogeny; it has been demonstrated by phylogenetic analysis of morphology (Legg et al., 2013; Wills et al.,

1717 1998), nuclear ribosomal and protein-coding genes (Giribet et al., 2001; Regier et al., 2010, 2005),
1718 transcriptomes (von Reumont et al., 2012), and combined analysis of molecular and morphological
1719 data (Lee et al., 2013; Oakley et al., 2013).

1720

1721 *48.1. Fossil specimens*

1722

1723 *Cinerocaris magnifica* Briggs et al., 2004. OUM C.29565 (holotype; **Fig. 14g**), and OUM
1724 C.29566 (serially ground and reconstructed specimen; **Fig. 14f**). Morphological data for Herefordshire
1725 fossils are published as 3D models of thin section photographs.

1726

1727 *48.2. Phylogenetic justification*

1728

1729 *C. magnifica* was found to be a member of the stem group of Leptostraca (therefore crown
1730 group Malacostraca) in analyses of morphology (Legg et al., 2013) and morphology combined with
1731 molecules (Oakley et al., 2013).

1732

1733 *48.3. Age justification*

1734

1735 As for 44.3.

1736

1737 *48.4. Discussion*

1738

1739 The position of other fossil phyllocarids with respect to extant malacostracans (and the
1740 monophyly of phyllocarids themselves) have not been significantly investigated. The position of the
1741 Devonian phyllocarid *Nahecaris stuarti* in a phylogenetic analysis (Oakley et al., 2013) was
1742 equivocally stem Leptostraca or stem Malacostraca, casting doubt on the position of at least rhinocarid

1743 phyllocarids within crown Malacostraca. As *N. stuarti* has the same relationship to crown
1744 Malacostraca as *A. inflata* (at least in the analysis of Collette and Hagadorn, 2010b), neither fossil can
1745 be confidently placed within crown-group Malacostraca. Recent reinvestigation of *Ceratiocaris* cf.
1746 *macroura* (related to *A. inflata* and *N. stuarti* in the analysis of Collette and Hagadorn, 2010b)
1747 suggests this Silurian ‘phyllocarid’ may be a stem eumalacostracan due to possession of an antennal
1748 scale, casting further doubt on the monophyly of fossil phyllocarids (Jones et al., 2015). The *C.*
1749 *macroura* study, however, assumes malacostracan identity of phyllocarids (partly defined by biramous
1750 antennules), which, as discussed above (section 42.2), may not be robust to phylogenetic analysis. If,
1751 however, *Ceratiocaris* is within crown Malacostraca (either alone or with other archaeostracans), the
1752 oldest Malacostraca would be amended to *Ceratiocaris winneshiekensis* Briggs et al., 2015 from the
1753 Darriwilian Winneshiek Lagerstätte of Iowa (~14 Myr older than *C. magnifica*).

1754 Thylacocephalans are an enigmatic fossil arthropod clade ranging from the Silurian to the
1755 Cretaceous (C. Haug et al., 2014; Schram, 2014). Some Cambrian fossils have been proposed as
1756 thylacocephalans, but their membership is generally discounted (Schram, 2014; Vannier et al., 2006).
1757 Thylacocephalans have been compared to several extant arthropod clades, including the
1758 malacostracan stomatopods and decapods (Schram, 2014; Schram et al., 1999; Secrétan and Riou,
1759 1983; Vannier et al., 2016), which would extend the minimum age of Malacostraca slightly older within
1760 the Silurian (~433 Ma). The Jurassic thylacocephalan *Dollocaris ingens* Van Straelen, 1923 was coded
1761 in a morphological matrix, and found to be a stem eumalacostracan (therefore crown malacostracan)
1762 by phylogenetic analysis (Legg et al., 2013). However, their malacostracan affinities have been
1763 questioned, especially by C. Haug et al. (2014) studying a Silurian species, noting divergent trunk
1764 tagmosis and similarities to remipedes. Continued uncertainty over thylacocephalan affinities make
1765 them poor calibration fossils.

1766

1767 **49. Crown Eumalacostraca**

1768

1769 This clade comprises Verunipeltata (mantis shrimp, partial total group called Stomatopoda),
1770 Peracarida, 'Syncarida' (itself comprising Anaspidacea and Bathynellacea) and Eucarida, their last
1771 common ancestor and all of its descendants (**Fig. 13**). Monophyly is demonstrated by phylogenetic
1772 analysis of morphology (Legg et al., 2013; Richter and Scholtz, 2001), nuclear ribosomal and protein-
1773 coding genes (Regier et al., 2010), transcriptomes (von Reumont et al., 2012), and combined analysis
1774 of molecular and morphological data (Lee et al., 2013; Oakley et al., 2013; Wills et al., 2009). Although
1775 stomatopods and/or syncarids were not sampled in some of the above analyses, the best taxon
1776 sampling still resulted in eumalacostracan monophyly (Legg et al., 2013; Wills et al., 2009).

1777

1778 *49.1. Fossil specimens*

1779

1780 *Palaeopalaemon newberryi* Whitfield, 1880. The holotype at the AMNH, figured by Schram et
1781 al. (1978: Plate 3 #1-3), has been lost (B. Hussaini, pers. comm.), thus we refer to specimen KSU
1782 3484 (**Fig. 14h,i**).

1783

1784 *49.2. Phylogenetic justification*

1785

1786 Schram and Dixon (2004) coded *P. newberryi* into the morphological matrix of Dixon et al.
1787 (2003), finding it sister to a clade including Anomura, Brachyura, and Achelata to the exclusion of
1788 Astacidea, Axiidea, Gebiidea and Glypheidea. This position is within the crown group of Reptantia,
1789 hence within the crown groups of Decapoda and Eumalacostraca.

1790

1791 *49.3. Age justification*

1792

1793 The specimen of *P. newberryi* was found in gray shale near "Paine's Creek," LeRoy, Lake
1794 County, Chagrin (Erie) Shale, northeastern Ohio, USA (Feldmann et al., 1978; Schram et al., 1978).

1795 The Chagrin Shale is dated to the late Fammenian based on presence of the index alga *Foerstia*
1796 (Murphy, 1973), which in Ohio lies 40-70 m below surface outcrops (Feldmann et al., 1978). The upper
1797 boundary of the Fammenian is 358.9 Ma \pm 0.4 Myr, giving a minimum of 358.5 Ma.

1798 Soft maximum as for 26.3.

1799

1800 **50. Crown Anaspidacea**

1801

1802 This clade comprises the families Anaspididae, Koonungidae, Psammaspididae and
1803 Stygocarididae, their last common ancestor and all of its descendants (**Fig. 13**). Phylogenetic studies
1804 including Anaspidacea are extremely rare, but morphology (Schram, 1984) and mitochondrial 16S
1805 sequences (Camacho et al., 2002) indicated monophyly of the clade.

1806

1807 *50.1. Fossil specimens*

1808

1809 *Anaspidites antiquus* Chilton, 1929. AMS F64765, holotype, complete specimen (**Fig. 14k**).

1810

1811 *50.2. Phylogenetic justification*

1812

1813 Although not included in a formal phylogenetic analysis, Schram (1984) justified the
1814 membership of *A. antiquus* as essentially indistinguishable from living Anaspididae. Fusion of the
1815 first thoracomere into the cephalon, uniramous pleopods, and absence of an antennal scale are noted
1816 as diagnostic characters (Schram, 1984). As the fossil lacks preservation of diagnostic mouthparts,
1817 exact family affinities within total-group Anaspidacea are uncertain.

1818

1819 *50.3. Age justification*

1820

1821 *A. antiquus* was found in the Hawkesbury Sandstone at the former Brookvale Brick Quarry,
1822 New South Wales, Australia (Schram, 1984). The Hawkesbury Sandstone overlies the Narrabeen
1823 Group and underlies the Wianamatta Group (Herbert, 1997). Sequence stratigraphy places the
1824 Hawkesbury in Sequence F, including the appearance of *Aratrisporites parvispinosus* spores (Helby,
1825 1973; Herbert, 1997). The *A. parvispinosus* spore zone indicates an age during the Anisian (middle
1826 Triassic) (Herbert, 1997). The upper boundary of the Anisian is estimated at 241.5 ± 1 Ma (Ogg,
1827 2012), providing a minimum age at 240.5 Ma.

1828 Soft maximum as for 26.3.

1829

1830 50.4. Discussion

1831

1832 ‘Syncarida’, the traditional taxon containing Anaspidacea, is purposely excluded from this
1833 review, as its monophyly has been substantially challenged. In phylogenetic analyses, syncarid
1834 monophyly was only supported by the morphological dataset of Richter and Scholtz (2001),
1835 emphasizing the absence of a dorsal carapace in Anaspidacea and Bathynellacea (‘Syncarida’). Each
1836 of a partial mitochondrial gene (Camacho et al., 2002), two mitochondrial genes and morphology
1837 (Jenner et al., 2009) and morphology including putative syncarid fossils (Schram and Hof, 1998; Wills
1838 et al., 2009) failed to recover a sister group relationship between Anaspidacea and Bathynellacea.
1839 Wills et al. (2009) suggested that a paraphyletic grade of ‘Syncarida’, including fossils (*Acanthotelson*,
1840 *Palaeocaris*) represented the first divergences of Eumalacostraca.

1841

1842 51. Crown Verunipeltata

1843

1844 This is the clade comprising Bathysquilloidea, Erythrosquilloidea, Eurysquilloidea,
1845 Parasquilloidea, Gonodactyloidea, Lysiosquilloidea and Squilloidea, their last common ancestor and
1846 all of its descendants (**Fig. 13**). Although the extant members are often referred to Stomatopoda, that

1847 clade includes a number of extinct members forming a paraphyletic grade (Fig. 1 of Haug et al., 2010).
1848 As membership of fossil species within a crown group is only possible if they branch along the stem
1849 lineage of a living clade that is part of the crown itself, we agree with the assertion that crown
1850 ‘Stomatopoda’ is equivalent to the clade Verunipeltata *sensu* Haug et al. (2010). The stomatopod
1851 clade as a whole may be defined by several apomorphies, such as five pairs of maxillipeds, and
1852 modification of the first two pleopods as gonopods (Richter and Scholtz, 2001).

1853 All living members form a clade in analyses of morphology including both fossil and extant taxa
1854 (Ahyong, 1997; Ahyong and Harling, 2000). Analysis of combined molecular and morphological data,
1855 with limited sampling of verunipeltatan clades, strongly supports monophyly of those members (Jenner
1856 et al., 2009). As well, representatives of Gonodactyloidea, Lysiosquilloidea and Squilloidea were
1857 sequenced for six housekeeping genes; these were monophyletic in a diverse sample of
1858 Pancrustacea (Bybee et al., 2011).

1859

1860 51.1. Fossil specimens

1861

1862 *Ursquilla yehoachi* Remy and Avnimelech, 1955. For calibration, we refer to two specimens.
1863 Based on new phylogenetically relevant details, we use a new specimen (SMNS 67703) from Fig. 1
1864 and 2 of Haug et al. (2013). The SMNS specimen, however, lacks locality and stratigraphic information
1865 beyond “Late Cretaceous Negev Desert, Israel” as it was privately donated (Haug et al., 2013). We
1866 also therefore refer to the holotype (MNHN R. 62691).

1867

1868 51.2. Phylogenetic justification

1869

1870 The uropod morphology of *U. yehoachi* indicates its membership in the crown group of
1871 Verunipeltata. The uropodal exopod of *U. yehoachi* specimen SMNS 67703 is bipartite, a
1872 synapomorphy of Verunipeltata (Haug et al., 2013). Furthermore, *U. yehoachi* shares several

1873 characters with Squillidae (Squilloidea), such as prelateral lobes, submedian teeth with fixed apices
1874 and a subquadrate telson (Haug et al., 2013). As *U. yehoachi* has not been included in a phylogenetic
1875 analysis, it is uncertain whether it falls within crown Squilloidea (Haug et al., 2013) or on its stem;
1876 either position would remain within the crown group of Verunipeltata.

1877

1878 51.3. Age justification

1879

1880 The holotype of *U. yehoachi* was collected from a chert bank in the Chert Member of the
1881 Mishash Formation, near the city of Arad, Israel (Hof, 1998). The chert banks are within the
1882 *Hoplitoplacenticeras marroti* ammonite biozone (Reiss et al., 1986). *H. marroti* co-occurs with
1883 *Baculites* sp. (smooth) (Lehmann and Murphy, 2001), which is dated to the uppermost early
1884 Campanian. Based on a spline-fit of interbedded bentonites, the base of the Tethyan *Baculites* sp.
1885 (smooth) Zone is dated to 79.64 Ma, with a duration of 0.63 Myr (Ogg et al., 2012), thus the minimum
1886 age of *U. yehoachi* is 79.01 Ma.

1887 Soft maximum as for 26.3.

1888

1889 52. Crown Peracarida

1890

1891 This clade comprises Amphipoda (scuds/beach fleas), Isopoda (wood lice/pill bugs), Cumacea,
1892 Lophogastrida, Bochusacea, Mictacea, Mysida (opossum shrimp), Stygiomysida, Spelaeogriphacea,
1893 Tanaidacea and Thermosbaenacea, their last common ancestor and all of its descendants (**Fig. 13**).
1894 Monophyly has been demonstrated by phylogenetic analysis of morphology (Jones et al., 2016;
1895 Poore, 2005; Richter and Scholtz, 2001; Wills et al., 2009; Wirkner and Richter, 2010), and combined
1896 morphology and molecular data (Jenner et al., 2009). Molecular phylogenies based on ribosomal
1897 genes reject the inclusion of Mysida within Peracarida (Jenner et al., 2009; Meland and Willassen,
1898 2007; Spears et al., 2005), while Lophogastrida and Stygiomysida are removed from Mysidacea and

1899 found comfortably within Peracarida (Meland and Willassen, 2007; Meland et al., 2015). Note
1900 ribosomal genes alone are insufficient markers for deep divergences (Giribet and Ribera, 2000), so we
1901 cautiously include Mysida within Peracarida pending multilocus investigations.

1902

1903 *52.1. Fossil specimens*

1904

1905 *Hesslerella shermani* Schram, 1970. FMNH PE 16527, holotype, lateral view (illustrated in
1906 Wilson, 2012 and **Fig. 14j**).

1907

1908 *52.2. Phylogenetic justification*

1909

1910 *H. shermani* was included in a morphological cladistic analysis by Wilson (2012). It occurred at
1911 the base of Phreatoicidea (Wilson, 2012), a position within the crown group of Isopoda and thus,
1912 crown Peracarida. Note that the assignment of our calibration fossil to crown Isopoda means that
1913 exclusion of Mysida from Peracarida (Jenner et al., 2009; Meland and Willassen, 2007; Spears et al.,
1914 2005) will not change the date assessed for Peracarida.

1915

1916 *52.3. Age justification*

1917

1918 As for 31.3.

1919

1920 *52.4. Discussion*

1921

1922 Pygocephalomorpha is a eumalacostracan fossil clade with a number of symplesiomorphic
1923 characters. Pygocephalomorpha were proposed as members of Peracarida; however, a recent
1924 phylogeny depicted them in a polytomy in any of three positions: sister to Mysidacea (Mysida +

1925 Lophogastrida), sister to all non-Mysidacea peracarids, or on the peracarid stem lineage (Jones et al.,
1926 2016). Note also the molecular analyses discussed above that exclude Mysida from Peracarida (e.g.
1927 Jenner et al., 2009), which would mean two of three equally parsimonious positions for
1928 Pygocephalomorpha may be outside the peracarid crown group. If Pygocephalomorpha were shown
1929 to be more likely within the crown group of Peracarida (e.g. as sister to non-mysid peracarids), one
1930 species in this clade, *Tealliocaris walloniensis* Gueriau et al., 2014, would become the oldest peracarid
1931 (from the Fammenian stage of the Devonian ~50 Myr older; Gueriau et al., 2014).

1932 Within Peracarida, several orders have putative Mesozoic calibration fossils that do not fully
1933 meet our requirements. Putative Lophogastrida fossils were described from the middle Triassic Falang
1934 Formation of China (Taylor et al., 2001) and Grès à Voltzia, France (Bill, 1914). These were attributed
1935 to the extant family Eucopiidae (Taylor et al., 2001), although they resolved outside crown
1936 Lophogastrida in an older phylogeny including only the French species (Taylor et al., 1998). Putative
1937 Mysida were described from the Late Jurassic Solnhofen Plattenkalk of Germany, but are poorly
1938 preserved (Schram, 1986). Fossils separately attributed to each of Lophogastrida and Mysida have
1939 also been described from the Middle Jurassic La Voulte-sur-Rhône of France (Secrétan and Riou,
1940 1986). Other fossils noted as “mysidaceans” have been mentioned, but not yet described, from the
1941 middle Triassic Luoping Biota of China (Feldmann et al., 2015; Hu et al., 2010). None of these fossils
1942 have been evaluated in the context of molecular discoveries, i.e. they assume a sister relationship
1943 between Mysida and Lophogastrida. Therefore, none can be used as calibrations until their
1944 relationships with respect to potential polyphyletic Mysidacea have been assessed.

1945 Fossils allied to Spelaeogriphacea have been described from the Cretaceous Yixian Formation
1946 of China (Shen et al., 1998; section 60.3 for revised stratigraphy) and Las Hoyas of Spain (Jaume et
1947 al., 2013). However, poor preservation of diagnostic characters indicates these are stem
1948 spelaeogriphaceans (Jaume et al., 2013).

1949 Although several Mesozoic fossils have been assigned to Amphipoda, none have sufficient or
1950 accurate morphological placement (Starr et al., 2016; Vonk and Schram, 2007). Thus no known

1951 Mesozoic fossil qualifies as a crown group amphipod.

1952

1953 **53. Crown Isopoda**

1954

1955 This clade comprises Asellota, Phoratopodidea, Cymothoida, Microcereberidea, Limnoridea,
1956 Sphaeromatidea, Valvifera, Oniscidea (wood lice/pill bugs), Phreatoicidea, Calabozoidea and
1957 Tainisopidea, their last common ancestor and all of its descendants (**Fig. 13**). The list of isopod
1958 suborders is derived from Boyko et al. (2008). Isopod monophyly was recovered in phylogenetic
1959 analysis of four housekeeping genes (Lins et al., 2012) and of combined ribosomal genes and
1960 morphology (Wilson, 2009).

1961

1962 *53.1. Fossil specimens*

1963

1964 As for 52.1.

1965

1966 *53.2. Phylogenetic justification*

1967

1968 As for 52.2.

1969

1970 *53.3. Age justification*

1971

1972 As for 31.3.

1973

1974 **54. Crown Tanaidacea**

1975

1976 This clade comprises Apseudomorpha, Neotanaidomorpha and Tanaidomorpha, their last

1977 common ancestor and all of its descendants (**Fig. 13**). Phylogenetic analysis of three molecular loci
1978 demonstrated monophyly of Apseudomorpha and Tanaidomorpha; Neotanaidomorpha could not be
1979 included (Drumm, 2010). More expansive outgroup sampling (without Neotanaidomorpha) did not
1980 recover monophyletic Tanaidacea with ribosomal and morphological data (Wilson, 2009). However, a
1981 nuclear ribosomal analysis including Neotanaidomorpha supported monophyly (Kakui et al., 2011).

1982

1983 *54.1. Fossil specimens*

1984

1985 *Alavatanais carabe* Vonk and Schram, 2007. MCNA 9537, holotype in amber, male (**Fig. 14l**).
1986 For additional morphological details, we also refer to MCNA 9846a and MCNA 13888 (**Fig. 14m**), both
1987 males.

1988

1989 *54.2. Phylogenetic justification*

1990

1991 Spanish amber tanaids were originally misidentified as amphipods (Alonso et al., 2000). The
1992 fossils were placed in a new family, Alavatanaidae, part of the superfamily Paratanaoidea within
1993 Tanaidomorpha (Sánchez-García et al., 2015; Vonk and Schram, 2007). Characters supporting affinity
1994 within Tanaidomorpha include the presence of an articulated ischium, articulation of the last two
1995 pleopods (may be reduced in males), and seven or fewer antennal articles (Sánchez-García et al.,
1996 2015).

1997

1998 *54.3. Age justification*

1999

2000 Amber inclusions bearing arthropod fossils were discovered from the Peñacerrada I outcrop,
2001 Basque-Cantabrian Basin, Álava, Spain (Alonso et al., 2000; Peñalver and Delclòs, 2010). The
2002 Peñacerrada I outcrop itself is divided into three intervals, with the lowest bearing the amber (Barrón

et al., 2015). Earlier palynological study assigned Peñacerrada I to the Escucha Formation, in the late Aptian (Barrón et al., 2001). Recent restudy, however, amended this outcrop to the Utrillas Group (Barrón et al., 2015). The presence of marine palynomorphs characterized by *Chichaouadinium vestitum* and *Palaeohystrichophora infusorioides*, and the terrestrial *Distaltriangulisporites mutabilis* and *Senectotetradites varireticulatus* together constrain a late Albian age for the Peñacerrada I (Barrón et al., 2015). The upper boundary of the Albian stage is 100.5 Ma \pm 0.4 Myr (Ogg et al., 2012), providing a minimum estimate for Álava amber fossils at 100.1 Ma.

Soft maximum as for 26.3.

55. Crown Eucarida

This clade comprises Euphausiacea (krill) and Decapoda (crabs, shrimp, lobsters), their last common ancestor and all of its descendants (**Fig. 13**). Monophyly of Euphausiacea and Decapoda is supported by phylogenetic analysis of transcriptomes (von Reumont et al., 2012), ribosomal genes (Spears et al., 2005), and combined molecular and morphological data (Jenner et al., 2009; Wills et al., 2009). Amphionidacea was represented as its own order within Eucarida based on morphology (Jenner et al., 2009; Wills et al., 2009), but recently the first molecular sequence data have become available, indicating that Amphionidacea are larval stages of Caridea (i.e. within Decapoda) (De Grave et al., 2015).

55.1. Fossil specimens

As for 49.1.

55.2. Phylogenetic justification

2029 As for 49.2.

2030

2031 *55.3. Age justification*

2032

2033 As for 49.3.

2034

2035 **56. Crown Decapoda**

2036

2037 This clade comprises Dendrobranchiata (shrimp/prawns) and Pleocyemata (caridean shrimp,
2038 mud shrimp, true crabs, hermit and king crabs, lobsters, spiny lobsters, etc.), their last common
2039 ancestor and all of its descendants (**Fig. 13**). Decapod monophyly is established by phylogenetic
2040 analysis of protein-coding genes (Bracken et al., 2009; Bybee et al., 2011; Timm and Bracken-
2041 Grissom, 2015), morphology (Legg et al., 2013; Richter and Scholtz, 2001), and combined
2042 morphology and molecular data (Jenner et al., 2009). Analyses of whole mitochondrial genomes place
2043 Euphausiacea (krill) within Decapoda (Shen et al., 2015), a result congruent with acquisition of a
2044 nauplius larval stage (though this is accepted as convergent: (Jirikowski et al., 2013; Scholtz, 2000).
2045 We apply caution in interpreting deep splits inferred from mitochondrial DNA (Simon and Hadrys,
2046 2013); hence, we accept decapod monophyly to the exclusion of krill.

2047

2048 *56.1. Fossil specimens*

2049

2050 As for 49.1.

2051

2052 *56.2. Phylogenetic justification*

2053

2054 As for 49.2.

2055

2056 *56.3. Age justification*

2057

2058 As for 49.3.

2059

2060 **57. Crown Allotriocarida**

2061

2062 This clade comprises Branchiopoda, Cephalocarida, Remipedia, and Hexapoda, their last
2063 common ancestor and all of its descendants (**Fig. 15**). Monophyly of this clade was proposed by a
2064 combined phylogenetic analysis of transcriptomes, nuclear protein-coding genes, and morphology
2065 (Oakley et al., 2013). As of this writing, a transcriptome remains to be sequenced for Cephalocarida.
2066 This clade is not recognized in GenBank taxonomy.

2067

2068 *57.1. Fossil specimens*

2069

2070 *Rehbachella kinnekullensis* Müller, 1983. UB 644, holotype, consisting of a complete larva
2071 (**Fig. 16a**). This species has been extensively documented by Walossek (1993).

2072

2073 *57.2. Phylogenetic justification*

2074

2075 Recent phylogenetic analyses including *R. kinnekullensis* have strongly indicated a position on
2076 the branchiopod stem lineage (morphology: Legg et al., 2013; combined morphology and molecular:
2077 Oakley et al., 2013) or the cephalocarid stem lineage (morphology: Wolfe and Hegna, 2014). Either
2078 relationship (or a strict consensus position on the stem of Branchiopoda + Cephalocarida) would still
2079 be within the crown group of Allotriocarida.

2080

2081 57.3. *Age justification*

2082

2083 As for 35.3.

2084

2085 **58. Crown Branchiopoda**

2086

2087 This clade comprises Anostraca (fairy/brine shrimp), Notostraca (tadpole shrimp) and
2088 Diplostraca, their last common ancestor and all of its descendants (**Fig. 15**). Monophyly of this clade is
2089 established by phylogenetic analysis of protein-coding genes (Regier et al., 2010; Spears and Abele,
2090 2000), transcriptomes (von Reumont et al., 2012), morphology (Legg et al., 2013), and combined
2091 molecular and morphological data (Oakley et al., 2013).

2092

2093 58.1. *Fossil specimens*

2094

2095 *Lepidocaris rhyniensis* Scourfield, 1926. BMNH IN. 24493, holotype (**Fig. 16b**).

2096

2097 58.2. *Phylogenetic justification*

2098

2099 *L. rhyniensis* has been included in several phylogenetic analyses, coded from a composite of
2100 holotype and paratype material (Scourfield, 1926). With morphology only, *L. rhyniensis* is sister to
2101 extant Anostraca (Hegna, 2012; Legg et al., 2013); with morphology and molecular data, it is within
2102 Anostraca (Oakley et al., 2013). Therefore, it is unequivocally a crown group member of
2103 Branchiopoda.

2104

2105 58.3. *Age justification*

2106

2107 Minimum as for 10.3. Soft maximum as for 26.3.

2108

2109 *58.4. Discussion*

2110

2111 *R. kinnekullensis* has been frequently used to polarize the evolution of Branchiopoda. Its fossils
2112 are known only from larval stages, which may confound discussions of its morphology (Wolfe and
2113 Hegna, 2014). Recent phylogenetic analyses have indicated a position on the branchiopod stem
2114 lineage (Legg et al., 2013; Oakley et al., 2013) or the cephalocarid stem lineage (Wolfe and Hegna,
2115 2014), excluded from the branchiopod crown. Nevertheless, divergence time analyses suggest
2116 Cambrian origins for crown Branchiopoda (Oakley et al., 2013), such that molecular clock estimates
2117 do not conflict with branchiopod affinities for Cambrian filter plate fossils (Harvey and Butterfield, 2008)
2118 or *R. kinnekullensis*.

2119

2120 **59. Crown Anostraca**

2121

2122 This clade comprises Artemiidae, Branchinectidae, Branchipodidae, Chirocephalidae,
2123 Parartemiidae, Streptocephalidae, Tanymastigidae and Thamnocephalidae, their last common
2124 ancestor and all of its descendants (**Fig. 15**). Monophyly of five sampled families is established by
2125 phylogenetic analysis of six housekeeping genes and morphology (Richter et al., 2007). Full sampling
2126 of families produced monophyletic Anostraca in an analysis of one ribosomal gene (Weekers et al.,
2127 2002).

2128

2129 *59.1. Fossil specimens*

2130

2131 *Palaeochirocephalus rasnitsyni* Trussova, 1975. TsGM 7a/10303 and 9/10303, preserving male
2132 antennae, and TsGM 2/10303, preserving a female body. The holotype does not preserve any

2133 diagnostic characters for the Anostraca crown group.

2134

2135 59.2. *Phylogenetic justification*

2136

2137 *P. rasnitsyni* (formerly *Chirocephalus rasnitsyni* Trussova, 1971) has not been included in a
2138 phylogenetic analysis. Taxonomic placement of its family, Palaeochirocephalidae, implicitly relates
2139 them to the extant family Chirocephalidae, though this family is considered *incertae sedis* by Rogers
2140 (2013). Morphological characters (shared with Chirocephalidae) supporting this relationship include 11
2141 thoracic appendages bearing two pre-epipodites, the nine-segmented abdomen, and the basally
2142 separated two-segmented antennae in males (Trussova, 1971). A possible position on the stem
2143 lineage of Chirocephalidae would therefore place *P. rasnitsyni* within the crown group of Anostraca.

2144

2145 59.3. *Age justification*

2146

2147 The type locality of *P. rasnitsyni*, briefly described by Trussova (1971), is the left bank of Daya
2148 River, upstream from Shiviya Falls, in eastern Transbaikalia, Russia. This locality, within the Unda-Daya
2149 Basin, has been assigned to the Glushkovo Formation (Sinitshenkova, 2005). The age of the
2150 Glushkovo Formation is poorly constrained, suggested as Late Jurassic (Sinitsa and Starukhina,
2151 1986), Early Cretaceous (Sinitshenkova, 2005; Zherikhin et al., 1998), or perhaps at the
2152 Jurassic/Cretaceous boundary (Rasnitsyn and Quicke, 2002). However, *P. rasnitsyni* itself (along with
2153 palaeopteran insects such as *Proameletus caudatus* and *Equisetum undense*) correlates the
2154 Glushkovo Formation to the Baigul locality, also in Transbaikalia (Ignatov et al., 2011). The Baigul
2155 locality preserves fossil *Bryokhutuliinia jurassica*, one of only five known genera of Jurassic mosses
2156 (Ignatov et al., 2011). Thus Baigul can be correlated to the Ulugey Formation of Mongolia, which also
2157 preserves *Bryokhutuliinia* fossils (Ignatov, 1992). The Ulugey Formation, in turn, is correlated to the La
2158 Cabrúia (Sierra del Montsec, Pyrenees, Spain) locality based on the shared presence of the

2159 coleopteran genus *Gobicar* (Gratshev and Zherikhin, 2000; Legalov, 2010; Soriano et al., 2006). Fossil
2160 charophyte algae (*Atopochara trivolis triquetra*) indicate an age of late Hauterivian-early Barremian
2161 for the freshwater deposits of La Cabrúa (Gomez et al., 2002; Martín-Closas and López-Morón, 1995).
2162 Although it has been proposed that a minimum age of the Montsec limestone may be as young as the
2163 end Maastrichtian (O'Reilly et al., 2015), recent biostratigraphic work proposes the last appearance of
2164 *A. trivolis triquetra* is correlated to the *Deshayesites weissi* ammonite Zone at its youngest (Martín-
2165 Closas et al., 2009). Revision of Tethyan ammonite dates indicates the *D. weissi* Zone, now the *D.*
2166 *forbesi* Zone, had an upper boundary of 125.71 Ma (Ogg et al., 2012a). This age is early Aptian, and
2167 provides a minimum for the correlated Glushkovo Formation.

2168 Soft maximum as for 26.3.

2169

2170 59.4. Discussion

2171

2172 Oakley et al. (2013) placed the Early Devonian *L. rhyniensis* in the crown group of Anostraca,
2173 having sampled extant members of Artemiidae and Streptocephalidae. Earlier descriptions (Sanders,
2174 1963; Scourfield, 1940a, 1926; Walossek, 1993) support this position. However, the most extensively
2175 sampled morphological analyses of Hegna (2012) consistently place *L. rhyniensis* as sister to all
2176 extant Anostraca. The Late Devonian *Haltinnaias serrata* Gueriau et al., 2016, described from both
2177 sexes, likely also belongs to the total group of Anostraca.

2178 Other fossils from the Late Jurassic Daohugou Beds of China (Huang et al., 2006; Shen and
2179 Huang, 2008) and Early Cretaceous Koonwarra Formation of Australia are likely to belong to the
2180 crown group of Anostraca, as they have been included in a morphological phylogenetic analysis
2181 (Hegna, 2012), but these have not been described in detail.

2182

2183 60. Crown Notostraca

2184

2185 This clade comprises two extant genera, *Triops* and *Lepidurus*, their last common ancestor and
2186 all of its descendants (**Fig. 15**). Monophyly is established by phylogenetic analysis of housekeeping
2187 genes (Mathers et al., 2013), morphology (Lagebro et al., 2015), and combined morphological and
2188 molecular data (Richter et al., 2007).

2189

2190 *60.1. Fossil specimens*

2191

2192 *Chenops yixianensis* Hegna and Ren, 2010. CNU-CAL-HP-2009001 (part; **Fig. 16c**) and CNU-
2193 CAL-HP-2009002 (counterpart), holotype.

2194

2195 *60.2. Phylogenetic justification*

2196

2197 In the morphological phylogenetic analysis of Lagebro et al. (2015), *C. yixianensis* was in a
2198 polytomy with other crown Notostraca, including *Lepidurus batesoni*. The equal size of thoracic
2199 endopods and fourth and fifth endites may exclude *C. yixianensis* from crown Notostraca (Hegna and
2200 Ren, 2010). However, in previous morphological phylogenies (Hegna, 2012), *C. yixianensis* was sister
2201 taxon to the extant *L. batesoni*. This is because *L. batesoni* lacks elongated endites on the first
2202 thoracic appendage, suggesting a synapomorphy between *C. yixianensis* and the extant species, and
2203 perhaps membership in an entirely different genus (Hegna, 2012; Hegna and Ren, 2010). If indeed *C.*
2204 *yixianensis* is, based on phylogenies and endite morphology, a sister group of *L. batesoni*, it would
2205 remain within the crown Notostraca.

2206

2207 *60.3. Age justification*

2208

2209 This fossil was discovered in the Yixian Formation of northeastern China (Hegna and Ren,
2210 2010). The Yixian Formation lies between the overlying Jiufotang Formation and underlying Tuchengzi

2211 Formation; together they comprise the Jehol Group (e.g. Chang et al., 2009a; Zhou, 2006). Dating of
2212 the Jehol Group has been contentious, varying from Late Jurassic to Early Cretaceous based on
2213 biostratigraphic and radiometric techniques. Recent $^{40}\text{Ar}/^{39}\text{Ar}$ dates yielded ages of $129.7 \text{ Ma} \pm 0.5$
2214 Myr for basaltic lava from the bottom of the Yixian Formation and $122.1 \text{ Ma} \pm 0.3$ Myr for tuff layers at
2215 the bottom of the overlying Jiufotang Formation (Chang et al., 2009a). Other age estimates have fallen
2216 within this range (reviewed by Zhou, 2006). This debate underscores the point that reasonably precise
2217 radiometric dates may still be quite inaccurate. We conservatively use the younger of these estimates,
2218 so a minimum age for Yixian fossils is 121.8 Ma.

2219 Soft maximum as for 26.3.

2220

2221 60.4. Discussion

2222

2223 *Strudops goldenbergi* Lagebro et al., 2015 was recently described from the Late Devonian,
2224 which would be the oldest notostracan. In a morphological phylogenetic analysis, however, it could
2225 only be identified as a member of the total group (Lagebro et al., 2015), and thus cannot assign a
2226 minimum age to crown Notostraca.

2227 Morphological conservatism (i.e. Permian and Triassic fossils erroneously attributed to the
2228 extant species *Triops cancriformis*) has led to the misleading name 'living fossil' for Notostraca
2229 (Hegna, 2012; Mathers et al., 2013). Once touted as the 'oldest living species,' *T. cancriformis*
2230 *permiensis*, from the Permian of France, is more similar to the co-occurring *Lepidurus occitaniacus*
2231 than extant *Triops* (Lagebro et al., 2015). Decay experiments on living *T. cancriformis* confirm that
2232 carapace characters and elongated endites of the first thoracic limb are phylogenetically meaningful,
2233 thus rejecting a referral of any fossil to the extant species (Hegna, 2012).

2234

2235 61. Crown Diplostraca

2236

2237 This clade comprises Laevicaudata, Spinicaudata, Cyclestherida (these three collectively:
2238 'clam shrimp') and Cladocera (water fleas), their last common ancestor and all of its descendants (**Fig.**
2239 **15**). Monophyly is supported by phylogenetic analysis of transcriptomes (von Reumont et al., 2012)
2240 and 62 nuclear protein-coding genes (Regier et al., 2010), and combined molecules and morphology
2241 (Oakley et al., 2013) although Cyclestherida was not sampled in these analyses. Smaller molecular
2242 analyses (Richter et al., 2007 with indel costs) and morphological analyses (Hegna, 2012; Legg et al.,
2243 2013; Olesen, 2009, 1998; Richter et al., 2007) including data for Cyclestherida also support
2244 monophyly of Diplostraca.

2245

2246 *61.1. Fossil specimens*

2247

2248 *Leaia chinensis* Shen, 1983. NIGP 51786, holotype, preserving a left valve (**Fig. 16d**).

2249

2250 *61.2. Phylogenetic justification*

2251

2252 *L. chinensis* has not been treated in a phylogenetic context. It is placed within the fossil family
2253 Leaidae primarily based on carapace shape, including the nearly straight ventral edge (Shen, 1978;
2254 Tasch, 1987). However, congeneric fossils, *L. gondwanella* Tasch, 1987 and *L. canadensis* Shen and
2255 Schram, 2014, may have preserved soft parts (Shen and Schram, 2014). These include biramous
2256 antennae, mandibles, as well as putative shell glands and digestive tubes, and radiating carinae (Shen
2257 and Schram, 2014). The short and delicate antennal flagella and radiating carinae of *L. chinensis*, in
2258 particular, are similar to extant Spinicaudata and Cyclestherida; the presence of growth lines is only
2259 known from Spinicaudata (Shen and Schram, 2014). However, the head shape of *L. chinensis* is more
2260 similar to Laevicaudata. This suggests phylogenetic positions either on the stem of Onychocaudata
2261 (Spinicaudata, Cyclestherida, and Cladocera) or on the stem of Laevicaudata. A position as stem
2262 Diplostraca would mean growth lines are ancestral for all diplostracans, and have been lost twice (in

the ancestors of Laevicaudata and Cyclestherida + Cladocera), which is unparsimonious. Hence we support *L. chinensis* within crown Diplostraca.

61.3. Age justification

L. chinensis was found in sediments of the Guitou Group, near Chengma village, Hepu county, Guangxi Zhuang Autonomous Region, southern China (Shen, 1978). The upper subgroup of the Guitou Group, bearing conchostracan fossils, has purple-grey sandy shales within mudstone lamination, and is overlain by the Tungkangling Formation (Shen, 1978). The brachiopod *Stringocephalus*, the stromatoporoid corals *Endophyllum* and *Sunophyllum*, and the ostracods *Samarella crassa* and *Tuberokloedenia bituberculata* together indicate a Givetian age for the upper Tungkangling Formation (Liao and Ruan, 2003). The underlying Yingtang Formation (as well as the lower Tungkangling Formation) are correlated to the Eifelian Stage by the ostracods *Bairdocypris biesenbachi* and *Flatiella subtrapezoidalis* (Liao and Ruan, 2003), the brachiopod *Bornhardtina* and the conodonts *Polygnathus australis*, *P. costatus*, and *P. partitus* (Ma et al., 2009). As the conchostracan-bearing sediments underlie the Tungkangling Formation, they are no younger than Eifelian in age. The upper boundary of the Eifelian is 387.7 Ma \pm 0.8 Myr, providing a minimum age of 386.9 Ma.

Soft maximum as for 26.3.

62. Crown Spinicaudata

This clade comprises Leptestheriidae, Cyzicidae and Limnadiidae, their last common ancestor and all of its descendants (**Fig. 15**). Clade names are defined in Schwentner et al. (2009). Monophyly is established by phylogenetic analysis of morphology (Hegna, 2012; Olesen, 1998; Richter et al., 2007), three housekeeping genes (Schwentner et al., 2009), and six housekeeping genes plus

2289 morphology (Richter et al., 2007).

2290

2291 62.1. Fossil specimens

2292

2293 *Dundgobiestheria mandalgobiensis* Li et al., 2014. ED-A-14-1, holotype (**Fig. 16e**).

2294

2295 62.2. Phylogenetic justification

2296

2297 Phylogenetic analysis of spinicaudatan fossils is rare, owing to difficulty in character
2298 identification (Astrop and Hegna, 2015; see also 62.3). Members of Leptestheriidae appear to share
2299 emergence of dendritic reticulation and anastomizing ridge ornamentation with the fossil spinicaudatan
2300 family Loxomegaglyptidae (Astrop and Hegna, 2015; Shen, 1994). *D. mandalgobiensis* is perhaps the
2301 oldest definitive Loxomegaglyptidae, based on large-sized reticulate ornamentation and weakly
2302 defined growth lines, shared with other members of the family (Li et al., 2014). Due to the above
2303 ornamentation characters (Astrop and Hegna, 2015; T. Astrop, pers. comm.), it can be placed on the
2304 stem lineage of Leptestheriidae, and thus within crown Spinicaudata.

2305

2306 62.3. Age justification

2307

2308 *D. mandalgobiensis* is from the Eedemt Formation, Khootiin Khotgor coal mine region,
2309 Dundgobi Province, southeast Mongolia (Li et al., 2014). The spinicaudatan genus *Triglypta* (co-
2310 occurring with *D. mandalgobiensis*) provides a biostratigraphic constraint on the Eedemt Formation, as
2311 *Triglypta* species also occur in both the (older) *Euestheria ziliujingensis* fauna and (younger)
2312 *Sinokontikia* fauna in lacustrine sequences of northwestern China (Li et al., 2014; Li and Matsuoka,
2313 2012). First, the *E. ziliujingensis* fauna is distributed throughout east Asia, dated to a Bajocian-
2314 Bathonian (Jurassic) age by the occurrence of *Euestheria trotternishensis* (Chen et al., 2007). *E.*

2315 *trotternishensis* co-occurs in the *Skyestheria* spinicaudatan fauna of Skye, Scotland; the Bajocian-
2316 Bathonian date for this locality comes from ammonite and palynological index fossils (Chen and
2317 Hudson, 1991). Although the *Sinokontikia* fauna was once thought stratigraphically equal to the late *E.*
2318 *ziliujingensis* fauna (Chen et al., 2007; Li and Matsuoka, 2012), *Sinokontikia* has been determined to
2319 be younger based on occurrence in the Qiketai Formation of the Turpan Basin, northwest China. The
2320 Qiketai Formation is constrained only to the Callovian. As Chinese *Triglypta* (the index genus for the
2321 Eedemt Formation) is absent from any higher strata, a minimum age comes from the upper boundary
2322 of the *Sinokontikia* fauna (Li et al., 2014). The upper boundary of the Callovian is 163.5 Ma \pm 1.0 Myr,
2323 giving a minimum age for the Eedemt Formation of 162.5 Ma.

2324 Soft maximum as for 26.3.

2325

2326 62.4. Discussion

2327

2328 Preservation of the calcified spinicaudatan carapace is extremely common (some fossil species
2329 are used as biostratigraphic indices), but characters diagnostic for extant taxa (i.e. soft parts) are
2330 rarely preserved (Hegna, 2012; Orr and Briggs, 1999). Uniquely among ‘conchostracans’ (and indeed
2331 most arthropods), Spinicaudata do not moult their carapace, instead preserving growth lines. The
2332 number of growth lines necessarily increases through ontogeny, so it is a poor character to
2333 demonstrate phylogenetic relationships. Therefore relationships among fossil taxa have been
2334 determined based on ornamentation of the carapace (e.g. Gallego, 2010); however, these characters
2335 have not yet been integrated with morphological study of extant carapaces. Ongoing work seeks to
2336 demonstrate the utility of carapace ornamentation as valid phylogenetic characters (Astrop and
2337 Hegna, 2015). Furthermore, integration of past descriptive work is hindered by language barriers
2338 between different workers (Chinese, Russian, and English; summarized by Astrop and Hegna, 2015).

2339 For example, some poorly known fossils from the Middle Devonian of Antarctica, described as
2340 members of the genus *Cyzicus* (*Euestheria*), may be assigned to Spinicaudata (Tasch, 1987), possibly

on the stem lineage of ‘non-Australian Cyzicidae’ *sensu* Schwentner et al. (2009). Characters linking the Antarctic fossils to the living clade, however, are dubious. There are reports of uncertain Late Devonian stem group members for Limnadiidae (Liu and Gao, 1985), and much more likely Permian stem Limnadiidae (Novojilov, 1970), but these fossils are insufficiently described, leaving any specific crown spinicaudatan character states debatable. Therefore we must caution that Jurassic age is likely a severe underestimate of crown spinicaudatan antiquity. Finally, the Sinemurian *Afrolimnadia sibiriensis* Tasch, 1987 was used to calibrate crown Spinicaudata in a divergence time analysis, but with limited justification of characters for Limnadiidae (Bellec and Rabet, 2016).

63. Crown Cladocera

This clade comprises Anomopoda, Ctenopoda, Onychopoda and Haplopoda, their last common ancestor and all of its descendants (**Fig. 15**). Monophyly of this clade is supported by phylogenetic analysis of housekeeping genes alone (Stenderup et al., 2006), morphology (Hegna, 2012; Olesen, 2009, 2007, 1998), and six housekeeping genes plus morphology (Richter et al., 2007).

63.1. Fossil specimens

Smirnovidaphnia smirnovi Kotov, 2007, illustrated by two specimens: PIN 1873/100 (holotype, preserving the second antenna; **Fig. 16f**) and PIN 1873/105 (paratype, preserving both second antennae and mandibles).

63.2. Phylogenetic justification

The setal armature of the second antenna is similar to that found in extant Ctenopoda (Kotov, 2007). In morphological phylogenetic analyses, *S. smirnovi* was either found in a basal polytomy with

all of crown Cladocera, or it was sister to all Cladocera except Anomopoda (Hegna, 2012). The polytomy could indicate a stem cladoceran position, but the analyses in which *S. smirnovi* was within crown Cladocera included a lesser amount of missing data, and thus may be more robust. Furthermore, Ctenopoda itself was not recovered as monophyletic in these analyses, but *S. smirnovi* was related to taxa that have been previously included in Ctenopoda (Hegna, 2012).

2372

63.3. Age justification

2374

S. smirnovi was found on the right bank of the Angara River, downstream of Ust'-Baley village in the Olonkovsky District of Asian Russia (Kotov, 2007). According to the presence of *Osmundacidites*-type plant spores, the Ust'-Baley outcrop of the Cheremkhovo or Cheremkhovskaya Formation is correlated to the late Toarcian stage of the Early Jurassic (Akulov et al., 2015). The upper boundary of the Toarcian is $174.1 \text{ Ma} \pm 1.0 \text{ Myr}$, therefore giving a minimum age of 173.1 Ma.

Soft maximum as for 26.3.

2381

63.4. Discussion

2383

Ebullitiocaris oviformis Anderson et al., 2003 from the Devonian Rhynie Chert and *E. elatus* Womack et al., 2012 from Carboniferous chert have both been described as Cladocera. Fragmentation patterns of both fossils are inconsistent with those observed from decay experiments, therefore casting doubt on their cladoceran membership (Hegna, 2012).

Other Jurassic/Cretaceous members of the fossil family Prochydoridae are known from Mongolia and Asian Russia (Kotov, 2009). However, the Prochydoridae have been proposed as a member of the stem lineage of Anomopoda, the stem of all non-Anomopoda Cladocera, as well as the stem of Cladocera itself (Kotov, 2013, 2009). Thus crown-group affinity cannot be confirmed.

2392

2393 **64. Crown Hexapoda**

2394

2395 This clade comprises Collembola (springtails), Protura (cone heads), Diplura (two-pronged
2396 bristletails) and Insecta (insects), their last common ancestor and all of its descendants (**Fig. 17**).
2397 Monophyly of Hexapoda is established by phylogenetic analysis of nuclear protein-coding genes
2398 (Regier et al., 2010, 2005; Sasaki et al., 2013), transcriptomes (Dell’Ampio et al., 2014; Misof et al.,
2399 2014), and morphology (Legg et al., 2013).

2400

2401 *64.1. Fossil specimens*

2402

2403 *Rhyniella praecursor* Hirst and Maulik, 1926. NHMUK IN. 27765, lectotype (*fide* Ross and York,
2404 2003), head capsule with mouthparts in chert (**Fig. 2f**). Paralectotypes NHMUK IN. 38225-38227.

2405

2406 *64.2. Phylogenetic justification*

2407

2408 The Rhynie Chert taxon *R. praecursor* Hirst and Maulik, 1926, was originally identified as an
2409 insect. Re-identification as a poduromorph collembolan was made by Tillyard (1928). Additional
2410 material was examined by Scourfield (1940a, 1940b), who considered *R. praecursor* to be a possible
2411 entomobryomorph rather than a poduromorph. Subsequent studies, including some additional
2412 specimens, were made by Massoud (1967), Whalley and Jarzembowski (1981), Greenslade (1988),
2413 and Greenslade and Whalley (1986). The most recent of these investigations favour membership of at
2414 least some specimens assigned to *R. praecursor* in the extant entomobryomorph family Isotomidae
2415 (Greenslade and Whalley, 1986). Greenslade (1988) indicated that three species could be
2416 represented in the sample that is currently assigned to *R. praecursor*. Identification as an
2417 entomobryomorph underpins an assignment to the crown groups of Collembola and Hexapoda. Other
2418 taxa from the Rhynie Chert (*Rhyniognatha* and *Leverhulmia*; Engel and Grimaldi, 2004; Fayers and

2419 Trewin, 2005) and thus as old as *R. praecursor* have also been identified as Hexapoda, and more
2420 precisely as Insecta.

2421

2422 *64.3. Age justification*

2423

2424 As for 58.3.

2425

2426 **65. Crown Collembola**

2427

2428 This clade comprises Entomobryomorpha, Neelipleona, Poduromorpha, Symphypleona and
2429 Tomoceroidea, their last common ancestor and all of its descendants (**Fig. 17**). Most studies with
2430 substantial outgroup sampling are based on only one or two subclades of Collembola; however,
2431 phylogenetic analysis of ribosomal genes including all subclades (Gao et al., 2008; Xiong et al., 2008)
2432 demonstrated monophyly. Additional support with limited sampling of Collembola subclades comes
2433 from transcriptomes (Dell’Ampio et al., 2014), mitochondrial genomes (Carapelli et al., 2007), and
2434 morphology (D’Haese, 2003).

2435

2436 *65.1. Fossil specimens*

2437

2438 As for 64.1.

2439

2440 *65.2. Phylogenetic justification*

2441

2442 As for 64.2.

2443

2444 *65.3. Age justification*

2445

2446 As for 58.3.

2447

2448 **66. Crown Diplura**

2449

2450 This clade comprises Projapygoidea, Japygoidea and Campodeoidea, their last common
2451 ancestor and all of its descendants (**Fig. 17**). Monophyly of Diplura has been demonstrated by
2452 phylogenetic analysis of ribosomal genes (Gao et al., 2008), whole mitochondrial genomes (Chen et
2453 al., 2014), and morphology (Koch, 1997).

2454

2455 *66.1. Fossil specimens*

2456

2457 *Ferrojapyx vivax* Wilson and Martill, 2001. SMNS 64276, holotype.

2458

2459 *66.2. Phylogenetic justification*

2460

2461 *F. vivax* is “morphologically indistinguishable” (Wilson and Martill, 2001) from extant
2462 Japygoidea, sharing characters such as 40-segmented antennules, abdominal tergites 1-8 with a
2463 median suture, abdominal tergite 9 significantly shorter, conical abdominal styli, and forcipate cerci
2464 with curved inner margins and lacking obvious denticles (Wilson and Martill, 2001). Monophyly of
2465 Japygoidea has been considered “beyond doubt” (Koch, 2009; Fig. 3 therein for cladogram), so a
2466 phylogenetic position for this fossil either within or closely related to that clade would place it within
2467 crown Diplura.

2468

2469 *66.3. Age justification*

2470

2471 As for 29.3.

2472

2473 **67. Crown Insecta**

2474

2475 This clade comprises Microcoryphia (jumping bristletails), Zygentoma (silverfish) and Pterygota
2476 (winged insects), their last common ancestor and all of its descendants (**Fig. 17**). Monophyly is
2477 established by phylogenetic analysis of nuclear protein-coding genes (Regier et al., 2010, 2005;
2478 Sasaki et al., 2013), transcriptomes (Dell’Ampio et al., 2014; Misof et al., 2014), and morphology
2479 (Legg et al., 2013).

2480

2481 *67.1. Fossil specimens*

2482

2483 *Rhyniognatha hirsti* Tillyard, 1928. BMNH IN. 38234, holotype, preserving the mandibles and
2484 their articulation (**Fig. 18d**). Redescribed and imaged by Engel and Grimaldi (2004).

2485

2486 *67.2. Phylogenetic justification*

2487

2488 The only known specimen (the holotype) of *R. hirsti* demonstrates that the preserved pair of
2489 mandibles articulate at two points, i.e. are dicondylic (Engel and Grimaldi, 2004). Dicondylic mandibles
2490 are a diagnostic synapomorphy of Insecta (including Microcoryphia; Blanke et al., 2015). Although *R.*
2491 *hirsti* has not been included in numerical phylogenetic analyses, its mandibular shape implies
2492 “metapterygote” affinities (Engel and Grimaldi, 2004) and accordingly crown group membership within
2493 Insecta.

2494

2495 *67.3. Age justification*

2496

2497 As for 58.3.

2498

2499 67.4. Discussion

2500

2501 A complete body fossil of a putative insect, *Strudiella devonica* Garrouste et al., 2012, was
2502 described from the Fammenian (372-359 Ma) of Strud, Belgium. Apomorphies supporting an insect
2503 affinity (such as the structure of the mandibles and the number of legs), however, are poorly preserved
2504 and potentially over-interpreted (Hörschemeyer et al., 2013).

2505

2506 68. Crown Microcoryphia

2507

2508 This clade comprises the families 'Machilidae' and Meinertillidae, their last common ancestor,
2509 and all of its descendants (**Fig. 17**). This clade is commonly referred to as Microcoryphia in taxonomic
2510 literature and Archaeognatha in phylogenetic literature (Gaju-Richart et al., 2015). Recently it was
2511 clarified that Archaeognatha includes the completely extinct order Monura (compound eyes not fused,
2512 paracercus only) and Microcoryphia (very small head vertex due to their fused compound eyes,
2513 terminalia composed of a median paracercus and two lateral cerci), and thus the crown group refers to
2514 Microcoryphia only (Gaju-Ricart et al., 2015). Monophyly is supported by phylogenetic analysis of
2515 transcriptomes (Misof et al., 2014), nuclear protein-coding genes (Regier et al., 2010), and
2516 morphology (Legg et al., 2013). Synapomorphies are discussed and mapped on cladograms by Larink
2517 (1997) and Koch (2003).

2518

2519 68.1. Fossil specimens

2520

2521 *Cretaceomachilis libanensis* Sturm and Poinar, 1998 (collection Milki No. 194/35, deposited at
2522 the American University of Beirut, Beirut, Lebanon), holotype, male in amber (**Fig. 18b**).

2523

2524 68.2. *Phylogenetic justification*

2525

2526 *C. libanensis* shares morphological characters with the extant family Meinertillidae. These
2527 include the the absence of scales on the scapus, pedicellus and flagellum, and the presence of a
2528 characteristic hook near the distal end of article 2 of the male maxillary palp (Sturm and Poinar, 1998).
2529 The latter character is a synapomorphy of crown Meinertillidae (Sturm and Poinar, 1998), therefore the
2530 fossil is within crown Microcoryphia.

2531

2532 68.3. *Age justification*

2533

2534 *C. libanensis* was discovered in Cretaceous amber, from a locality in Lebanon that was not
2535 recorded (Sturm and Poinar, 1998). We therefore use a minimum age constraint from the youngest of
2536 the several known Lebanese amber localities, which all bear the same age within the early Barremian
2537 (Maksoud et al., 2016). The upper boundary of the early Barremian is proposed to be the first
2538 appearance of the ammonite *Ancyloceras vandenheckii* (Ogg et al., 2012). Cyclostratigraphy dates the
2539 *A. vandenheckii* Zone beginning at 129.41 Ma (Ogg et al., 2012), providing a minimum age for Jezzine
2540 Lebanese amber fossils.

2541 Soft maximum as for 26.3.

2542

2543 68.4. *Discussion*

2544

2545 Body imprint and trackway trace fossils from the Pennsylvanian have been attributed to both
2546 Archaeognatha and Zygentoma (Getty et al., 2013). Experiments with extant species of both clades
2547 indicate that archaeognathans produced fossil body imprints, as well as trackways exhibiting opposite
2548 symmetry (Getty et al., 2013). However, it is not possible to distinguish specific crown group

2549 apomorphies for these traces.

2550 Dasyleptidae, a diverse fossil group known from the Carboniferous-Triassic, has been
2551 proposed as the sister group of Ectognatha (Collembola, Diplura, Protura) as well as part of
2552 Archaeognatha. Recent classifications place Dasyleptidae in Monura, a separate extinct suborder of
2553 Archaeognatha, and thus outside its crown group (Bechly and Stockar, 2011; Gaju-Ricart et al., 2015).

2554

2555 **69. Crown Zygentoma**

2556

2557 This clade comprises the families Lepismatidae, Nicoletiidae, Lepidotrichidae, Maindroniidae,
2558 and Protrinemuridae, their last common ancestor and all of its descendants (**Fig. 17**). Phylogenetic
2559 analyses of transcriptomes (Misof et al., 2014), protein-coding genes (Regier et al., 2010; Sasaki et
2560 al., 2013), morphology (Blanke et al., 2014), and combined molecular and morphological data (Kjer et
2561 al., 2006) with partial taxon sampling support monophyly.

2562

2563 *69.1. Fossil specimens*

2564

2565 *Burmalepisma cretacicum* Mendes and Poinar, 2008 (specimen B-TH-1 deposited in the Poinar
2566 amber collection maintained at Oregon State University; B-TH refers to Burma-Thysanura), holotype, a
2567 female in amber (**Fig. 18c**).

2568

2569 *69.2. Phylogenetic justification*

2570

2571 Although it has not been included in a phylogenetic analysis, *B. cretacicum* bears several
2572 morphological similarities to the extant family Lepismatidae. These include the presence of compound
2573 eyes, absence of ocelli, coxal, femur, and tarsal morphology, absence of a pronotal setal collar, and
2574 presence of only smooth macrochaetae (Mendes and Poinar, 2008). A phylogenetic position either on

2575 the stem or within the crown of Lepismatidae is within the crown group of Zygentoma.

2576

2577 69.3. *Age justification*

2578

2579 As for 33.3.

2580

2581 69.4 *Discussion*

2582

2583 A possible Zygentoma fossil has been recorded from the older Aptian Crato Formation of Brazil
2584 (Sturm, 1998), but is not sufficiently characterized to be a calibration fossil. Another fossil from
2585 Burmese amber, *Cretolepisma kachinicum* Mendes and Wunderlich, 2013, is also identified as
2586 Lepismatidae. This fossil is of equal age and affinity, and is therefore also an acceptable calibration for
2587 Zygentoma.

2588

2589 **70. Crown Pterygota**

2590

2591 This clade comprises Palaeoptera (mayflies, dragonflies) and Neoptera (flexible winged
2592 insects), their last common ancestor and all of its descendants (**Fig. 17**). Monophyly is established
2593 based on phylogenetic analysis of nuclear protein-coding genes (Regier et al., 2010, 2005; Sasaki et
2594 al., 2013), transcriptomes (Misof et al., 2014; Simon et al., 2012), and morphology (Legg et al., 2013).

2595

2596 70.1. *Fossil specimens*

2597

2598 *Delitzschala bitterfeldensis* Brauckmann and Schneider, 1996 (BGR X 9216), holotype,
2599 preserving a forewing, a hindwing, cerci, and part of the abdomen (**Fig. 18a**).

2600

2601 70.2. *Phylogenetic justification*

2602

2603 *D. bitterfeldensis* is considered a member of the family Spilapteridae, in the clade
2604 Palaeodictyoptera (Brauckmann and Schneider, 1996). Morphological characters supporting this
2605 relationship include the concave anterior wing margin and deeply bifurcate MA vein ending with two
2606 long branches (Brauckmann and Schneider, 1996; Li et al., 2013b). Other fossils of Spilapteridae have
2607 also preserved the distinctive colour patterns and long cerci observed in *D. bitterfeldensis* (Li et al.,
2608 2013b). Palaeodictyoptera have previously assumed to be related to extant Palaeoptera as they share
2609 the inability to fold their wings over the abdomen (a character observed in *D. bitterfeldensis*). However,
2610 a recent morphological phylogenetic analysis controversially recognized Palaeodictyoptera as the
2611 fossil sister group of Neoptera (Sroka et al., 2015). In this evolutionary scenario, palaeopterous wings
2612 are presumably a symplesiomorphy. Nonetheless, the position of Palaeodictyoptera suggested by
2613 Sroka et al. (2015) remains within crown Pterygota.

2614

2615 70.3. *Age justification*

2616

2617 *D. bitterfeldensis* was preserved in a core extracted from the locality Bore WISABAW 1315, in
2618 the Sandersdorf Formation of Bitterfeld, Germany (Brauckmann and Schneider, 1996). The core was
2619 correlated with the E2 ammonite zone, i.e. Arnsbergian (middle Namurian A) based on the co-
2620 occurrence of ostracods and conchostracans (Brauckmann et al., 1994). The Arnsbergian is further
2621 correlated to the late Serpukhovian stage at the end of the Mississippian (Pointon et al., 2012). The
2622 upper boundary of the Serpukhovian (base of the Pennsylvanian) is estimated at 323.23 Ma \pm 0.4 Myr
2623 (Davydov et al., 2012), giving a minimum age of 322.83 Ma.

2624 Soft maximum as for 26.3.

2625

2626 70.4. *Discussion*

2627

2628 An undescribed Namurian A (latest Mississippian) member of Archaeorthoptera was initially
2629 attributed to Orthoptera (Prokop et al., 2005). It was noted that the veins are strongly deformed,
2630 enough so that the authors were reluctant to make a formal systematic description (Prokop et al.,
2631 2005). Therefore, we regard the fossil as insufficiently characterized for dating. See section 67.4 for
2632 refutation of the even older *Strudiella devonica* (Garrouste et al., 2012).

2633

2634 **71. Crown Palaeoptera**

2635

2636 This clade comprises Euplectoptera (mayflies) and Odonata (dragonflies), their last common
2637 ancestor and all of its descendants (**Fig. 17**). Monophyly of this group has been challenged by
2638 morphology (Kristensen 1981) and some transcriptome data (Simon et al., 2012, 2009), though recent
2639 analyses of nuclear protein-coding genes (Regier et al., 2010) and transcriptomes have supported
2640 Palaeoptera (Misof et al., 2014; von Reumont et al., 2012), the former weakly, only in maximum
2641 likelihood analyses of the total dataset. Recent detailed morphological analyses of head morphology
2642 corroborate the monophyly of Palaeoptera (Blanke et al., 2013, 2012). Although a morphological
2643 phylogenetic analysis (Sroka et al., 2015) claims to reject palaeopteran monophyly, its constituent
2644 extant members, Euplectoptera and Odonata, are each others' closest living relative and named
2645 therein as a new clade, Euhydrolaeoptera. We therefore cautiously endorse Palaeoptera as a clade
2646 of interest for dating.

2647

2648 *71.1. Fossil specimens*

2649

2650 *Oligotypus huangheensis* Li et al., 2013a (CNU-NX2006003), holotype, a forewing.

2651

2652 *71.2. Phylogenetic justification*

2653

2654 This species was originally described as *Sinomeganeura huangheensis* within the family
2655 Meganeuridae, part of Protodonata (Ren et al., 2008). Meganeurids include the “giant” dragonflies
2656 (with wings up to 710 mm), though *O. huangheensis* is much smaller at 70 mm (Ren et al., 2008).
2657 Despite the size difference, wing venation characters are consistent with classification in Protodonata,
2658 including the fusion of stems of CuP and CuA to a single oblique vein, distinctly stronger than the
2659 crossveins (Ren et al., 2008). This character, previously assumed to be synapomorphic for
2660 Meganeuridae, is more widespread within Protodonata (Li et al., 2013a). The group “Protodonata”
2661 itself is a paraphyletic stem group to crown Odonata, together within the total group Odonatoptera,
2662 defined by the simple MP vein (Sroka et al., 2015). Regardless of the precise relationship of
2663 Protodonata to crown Odonata, its members are definitively within crown Palaeoptera.

2664

2665 71.3. Age justification

2666

2667 The insect beds where this species was located are near Xiaheyan Village in the Qilianshan
2668 Mountains, Zhongwei County, Ningxia Huizu Autonomous Region, northwest China (Zhang et al.,
2669 2013). The insect fossil deposits are within the uppermost unit of the upper Tupo Formation
2670 (synonyms Hongtuwa or Zhongwei Formation). The presence of the ammonoids *Reticuloceras*
2671 *reticulatum*, *Gastrioceras listeri* and *G. montgomeryense* and conodonts *Declingnathodus noduliferous*
2672 and *Neognathodus symmetricus* indicate a Namurian B/C age (Xie et al., 2004; Yang, 1987; Yang et
2673 al., 1988; Zhang et al., 2013). The (late) Namurian-(early) Westphalian boundary is defined by the
2674 earliest occurrence of the goniatite *Gastrioceras subcrenatum* (Waters and Davies, 2006), but lacks a
2675 precise isotopic date. Pointon et al. (2012) estimated an age of c. 319.9 Ma for the base of the
2676 Westphalian (top of the Namurian, only slightly younger than the Marsdenian) based on Milankovitch
2677 cycles of sedimentation, giving a minimum age for Xiaheyan fossils.

2678 Soft maximum as for 26.3.

2679

2680 71.4. Discussion

2681

2682 Due to the controversial status of Palaeoptera as a clade, there are several fossil groups that
2683 have been considered for membership: Palaeodictyoptera, Paoliida, stem mayflies (Ephemeroptera,
2684 see section 72), and stem dragonflies (Protodonata, including Geroptera) (Grimaldi and Engel, 2005).
2685 Each is discussed below.

2686 Palaeodictyoptera, an abundant clade from the Carboniferous and Permian, have been
2687 assumed to be related to extant Palaeoptera as they share the inability to fold their wings over the
2688 abdomen. The oldest member, *Delitzschala bitterfeldensis*, predates all other Palaeoptera (and all
2689 other Pterygota with preserved wings), as it is from the Mississippian (Brauckmann et al., 1994;
2690 Pointon et al., 2012). In cladograms in which Palaeodictyoptera is the fossil sister group of
2691 Neoptera (Sroka et al., 2015), palaeopterous wings are presumably a symplesiomorphy. The presence
2692 of nymphal wing pads is probably also a symplesiomorphy of Pterygota (Haug et al., 2016). Therefore
2693 Palaeodictyoptera may be outside the crown and even stem group of Palaeoptera.

2694 Paoliida is an extinct clade known mainly from wings of the Westphalian A stage of the
2695 Pennsylvanian. The group has been attributed to the Palaeodictyoptera and later removed (Prokop et
2696 al., 2012; Prokop and Nel, 2007). It has been subsequently proposed that Paoliida is the fossil sister
2697 group of Dictyoptera (Prokop et al., 2014), and thus are within crown Polyneoptera. This would refute
2698 a relationship with Palaeoptera or any of its members.

2699 A full body impression of a putative Carboniferous (Westphalian B/C) mayfly is subject to
2700 controversy (Benner et al., 2013; Knecht et al., 2011; Marden, 2013a, 2013b). *Bojophlebia prokopi*
2701 Kukalová-Peck, 1985 (Westphalian C) is likely outside of Palaeoptera, according to descriptions and
2702 phylogenetic analysis (Prokop et al., 2010; Sroka et al., 2015; Staniczek et al., 2011). The Stephanian
2703 B/C fossil *Triplosoba pulchella* Brongniart, 1883, originally described as a mayfly, has been
2704 redescribed as Palaeodictyoptera (Prokop and Nel, 2009). The oldest body fossils belonging to the

mayfly stem group are therefore members of the Syntonopteroidea. The oldest Syntonopteroidea are *Lithoneura lameerei* Carpenter, 1938 and *Syntonoptera schucherti* Handlirsch, 1911, from the Westphalian D Mazon Creek (younger than Xiaheyan) (Nicholson et al., 2015; Prokop et al., 2010).

Putative older members of Odonatoptera are Geroptera, represented by the species *Eugeropteron lunatum* and *Geropteron arcuatum* (both Riek and Kukalová-Peck, 1984), are known from the late Namurian of Argentina (Gutiérrez et al., 2000; Riek and Kukalová-Peck, 1984). *G. arcuatum* was included in a morphological phylogenetic analysis, but was resolved outside Protodonata, in a polytomy with Odonata, Ephemeroptera, and Neoptera, thus outside Palaeoptera (Bybee et al., 2008). It need, however, be noted that morphological characters were polarized *a priori* with respect to *G. arcuatum* (Bybee et al., 2008).

72. Crown Euplectoptera

This clade comprises the families Siphuriscidae, Baetidae, Isonychiidae, Ametropodidae, Acanthametropodidae, Coloburiscidae, Siphlaenigmatidae, Ameletopsidae, Heptageniidae, Metretopodidae, Siphonuridae, Oniscigastriidae, Rallidentidae, Nesameletidae, and the larger clades Carapacea and Furcatergalia, their last common ancestor and all of its descendants (**Fig. 17**). A variety of different classification schemes have been proposed (Kluge, 2004, 1998; McCafferty, 1991; Ogden and Whiting, 2005), but we follow the consensus based on combined phylogenetic analysis of two nuclear genes, two mitochondrial genes, and morphology (Ogden et al., 2009). Although the extant members are often referred to as Ephemeroptera, that clade includes a number of extinct members forming a paraphyletic grade (Kluge, 2004, 1998). As membership of fossil species within a crown group is only possible if they branch along the stem lineage of a living clade that is part of the crown itself, we treat crown 'Ephemeroptera' as equivalent to the clade Euplectoptera *sensu* Tillyard (1932).

Monophyly has been supported by the aforementioned combined data study (Ogden et al.,

2731 2009), as well as analyses of transcriptomes (with limited but representative taxon sampling: Misof et
2732 al., 2014) and morphology (Ogden et al., 2009 Fig. 4: note this is monophyletic, but the root is shown
2733 intervening).

2734

2735 72.1. Fossil specimens

2736

2737 *Triassonurus doliiformis* Sinitshenkova et al., 2005 (part of the private Louis Grauvogel
2738 collection, Ringendorf, Bas-Rhin, France, No. 9304), holotype, an incomplete nymph (**Fig. 18e**).

2739

2740 72.2. Phylogenetic justification

2741

2742 *T. doliiformis* has not been explicitly included in a phylogenetic analysis. It bears several
2743 morphological characters indicating affinity with the extant family Siphonuridae: a large nymph with a
2744 non-flattened body, head longer than short prothorax, massive mesothorax with considerably shorter
2745 metathorax, large and wide forewing pads almost completely covering the hind ones, short and
2746 slender legs, abdominal segments without sharp denticles, large rounded tergaliae, and cerci and
2747 paracercus long (Sinitshenkova et al., 2005). The family Siphonuridae is not accepted as
2748 monophyletic by all authors (J.-D. Huang et al., 2008; Kluge, 2004; McCafferty, 1991) although it is
2749 supported in total evidence and morphological analyses of Ogden et al. (2009). Siphonuridae is within
2750 the crown of Euplectoptera, in the clade of families outside Carapacea + Furcatergalia (Ogden et al.,
2751 2009). Therefore, *T. doliiformis* is also crown Euplectoptera.

2752

2753 72.3. Age justification

2754

2755 The fossil is derived from the silt-clay Grès à Meules unit (lowermost layer) of the Grès-a-
2756 Voltzia Formation, Vosges, northeastern France (Gall and Grauvogel-Stamm, 1993). Grès à Meules

2757 represents the last stage of the fluviatile facies prevalent in the Buntsandstein (Gall, 1985). Based on
2758 sequence stratigraphy, Bourquin et al. (2007, 2006) correlate the Grès-a-Voltzia Formation to the
2759 middle Anisian stage of the Triassic. Globally, the uppermost boundary of the Anisian is 241.5 ± 1 Ma
2760 (Ogg, 2012), providing a minimum age at 240.5 Ma.

2761 Because the monophyly of Palaeoptera is under debate (Simon et al., 2012, 2009), we assign
2762 a soft maximum age that allows its constituent extant orders to be older than the Rhynie Chert, as for
2763 26.3.

2764

2765 72.4. Discussion

2766

2767 The Permian fossils *Protereisma permianum* Sellards, 1907 and *Kukalova americana*
2768 Demoulin, 1970 were coded in the morphology matrix (larval and adult characters) of Odgen et al.
2769 (2009), but their relationships to the crown remain uncertain. *P. permianum* was resolved on the stem
2770 lineage of the extant families Euthyplociidae, Ephemeridae, and Potamanthidae with morphology only,
2771 but outside crown Euplectoptera in a total evidence analysis (Ogden et al., 2009). More generally,
2772 Kluge (Kluge, 2004, 1998) considered the Permian-Triassic members to form a plesion,
2773 Permoplectoptera, outside the crown group Euplectoptera. The relationship of Permoplectoptera to the
2774 crown group remains to be tested by morphological phylogenetics.

2775 Furthermore, many mayfly fossils are of nymphs, and linking characters between fossil and
2776 extant nymphs (or fossil nymphs and extant adults) is challenging, though not impossible (e.g. Haug et
2777 al., 2016; Wolfe and Hegna, 2014). The nymphal fossils include *Fuyous gregarius* and *Shantous*
2778 *lacustris* (both Zhang and Kluge, 2007), two species from the Jurassic Daohugou biota that have been
2779 used as crown group calibrations in previous divergence time analyses (Thomas et al., 2013). They
2780 are, however, younger than *T. doliiformis*.

2781

2782 73. Crown Odonata

2783

2784 This clade comprises Epiprocta (dragonflies; comprising Anisozygoptera and Anisoptera) and
2785 Zygoptera (damselflies), their last common ancestor and all of its descendants (**Fig. 17**). Monophyly of
2786 Odonata is supported by phylogenetic analysis of transcriptomes (Misof et al., 2014), combined
2787 morphology and housekeeping genes (Bybee et al., 2008), and a supertree including morphological
2788 and molecular input trees (Davis et al., 2011).

2789

2790 *73.1. Fossil specimens*

2791

2792 *Triassothemis mendozensis* Carpenter, 1960. MACN No. 18040, holotype, preserving the distal
2793 portion of two wings.

2794

2795 *73.2. Phylogenetic justification*

2796

2797 *T. mendozensis* is the oldest known member of the fossil family Triassolestidae (Nel et al.,
2798 2002; Nicholson et al., 2015). A family-level supertree, incorporating molecular and morphological
2799 input trees, found Triassolestidae within crown group Epiprocta (Davis et al., 2011, largest tree in their
2800 Fig. 1). This fossil is therefore also a member of crown group Odonata. Of all the fossil families
2801 included in the supertree analysis and placed within crown Odonata (Davis et al., 2011),
2802 Triassolestidae (represented by *T. mendozensis*) has the oldest member. Furthermore, this family (and
2803 its approximate date) was used to calibrate Odonata in multiple recent divergence time analyses
2804 (Rota-Stabelli et al., 2013a; Thomas et al., 2013).

2805

2806 *73.3. Age justification*

2807

2808 *T. mendozensis* was discovered in dark grey siltstone of the Potrerillos Formation, at Quebrada

2809 del Durazno, Mendoza Province, Argentina (Martins-Neto et al., 2008). The insect-bearing beds are
2810 from the upper part of the Potrerillos Formation. U-Pb SHRIMP dates have been measured for zircons
2811 from tuff layers in the middle section of the Potrerillos Formation. The uppermost tuff layer estimated
2812 an age of 230.3 Ma \pm 2.3 Myr (Spalletti et al., 2009), corresponding to the Carnian, late Triassic. Thus
2813 a minimum age of *T. mendozensis* is 228.0 Ma.

2814 Because the monophyly of Palaeoptera is under debate (Simon et al., 2009, 2012), we assign
2815 a soft maximum age that allows its constituent extant orders to be older than the Rhynie Chert, as for
2816 26.3.

2817

2818 73.4. Discussion

2819

2820 The internal taxonomy and placement of odonate fossils is highly contentious. Triassic
2821 members of the fossil family Triadophlebiidae are of approximately equal age to *T. mendozensis* (i.e.
2822 Carnian; Nicholson et al., 2015), however, they appear outside the crown group of Odonata in a
2823 supertree (Davis et al., 2011). Triadophlebiidae were not included in the total evidence analysis of
2824 Bybee et al. (2008). Most fossils in the latter analysis that had membership within crown Odonata
2825 were Jurassic or younger (Bybee et al., 2008).

2826 The Madygen fauna of Kyrgyzstan yields two possible calibrations for crown group Odonata.
2827 *Triassolestodes asiaticus* Pritykina, 1981 (family Triassolestidae, preserving a hindwing) was recently
2828 justified as the oldest odonate by Kohli et al. (2016). As well, fossil members of Lestidae, crown group
2829 Odonata in the analysis of Bybee et al. (2008), are inferred from oviposition scars on plant fossils from
2830 Madygen (Moisan et al., 2012). Aside from challenges associated with interpreting crown group
2831 affinities of trace fossils, the Madygen fauna is, according to our stratigraphy, dated to the Carnian
2832 (see section 90.3), substantially younger than the 237 Ma age argued by Kohli et al. (2016) based on
2833 megaflora. Our age would give a minimum age of 226.4 Ma for Madygen fossils, which is very slightly
2834 younger than the 228.0 Ma estimated for *T. mendozensis*. Note, however, that the mean age estimate

2835 for Madygen is 228.4 Ma (also younger than the mean of 230.3 Ma for the Potrerillos Formation).

2836 *Triassolestes epiophlebioides* Tillyard, 1918, a member of Triassolestidae used as a calibration
2837 fossil by Rota-Stabelli et al. (2013), is also known from the Carnian (Nicholson et al., 2015). Another
2838 fossil, *Pseudotriassothemis nipponensis* Bechly, 1997 (formerly *Triassoneura okafujii*), from the
2839 Carnian of Japan is also approximately coeval. We select *T. mendozensis* because its preservation is
2840 better, and radiometric dates for the Potrerillos Formation may be more precise.

2841

2842 **74. Crown Neoptera**

2843

2844 This clade comprises Polyneoptera (**Figs. 19 and 20**) and Eumetabola, their last common
2845 ancestor and all of its descendants (**Fig. 21**). Monophyly is supported by phylogenetic analysis of
2846 transcriptomes (Letsch and Simon, 2013; Misof et al., 2014), protein-coding genes (Ishiwata et al.,
2847 2011; Sasaki et al., 2013), and combined molecular and morphological data (Terry and Whiting, 2005).

2848

2849 *74.1. Fossil specimens*

2850

2851 *Protoprosbole straeleni* Laurentiaux, 1952. IRSNB a9885, holotype, preserving a forewing.
2852 Figured in Nel et al. (A. Nel et al., 2012), Fig. 3h.

2853

2854 *74.2. Phylogenetic justification*

2855

2856 The original description of *P. straeleni* as a member of Hemiptera by Laurentiaux (1952) has
2857 been rejected several times (Hennig, 1981; A. Nel et al., 2012; Shcherbakov, 1995). Nel et al. (2012)
2858 summarize the phylogenetic position of *P. straeleni* as being within Paraneoptera (a clade
2859 unsupported by recent molecular studies, but comprising Psocodea and Condylgnatha). The cua-cup
2860 contact with CuP and the flexion or nodal line following the course of RA are both similar to those

2861 observed in extant Hemiptera (A. Nel et al., 2012). However, the presence of three veins in the anal
2862 area is argued as a hemipteran autapomorphy that is lacking in *P. straeleni* (A. Nel et al., 2012).
2863 Conservatively, this fossil species can be thus assigned to the stem group of Condylgnatha, and thus
2864 crown Eumetabola and Neoptera.

2865

2866 74.3. Age justification

2867

2868 *P. straeleni* was discovered in Charbonnage de Monceau-Fontaine, Charleroi Coal Basin,
2869 Belgium (Brauckmann et al., 1994). The specimen was likely found in latest Marsdenian strata about 3
2870 m below the base of the Yeadonian (discussed by Brauckmann et al., 1994). The fossil-bearing
2871 deposits are assigned to the late Namurian B (Marsdenian) based on the *Bilinguites superbilinguis*
2872 R2c2 subzone of goniatite ammonoid stratigraphy (Brauckmann et al., 1994). The (late) Namurian-
2873 (early) Westphalian boundary is defined by the earliest occurrence of the goniatite *Gastrioceras*
2874 *subcrenatum* (Waters and Davies, 2006), but lacks a precise isotopic date. Pointon et al. (2012)
2875 estimated an age of c. 319.9 Ma for the base of the Westphalian (top of the Namurian, only slightly
2876 younger than the Marsdenian) based on Milankovitch cycles of sedimentation, giving a minimum age
2877 for *P. straeleni*.

2878 Soft maximum as for 26.3.

2879

2880 74.4. Discussion

2881

2882 *Qilianiblatia namurensis* Zhang et al., 2013 has an equal claim to being the earliest record of
2883 Neoptera (as *Q. namurensis* is a member of crown Polyneoptera), but it is of equal age to *P. straeleni*.
2884 The Qilianshan entomofauna at Xiaheyan, China, yields many other likely neopterans (e.g. Béthoux et
2885 al., 2011; Liu et al., 2009a; Prokop and Nel, 2007; Zhang et al., 2013).

2886 *Ctenoptilus elongatus* Béthoux and Nel, 2005 from the Stephanian B/C of France has been

2887 used as the putative oldest calibration fossil for crown Neoptera (e.g. O'Reilly et al., 2015). However,
2888 the Stephanian is a European stage of the Pennsylvanian, corresponding to the globally used
2889 Gzhelian, which is substantially younger than the Bashkirian age of both *P. straeleni* and *Q.*
2890 *namurensis* (with an upper boundary of 298.75 Ma).

2891

2892 **75. Crown Polyneoptera**

2893

2894 This clade comprises Zoraptera (ground lice), Dermaptera (earwigs), Plecoptera (stoneflies),
2895 Orthoptera (crickets, katydids), Notoptera, Eukinolabia and Dictyoptera, their last common ancestor
2896 and all of its descendants (**Fig. 19**). Monophyly has been demonstrated by phylogenetic analysis of
2897 transcriptomes (Letsch and Simon, 2013; Misof et al., 2014), protein-coding genes (Ishiwata et al.,
2898 2011), and wing morphology (Yoshizawa, 2011). This clade is not recognized in GenBank taxonomy.

2899

2900 *75.1. Fossil specimens*

2901

2902 *Qilianiblatia namurensis* Zhang et al., 2013. GMCB 04GNX1001-1, holotype, preserving the
2903 right forewing. We also refer to a second specimen (CNU-NX1-303; **Fig. 20a**), preserving paired
2904 forewings and hindwings (Guo et al., 2013).

2905

2906 *75.2. Phylogenetic justification*

2907

2908 *Q. namurensis* has not been included in formal phylogenetic analysis, but the fossil exhibits
2909 some apomorphic characters uniting it with crown group Blattodea, specifically presence of a deeply
2910 concave CuP in the forewing (Prokop et al., 2014). Additional data from forewings of the CNU
2911 specimen shows the RA with branches translocated to RP, as in cockroaches, suggesting this species
2912 could be stem Blattodea (Guo et al., 2013). However, there has not been a cladistic analysis of wing

2913 venation characters for both fossil and extant Blattodea and/or Dictyoptera, thus we agree with the
2914 more conservative view (Kjer et al., 2015; Legendre et al., 2015; Prokop et al., 2014) that roachoids
2915 likely represent a diverse and speciose fauna on the stem group of Dictyoptera. See also section 82.4.
2916 Nonetheless, placement of *Q. namurensis* on the stem lineage of Dictyoptera identifies it as a member
2917 of crown Polyneoptera.

2918

2919 75.3. Age justification

2920

2921 Minimum as for 71.3.

2922 A soft maximum age is estimated from *R. praecursor*, the oldest hexapod, from the Early
2923 Devonian (Pragian) Rhynie Chert of Aberdeenshire, Scotland. Spore assemblages of the Windyfield
2924 and stratigraphically underlying Rhynie Chert are dated to the early but not earliest Pragian to early
2925 (earliest?) Emsian (polygonalis-emsianensis Spore Assemblage Biozone) (Parry et al., 2011).
2926 Radiometric dating of the underlying Milton of Noth Andesite at ca. 411 Ma (Parry et al., 2013, 2011)
2927 has been subject to a dispute over its temporal relationship to hot spring activity associated with the
2928 cherts (Mark et al., 2013, 2011) and predates the biostratigraphic dating of the Rhynie Chert relative to
2929 the global dating of the base of the Pragian Stage. Therefore, a soft maximum constraint may be
2930 defined at 411 Ma for the Rhynie Chert.

2931

2932 76. Crown Dermaptera

2933

2934 This clade comprises Protodermaptera and Epidermaptera, their last common ancestor and all
2935 of its descendants (**Fig. 19**). Monophyly is supported based on phylogenetic analysis of
2936 transcriptomes (Misof et al., 2014), nuclear genes (Kocarek et al., 2013), and combined molecular and
2937 morphological data (Jarvis et al., 2005).

2938

2939 76.1. *Fossil specimens*

2940

2941 *Rhadinolabis phoenicica* Engel et al., 2011. Holotype preserving a female in amber, 1013 in the
2942 private collection of D. Azar in Fanar (Matn), Lebanon (**Fig. 20e**). Provisionally housed at MNHN.

2943

2944 76.2. *Phylogenetic justification*

2945

2946 *R. phoenicica* is assigned only to Neodermaptera (= Protodermaptera + Epidermaptera), and
2947 not to any extant family. Membership within Neodermaptera is based on the presence of
2948 morphological characters: trimerous tarsi, absence of a well-developed ovipositor, and tarsal structure
2949 (Engel et al., 2011). These characters are sufficient to confirm the fossil belongs within crown
2950 Dermaptera.

2951

2952 76.3. *Age justification*

2953

2954 This fossil was discovered in amber from the Mdeyrij-Hammana outcrop of the Baabda district,
2955 Mount Lebanon (Azar et al., 2010). Recent revision of the stratigraphy of Lebanese amber deposits
2956 places the Hammana fossils in the upper interval of the Grès du Liban (Maksoud et al., 2016). This is
2957 below the Jezzian regional stage (Maksoud et al., 2014) and above the Banc de Mrejatt subunit
2958 (indicated as Ba3-Ba4 in Fig. 4 of Maksoud et al., 2016). Despite the lack of microfossils to further
2959 constrain the oldest boundary of the Jezzian within the late Barremian, there is evidence that later
2960 Lebanese amber deposits bear the same age as Jezzine amber (see 26.3) because the amber itself
2961 has been reworked (Maksoud et al., 2016). We adopt the early Barremian minimum age proposed by
2962 Maksoud et al. (2016). The upper boundary of the early Barremian is proposed to be the first
2963 appearance of the ammonite *Ancyloceras vandenheckii* (Ogg et al., 2012). Cyclostratigraphy dates the
2964 *A. vandenheckii* Zone beginning at 129.41 Ma (Ogg et al., 2012), providing a minimum age for Jezzine

2965 Lebanese amber fossils.

2966 Soft maximum as for 75.3.

2967

2968 **77. Crown Plecoptera**

2969

2970 This clade comprises Antartoperlaria, Euholognatha and Systellognatha, their last common
2971 ancestor and all of its descendants (**Fig. 19**). This classification and its morphological evidence is
2972 reviewed by Zwick (2000). Monophyly of Plecoptera is supported by phylogenetic analysis of
2973 transcriptomes (Misof et al., 2014) and combined ribosomal genes, H3, and morphology (Terry and
2974 Whiting, 2005).

2975

2976 *77.1. Fossil specimens*

2977

2978 *Palaeotaeniopteryx elegans* Sharov, 1961. PIN 1197/333, holotype, preserving a forewing.

2979

2980 *77.2. Phylogenetic justification*

2981

2982 *P. elegans* is classified in the fossil family Palaeonemouridae, suborder Nemourina
2983 (Sinitshenkova, 1987). At that time, Nemourina was one of only two suborders, the other being Perlina
2984 (Rasnitsyn and Quicke, 2002). Zwick (2000) summarized Nemourina as containing the (extant)
2985 families Notonemouridae, Nemouridae, Taeniopterygidae, Capniidae, and Leuctridae, therefore
2986 equivalent to the new suborder Euholognatha. Grimaldi and Engel (2005; Fig. 7.6) prefer a placement
2987 of Palaeonemouridae outside the crown group of Plecoptera, on the basis that diagnostic characters
2988 for crown group suborders within Plecoptera are rarely preserved (e.g. muscles, cellular structures).
2989 While no formal phylogenetic hypothesis illustrates the relationship of Palaeonemouridae to other
2990 Euholognatha, synapomorphies are identified linking *P. elegans* to the crown group of Plecoptera

2991 (Béthoux, 2005, pers. comm.).

2992

2993 *77.3. Age justification*

2994

2995 The oldest specimen of *P. elegans* was discovered from the Mitino Horizon at the Kaltan
2996 locality in the Kuznetsk Basin, Kemerovo, Russia (Sharov, 1961; Shcherbakov, 2000). Correlation of
2997 insect faunas suggests the Kaltan locality is late early Kazanian (Lozovsky et al., 2009; Shcherbakov,
2998 2008). The Kazanian is a regional stage of the Russian Permian, which has been correlated to both
2999 the Wordian (Menning et al., 2006) and the Roadian global Stages (Lozovsky et al., 2009). Evidence
3000 for an age in the Roadian is stronger, demarcated by presence of ammonites such as *Sverdrupites*
3001 *harkeri* and *S. amundseni* (Lozovsky et al., 2009). These ammonites, and associated conodonts
3002 *Kamagnathus khalimbadzhai* and *K. volgensis*, correlate globally to the Roadian (Barskov et al., 2014;
3003 Leonova, 2007; Leonova and Shilovsky, 2007). The upper boundary of the Roadian is 268.8 Ma \pm 0.5
3004 Myr, so a minimum age is 268.3 Ma.

3005 Soft maximum as for 75.3.

3006

3007 *77.4. Discussion*

3008

3009 *Gulou carpenteri* Béthoux et al., 2011, from the Pennsylvanian Qilianshan entomofauna of
3010 China, is identified as a member of the stem group to Plecoptera (Béthoux et al., 2011), and thus
3011 cannot be used to calibrate a minimum age of the crown group. Moreover, other Permian plecopterans
3012 had terrestrial nymphs; an aquatic nymph is a synapomorphy uniting crown group Plecoptera (Zwick,
3013 2000), relegating any fossil without it to the stem group.

3014 O. Béthoux (pers. comm.) cautioned that a Jurassic minimum age for crown Plecoptera, as
3015 used by Misof et al. (2014), would underestimate their age significantly. The calibrating fossil
3016 *Pronemoura angustithorax* Liu et al., 2011 used by Misof et al. (2014), from the Daohugou Beds, is

likely a member of total group Euholognatha (Liu et al., 2011). Other crown Plecoptera groups are also known from the same locality (Liu et al., 2009b), suggesting diversification of the crown group was significantly earlier.

78. Crown Orthoptera

This clade comprises Ensifera (crickets, katydids) and Caelifera (grasshoppers), their last common ancestor and all of its descendants (**Fig. 19**). Monophyly is demonstrated by phylogenetic analysis of transcriptomes (Misof et al., 2014), mitochondrial genomes plus four nuclear genes (Song et al., 2015), morphology (Béthoux and Nel, 2002), and combined molecular and morphological data (Terry and Whiting, 2005).

78.1. Fossil specimens

Raphogla rubra Béthoux et al., 2002. Ld LAP 415 B, holotype, preserving the counterpart of a forewing (**Fig. 20c**).

78.2. Phylogenetic justification

Although no cladistic analysis exists combining extant and fossil Ensifera, *R. rubra* may be assigned to crown Ensifera based on forewing venation characters (Béthoux et al., 2002). It likely belongs to the stem group of the clade (Gryllidea + Tettigoniidea), based on the following characters: very broad area between anterior margin and Sc; RS moderately long basal of a short fusion with the anterior branch MA1a of MA; MP + CuA1 with only one simple anterior branch (Béthoux et al., 2002). As both Gryllidea and Tettigoniidea are crown clades within crown Ensifera, *R. rubra* is within crown group Orthoptera.

3043

3044 78.3. Age justification

3045

3046 *R. rubra* was found at the fossiliferous site F21 D, at “Le Moural D”, in the basal Mérifrons
3047 Member of the Salagou Formation (Saxonian Group), near village Octon, Lodève Basin, Hérault,
3048 France (Béthoux et al., 2002; Nel et al., 1999; Schneider et al., 2006). U-Pb dates have been recently
3049 measured from zircons lying in tuff beds near the lower two-thirds of the Salagou Formation (Octon
3050 Member), in the Artinskian (Michel et al., 2015). The Mérifrons Member, overlying the Octon, is
3051 therefore inferred to be Artinskian at its base but continuing up through the Kungurian (Michel et al.,
3052 2015). As the exact stratum of the F21 site is not indicated within the Mérifrons member (Michel et al.,
3053 2015; Schneider et al., 2006), we apply a conservative minimum estimate from the upper boundary of
3054 the Kungurian (272.3 Ma \pm 0.5 Myr), at 271.8 Ma.

3055 Soft maximum as for 75.3.

3056

3057 78.4. Discussion

3058

3059 An undescribed Namurian member of Archaeorthoptera was initially attributed to crown group
3060 Orthoptera (Prokop et al., 2005). However, an affinity with Archaeorthoptera is supported in the stem
3061 group of Orthoptera based on phylogenetic analysis (Béthoux and Nel, 2002), thus it cannot be used
3062 to calibrate the crown. Similarly, *Oedischia williamsoni* Brongniart, 1885, from the Pennsylvanian of
3063 France, is recognized as a stem group member of Orthoptera by cladistic analysis (Béthoux and Nel,
3064 2002). Together these fossils suggest a long stem branch for Orthoptera.

3065 The fossil *Eolocustopsis primitiva* Riek, 1976 from Natal, South Africa was listed as the oldest
3066 crown group member of Caelifera, and thus another Permian crown group member of Orthoptera
3067 (Song et al., 2015). However, the fossil comes from strata of the Normandien Formation,
3068 Changhsingian stage, latest Permian (due to the co-occurrence of the vertebrate fossil *Dicynodon*;

3069 e.g. Catuneanu et al., 2005), which is younger than the Kungurian.

3070

3071 **79. Crown Notoptera**

3072

3073 This clade comprises Mantophasmatodea (rock crawlers) and Grylloblattodea (ice crawlers),
3074 their last common ancestor and all of its descendants (**Fig. 19**). The monophyly of Notoptera is
3075 supported by phylogenetic analysis of transcriptomes (Misof et al., 2014), morphology (Wipfler et al.,
3076 2011), and combined molecular and morphological data (Terry and Whiting, 2005).

3077

3078 *79.1. Fossil specimens*

3079

3080 *Juramantophasma sinica* D. Huang et al., 2008. NIGP 142171, holotype, preserving a nearly
3081 complete adult female (**Fig. 20g**).

3082

3083 *79.2. Phylogenetic justification*

3084

3085 *J. sinica* has several characters in common with crown Mantophasmatodea. These include: a
3086 third tarsomere with a sclerotized elongated dorsal process, enlarged and fanlike pretarsal arolia, last
3087 tarsomere at right angle to the others, female gonoplasts short and claw shaped, and egg with a
3088 circular ridge (D. Huang et al., 2008). As no morphological matrix exists for Mantophasmatodea,
3089 relationships to extant lineages are not possible to test (D. Huang et al., 2008). The fossil is excluded
3090 from the crown group of Grylloblattodea as it lacks segmented cerci. Thus, conservatively, a position
3091 on the stem lineage of Mantophasmatodea is likely (although *J. sinica* could be amended to within the
3092 crown of Mantophasmatodea). This would, in any case, mean it is a member of crown Notoptera.

3093

3094 *79.3. Age justification*

3095

3096 This fossil was found in deposits of the Daohugou Beds, Ningcheng County, Inner Mongolia,
3097 China (D. Huang et al., 2008). There has been controversy about the accuracy and precise age and
3098 stratigraphic position of the Daohugou Beds (Gao and Ren, 2006; Wang et al., 2005; Zhang, 2015).
3099 The beds consist of 100–150 m thick succession of grey-white or locally reddish, thinly bedded
3100 claystones, shales, siltstones and sandy mudstones with intercalated ash-fall tuffs and ignimbrites.
3101 Ages have been proposed from Aalenian (Middle Jurassic) to Early Cretaceous (Liu et al., 2014; Wang
3102 et al., 2000), with several studies converging on Callovian-Oxfordian (Late Jurassic; Zhang, 2015).
3103 Radiometric dating of the ignimbrites with $^{40}\text{Ar}/^{39}\text{Ar}$ and SHRIMP U-Pb variously yields dates
3104 between $165 \text{ Ma} \pm 2.5 \text{ Myr}$ and $158.7 \text{ Ma} \pm 0.6 \text{ Myr}$ (Chang et al., 2009b; Gao and Ren, 2006; He et
3105 al., 2004; Peng et al., 2012). The fossiliferous shales overlay the volcanic deposits (Gao and Ren,
3106 2006), and are thus younger. The isotopic dates nonetheless provide a reasonable refutation of
3107 Cretaceous age estimates. Furthermore, the Daohugou Beds may be correlated to sediments from
3108 Oxfordian localities in China and Kazakhstan (Zhang, 2015). The most conservative (i.e. youngest) of
3109 the direct radiometric dates is 158.1 Ma (within the Oxfordian), giving a minimum age.

3110 Soft maximum as for 75.3.

3111

3112 *79.4. Discussion*

3113

3114 Stem group Grylloblattodea are uncommon, and extant grylloblattids (and mantophasmids) are
3115 wingless (Wipfler et al., 2014). A putative grylloblattid insect was described from the Pennsylvanian
3116 Montceau-les-Mines Lagerstätte, about 130 Myr older than *J. sinica* (Béthoux and Nel, 2010);
3117 however, the fossil preserved only the wings. We take the parsimonious view that there was a single
3118 loss of wings in the common ancestor of Grylloblattodea and Mantophasmatodea, i.e. in the crown
3119 group of Notoptera (Grimaldi and Engel, 2005). Therefore, any fossil bearing wings, such as the
3120 Pennsylvanian and Permian members, would be on the stem branch of Notoptera.

3121

3122 **80. Crown Eukinolabia**

3123

3124 This clade comprises Embioptera (webspinners) and Phasmatodea (stick and leaf insects),
3125 their last common ancestor and all of its descendants (**Fig. 19**). Monophyly of Eukinolabia is
3126 supported by phylogenetic analyses of transcriptomes (Letsch and Simon, 2013; Misof et al., 2014)
3127 and ribosomal and H3 sequences (Terry and Whiting, 2005).

3128

3129 *80.1. Fossil specimens*

3130

3131 *Cretophasmomima melanogramma* Wang et al., 2014. CNU-PHA-NN2012002, holotype,
3132 preserving a male (**Fig. 20d**).

3133

3134 *80.2. Phylogenetic justification*

3135

3136 *C. melanogramma* shares the 'shoulder pad' structure, and twig-like appearance (elongated
3137 meso- and metathorax) diagnostic of total group Phasmatodea (Wang et al., 2014). Crown
3138 membership within Phasmatodea is questionable, as important synapomorphies, the vomer and
3139 forceps-like extensions of the 10th abdominal tergum, are absent from *C. melanogramma* (Wang et
3140 al., 2014). The position of *C. melanogramma* on the stem lineage of Phasmatodea therefore places it
3141 within the crown group of Eukinolabia.

3142

3143 *80.3. Age justification*

3144

3145 As for 76.3.

3146

3147 80.4. Discussion

3148

3149 *Renphasma sinica* Nel and Delfosse, 2011 is of equal age, also from the Yixian Formation, and
3150 also a member of stem Phasmatodea, and thus crown Eukinolabia.

3151

3152 **81. Crown Phasmatodea**

3153

3154 This clade comprises Timematodea and Euphasmatodea, their last common ancestor and all
3155 of its descendants (**Fig. 19**). Monophyly of Phasmatodea is supported by phylogenetic analyses of
3156 transcriptomes (Misof et al., 2014), ribosomal and H3 sequences (Terry and Whiting, 2005), and
3157 morphology (Friedemann et al., 2012).

3158

3159 81.1 Fossil specimens

3160

3161 *Echinosomiscus primoticus* Engel et al., 2016c. NIGP 163536, holotype, preserving a male in
3162 amber (**Fig. 20f**).

3163

3164 81.2 Phylogenetic justification

3165

3166 Until recently, no Mesozoic fossil qualified for membership in the crown group of Phasmatodea
3167 (Bradler and Buckley, 2011). *E. primoticus* bears morphological characters shared with extant
3168 members of Euphasmatodea, in particular Heteropterygidae and Aschiphasmataidae, but lack the area
3169 apicalis on the tibiae (Engel et al., 2016c). It also shares characters with Lonchodinae, such as absent
3170 areole on all tibiae, comparatively long antennae, the absence of wings, and the division of the tenth
3171 abdominal tergum into moveable hemitergites (Engel et al., 2016c). Although a new family was
3172 erected to accommodate the unique character combination for *E. primoticus*, it is very clearly within

3173 Euphasmatodea (Phasmatidae s.l.), and thus a member of crown Phasmatodea (Engel et al., 2016c).

3174

3175 *81.3 Age justification*

3176

3177 Minimum as for 12.3. Soft maximum as for 75.3.

3178

3179 **82. Crown Dictyoptera**

3180

3181 This clade comprises Mantodea (praying mantids) and Blattodea (cockroaches, termites), their
3182 last common ancestor and all of its descendants (**Fig. 19**). Phylogenetic analysis of transcriptomes
3183 (Misof et al., 2014), mitochondrial genes (Legendre et al., 2015), and combined molecular and
3184 morphological data (Djernæs et al., 2015; Ware et al., 2008), support monophyly of Dictyoptera.

3185

3186 *82.1. Fossil specimens*

3187

3188 *Valditermes brenanae* Jarzembowski, 1981. BMNH In. 64588, holotype, preserving a forewing.

3189

3190 *82.2. Phylogenetic justification*

3191

3192 The position of *V. brenanae* was confirmed by morphological phylogenetic analysis (Engel et
3193 al., 2009). *V. brenanae* was resolved on the stem lineage of Mastotermitidae (Engel et al., 2009). This
3194 position was separately found for a congeneric species in the combined morphological and molecular
3195 phylogeny of Ware et al. (2010). Mastotermitidae is a monotypic family, sister to all other termites
3196 (Djernæs et al., 2015; Ware et al., 2010), so this phylogeny would also place *V. brenanae* in the
3197 crowns of Isoptera and Blattodea.

3198

3199 82.3. Age justification

3200

3201 The fossil is from the Clockhouse Brickworks pit site, Surrey, England (Jarzembowski, 1981).
3202 The Clockhouse Brickworks belongs to the Lower Weald Clay, as indicated by the presence of the
3203 ostracods *Cytheridea clavata*, *C. tuberculata*, and *C. valdensis* (Anderson, 1985). Of these, *C.*
3204 *tuberculata* has the narrowest range, and is restricted to the middle portion of the Lower Weald Clay,
3205 at BGS Bed 3a (Anderson, 1985; Ross and Cook, 1995). This faunal Zone is now assigned to the
3206 lower portion of the *C. pumila* Subzone of the *Theriosynoecum fittoni* Zone (Horne, 1995). Based on
3207 palynomorph stratigraphy, the boundary between Lower and Upper Weald Clay at the base of BGS
3208 Bed 3a corresponds accurately to the boundary between the Hauterivian and Barremian Stages (Ross
3209 and Cook, 1995). The upper boundary of the Hauterivian is 130.8 Ma \pm 0.5 Myr (Ogg et al., 2012a),
3210 therefore a minimum age of the Lower Weald Clay is 130.3 Ma.

3211 Soft maximum as for 75.3.

3212

3213 82.4. Discussion

3214

3215 There is ongoing debate over whether various Palaeozoic “roachoid” fossils, such as
3216 *Qilianiblattea namurensis* and *Homocladus grandis* Carpenter, 1966 (known only from wing venation
3217 characters), truly represent crown group members of Dictyoptera (e.g. Guan et al., 2016; Kjer et al.,
3218 2015; Legendre et al., 2015; Tong et al., 2015). If roachoids are indeed within crown group
3219 Dictyoptera, their antiquity may push back the origins of crown Dictyoptera and crown Polyneoptera by
3220 80-88 Myr (Legendre et al., 2015; Tong et al., 2015). However, wing venation alone may be insufficient
3221 to place most fossils within the crown group of Blattodea or even Dictyoptera. Particularly in
3222 cockroaches, asymmetry at the individual level and convergence at higher taxonomic levels are
3223 impediments to wing venation taxonomy, as well as the paucity of comparative venation data for extant
3224 species (e.g. Béthoux et al., 2010; Béthoux and Wieland, 2009; Garwood and Sutton, 2010; Gorochoy,

3225 2013; Guan et al., 2016).

3226 In the absence of detailed cladistic analysis of fossil roachoid wings together with extant
3227 Dictyoptera and other outgroups, we take the conservative view (Guan et al., 2016; Kjer et al., 2015;
3228 Prokop et al., 2014) that roachoids (including the family Anthracoptilidae/Strephocladidae, containing
3229 *H. grandis*) likely represent a diverse and speciose fauna on the stem group of Dictyoptera, perhaps
3230 with some members on the stem group of Neoptera or Polyneoptera (Grimaldi and Engel, 2005). At
3231 least some such roachoids may be used to calibrate crown group Polyneoptera (as done herein by
3232 assigning *Q. namurensis*), but they cannot calibrate crown Dictyoptera. As a consequence, many
3233 recent analyses have begun to rewrite the traditional assumption of extremely old crown ages for
3234 Dictyoptera, with crown origins likely in the Jurassic (Misof et al., 2014).

3235 Morphological phylogenetic analyses have excluded all Cretaceous fossils from the crown
3236 group of Mantodea, although they remain as likely crown Dictyoptera (Delclòs et al., 2016; Grimaldi,
3237 2003). Given that the analysed morphological matrix has fewer characters than taxa and has
3238 substantial missing data, it is not definitive (Delclòs et al., 2016). A recently discovered fossil from
3239 Crato (Aptian of Brazil), *Cretophotina santanensis* Lee, 2014, may be a stem group Chaeteessidae,
3240 which may be the most basal crown family of Mantodea (Svenson and Whiting, 2009). The position of
3241 Chaeteessidae may be within polyphyletic Mantidae (Legendre et al., 2015), but we exercise caution
3242 and do not place *C. santanensis* in the crown group, as recommended by Lee (2014).

3243

3244 **83. Crown Blattodea**

3245

3246 This clade comprises Lamproblattidae, Blaberoidea, Blattidae, Nocticolidae, Polyphagidae,
3247 Cryptocercidae and Isoptera, their last common ancestor and all of its descendants (**Fig. 19**). The
3248 position of Isoptera (termites) within a paraphyletic Blattodea was first identified by Inward et al. (2007)
3249 with six molecular loci. Further support for the monophyly of the new concept of Blattodea comes from
3250 transcriptomes (Misof et al., 2014), mitochondrial genes (Legendre et al., 2015), housekeeping genes

3251 (Djernæs et al., 2012), and combined molecular and morphological data (Djernæs et al., 2015; Ware
3252 et al., 2008).

3253

3254 83.1. *Fossil specimens*

3255

3256 As for 82.1.

3257

3258 83.2. *Phylogenetic justification*

3259

3260 As for 82.2.

3261

3262 83.3. *Age justification*

3263

3264 As for 82.3.

3265

3266 83.4. *Discussion*

3267

3268 *Baissatermes lapideus* Engel et al., 2007 is a crown group member of Isoptera, and
3269 *Mastotermes nepropadyom* Vršanský and Aristov, 2014 is crown Blattodea (Engel et al., 2016a); both
3270 have been used to calibrate Isoptera and Blattodea (Djernæs et al., 2015; Ware et al., 2010). Note that
3271 fossil *Mastotermes* are likely polyphyletic (Engel et al., 2016a). Although these are appropriate
3272 calibration fossils, they are not the oldest Blattodea. *B. lapideus* is from the Zaza Formation
3273 (Transbaikalian Russia), and *M. nepropadyom* is from Chernovskie Kopi, also in Transbaikalia and
3274 similar in age to the Turga Formation (Sukatsheva and Vassilenko, 2011; Vršanský and Aristov, 2014).
3275 The Turga Formation has been correlated to the Baissa locality, Zaza Formation; this is based on
3276 shared presence of *Asteropollis asteroides* spores (Vakhrameev and Kotova, 1977). As discussed in

3277 section 86.3, the Zaza Formation may be much younger than initially described, with a minimum age
3278 of Campanian (71.9 Ma). Therefore both Russian fossils are younger than *V. brenanae*.

3279

3280 **84. Crown Eumetabola**

3281

3282 This clade comprises Condylgnatha, Psocodea and Holometabola, their last common
3283 ancestor and all of its descendants (**Fig. 21**). Monophyly of the clade is supported by transcriptomes
3284 (Letsch and Simon, 2013; Misof et al., 2014) and protein-coding genes (Ishiwata et al., 2011). Some
3285 morphological analyses do not support monophyly of Eumetabola (Kristensen, 1981; Wheeler et al.,
3286 2001), although it is recovered (Kristensen, 1991; Kukalová-Peck, 1991) and assumed (Yoshizawa
3287 and Saigusa, 2001) in other analyses. Note also that support for Psocodea as the sister clade of
3288 Holometabola was statistically weak in analyses of transcriptomes (Misof et al., 2014), although
3289 monophyly of Eumetabola was well supported.

3290

3291 *84.1. Fossil specimens*

3292

3293 As for 74.1.

3294

3295 *84.2. Phylogenetic justification*

3296

3297 As for 74.2.

3298

3299 *84.3. Age justification*

3300

3301 Minimum as for 74.3. Soft maximum as for 75.3.

3302

3303 **85. Crown Condylgnatha**

3304

3305 This clade comprises Hemiptera (true bugs) and Thysanoptera (thrips), their last common
3306 ancestor and all of its descendants (**Fig. 21**). Monophyly is determined by phylogenetic analysis of
3307 transcriptomes (Misof et al., 2014), nuclear protein-coding genes (Ishiwata et al., 2011), and wing
3308 morphology (Yoshizawa and Saigusa, 2001).

3309

3310 *85.1. Fossil specimens*

3311

3312 *Aviorrhyncha magnifica* Nel et al., 2013, holotype Avion No. 2 (provisionally stored in the
3313 collection of Entomological Laboratory, MNHN; to be deposited in the Musée Géologique Pierre Vetter,
3314 Decazeville, France), preserving a single forewing (**Fig. 22a**).

3315

3316 *85.2. Phylogenetic justification*

3317

3318 Nel et al. (2013) diagnose *A. magnifica* as stem Euhemiptera (the clade sister to
3319 Sternorrhyncha containing all other living Hemiptera; Cryan and Urban, 2012; Cui et al., 2013). At least
3320 two forewing characters in *A. magnifica* are synapomorphies of Euhemiptera, including presence of an
3321 ambient vein and a well-developed concave CP (its presence is a synapomorphy) (Nel et al., 2013).
3322 Unlike many extant Euhemiptera, the cua-cup vein is not zigzagged. Given that much of fossil insect
3323 taxonomy is conducted with only preserved wings, an assignment to the crown group of Hemiptera
3324 and thus Condylgnatha is reasonable.

3325

3326 *85.4. Age justification*

3327

3328 *A. magnifica* was found in “Terril No. 7”, a layer containing rocks from the slag heap of coal

3329 mines 3 and 4 of Liévin, in the Avion outcrop of Pas-de-Calais, France (Nel et al., 2013). The coal
3330 mines are dated to the Westphalian C/D, or Bolsovian/Asturian, which has a youngest boundary
3331 equivalent to the latest Moscovian stage of the Pennsylvanian (Nel et al., 2013; Richards, 2013). As
3332 the upper boundary of the Moscovian is $307.0 \text{ Ma} \pm 0.1 \text{ Myr}$, this provides a minimum age of 306.9
3333 Ma.

3334 Soft maximum as for 75.3.

3335

3336 **86. Crown Thysanoptera**

3337

3338 This clade comprises Tubulifera and Terebrantia, their last common ancestor and all of its
3339 descendants (**Fig. 21**). Monophyly is established based on phylogenetic analysis of transcriptomes
3340 (Misof et al., 2014) and five nuclear protein-coding genes (Buckman et al., 2013). There is no
3341 adequate phylogenetic test of thysanopteran monophyly using morphology (reviewed by Mound and
3342 Morris, 2007).

3343

3344 *86.1. Fossil specimens*

3345

3346 *Fusithrips crassipes* Shmakov, 2009. PIN 3064/8547, holotype, preserving a female body (**Fig.**
3347 **22b**).

3348

3349 *86.2. Phylogenetic justification*

3350

3351 *F. crassipes* has not been included in a phylogenetic analysis, however, Shmakov (2009)
3352 describes characters placing it in the crown of Thysanoptera. In particular, Rs1 and M2 as crossveins
3353 rather than oblique veins suggest membership in the family Aeolothripidae (Shmakov, 2009). Whether
3354 crown or stem Aeolothripidae, the family is a part of Terebrantia, indicating crown group membership in

3355 Thysanoptera.

3356

3357 86.3. Age justification

3358

3359 The fossil *F. crassipes* was found in Layer 31 on the left bank of the Vitim River, 3 km
3360 downstream from the mouth of the Baissa River, Buryatia, Transbaikalian Russia (Shmakov, 2009).
3361 The fossiliferous lacustrine deposits are part of the Zaza Formation, Baissa locality. The Zaza
3362 Formation was once assigned to the Valanginian, based on correlation of fossil insect species,
3363 however palynological data from the appearance of *Asteropollis* spores suggests a younger date
3364 (O'Reilly et al., 2015; Zherikhin et al., 1998). *A. asteroides*, one of the earliest angiosperms, has a
3365 worldwide distribution during the Early and mid Cretaceous (Friis et al., 2005), and has been
3366 biostratigraphically assigned to the Barremian-Aptian (Friis et al., 1999; Zherikhin et al., 1998). This
3367 range has since been completely revised to Albian-Campanian, on the basis of pollen morphology
3368 (Doyle and Endress, 2014) and younger appearances of *Asteropollis* (Dettmann and Thomson, 1987;
3369 Eklund et al., 2004; Martínez et al., 2013). A minimum age can thus be estimated by the upper
3370 boundary of the Campanian, 72.1 Ma \pm 0.2 Myr, or 71.9 Ma.

3371 Soft maximum as for 75.3.

3372

3373 86.4. Discussion

3374

3375 *Triassothrips virginicus* Grimaldi et al., 2004 was described from the Late Triassic of Virginia.
3376 Although it was used as a calibration for Thysanoptera by Misof et al. (2014), *T. virginicus* is found in a
3377 basal polytomy outside of any crown group members in a morphological phylogeny (P. Nel et al.,
3378 2012). *Liassothrips crassipes* Martynov, 1927 is known from the Late Jurassic of Kazakhstan, but is
3379 classified in an extinct family, Liassothripidae (Shmakov, 2008). While Shmakov (2008) suggests
3380 Liassothripidae is the oldest family in the Tubulifera, making it crown Thysanoptera, characters are

3381 also listed linking it with Terebrantia; without a phylogenetic analysis it is difficult to assess their
3382 polarity and thus crown affinity.

3383

3384 **87. Crown Hemiptera**

3385

3386 This clade comprises Sternorrhyncha (aphids, scale insects), Fulgoromorpha (planthoppers),
3387 Cicadomorpha (cicadas, leafhoppers, treehoppers), Coleorrhyncha (moss bugs) and Heteroptera
3388 (typical bugs), their last common ancestor and all of its descendants (**Fig. 21**). Monophyly of
3389 Hemiptera is established by phylogenetic analysis of housekeeping genes (Cryan and Urban, 2012),
3390 whole mitochondrial genomes (Cui et al., 2013), transcriptomes (Misof et al., 2014; Simon et al.,
3391 2012), and wing morphology (Yoshizawa and Saigusa, 2001).

3392

3393 *87.1. Fossil specimens*

3394

3395 As for 85.1.

3396

3397 *87.2. Phylogenetic justification*

3398

3399 As for 85.2.

3400

3401 *87.3. Age justification*

3402

3403 As for 85.3.

3404

3405 **88. Crown Psocodea**

3406

3407 This clade comprises Psocoptera (barklice) and Phthiraptera (true lice), their last common
3408 ancestor and all of its descendants (**Fig. 21**). Monophyly of this clade is supported by phylogenies of
3409 transcriptomes (Misof et al., 2014), nuclear protein-coding genes (Ishiwata et al., 2011), mitochondrial
3410 genes (Yoshizawa and Johnson, 2003), and morphology (Lyal, 1985).

3411

3412 *88.1. Fossil specimens*

3413

3414 *Cretoscelis burmitica* Grimaldi and Engel, 2006. AMNH Bu912, holotype, female in amber.

3415

3416 *88.2. Phylogenetic justification*

3417

3418 In a morphological phylogenetic analysis, *C. burmitica* was a stem group member of
3419 Liposcelididae (Grimaldi and Engel, 2006). Liposcelididae is an extant family of Psocoptera, thus
3420 within the crown group of Psocodea.

3421

3422 *88.3. Age justification*

3423

3424 As for 81.3.

3425

3426 **89. Crown Holometabola**

3427

3428 This clade comprises Hymenoptera (sawflies, ants, bees, wasps) and Aparaglossata, their last
3429 common ancestor and all of its descendants (**Figs. 23 and 24**). Support for monophyly comes from
3430 phylogenetic analysis of transcriptomes (Misof et al., 2014; Peters et al., 2014), morphology (Beutel et
3431 al., 2011), and morphology plus molecules (Oakley et al., 2013). This clade exists in GenBank, but as
3432 Endopterygota.

3433

3434 89.1. *Fossil specimens*

3435

3436 *Westphalomerope maryvonneae* Nel et al., 2007. MNHN-LP-R.55181, holotype, preserving a
3437 hindwing. Pictured in Nel et al. (2007; Fig. 1a).

3438

3439 89.2. *Phylogenetic justification*

3440

3441 *W. maryvonneae* has not been included in a phylogenetic analysis, nor have any other
3442 members of its family, Protomeropidae. Mostly Permian members of Protomeropidae have been
3443 proposed to have affinities with a variety of holometabolan clades, including the total groups of
3444 Trichoptera, Mecoptera, and more generally Amphiesmenoptera or Antliophora (Grimaldi and Engel,
3445 2005; Kukalova-Peck and Willmann, 1990; Morse, 1997; Nel et al., 2013, 2007; Sukatsheva et al.,
3446 2007). Crown amphiesmenopteran (and thus trichopteran) affinity may be unlikely, as Protomeropidae
3447 lack a key synapomorphy, a true 'double-Y loop' arrangement of the anal veins on the forewing
3448 (Labandeira, 2011; Minet et al., 2010). However, Permian Protomeropidae possess Carpenter's
3449 organs in the male, a probable apomorphy for total group Mecoptera (Minet et al., 2010).
3450 Protomeropidae (with a younger date) was subsequently used to calibrate the basal split of
3451 Mecopterida for divergence time estimation (Rehm et al., 2011). Pending phylogenetic analysis of
3452 wing morphology, it is difficult to assign a specific placement for Protomeropidae, however, even with a
3453 conservative view all these possibilities are within crown Aparaglossata, and therefore crown
3454 Holometabola.

3455

3456 89.3. *Age justification*

3457

3458 *W. maryvonneae* was collected from black shales in the "Terril no. 5" horizon at the "Faisceau

3459 de Modeste", "Veine Maroc" locality in Bruay-la-Bussière, Pas-de-Calais, France (Nel et al., 2007).
3460 The locality is dated as early Langsettian (Nel et al., 2007), equivalent to the Westphalian A stage
3461 (Pointon et al., 2012). There is a SHRIMP U-Pb date within the middle Langsettian estimated at
3462 317.63 Ma \pm 0.12 Myr, however, the stratigraphy of Bruay-la-Bussière is not precise enough to
3463 determine when in the Westphalian A the fossil occurred (Nel et al., 2007; Pointon et al., 2012).
3464 Therefore, we use a date inclusive of the upper boundary of the Westphalian A, which is the upper
3465 boundary of Westphalian B. U-Pb dating of zircons constrains the upper boundary of the Westphalian
3466 B to 313.78 Ma \pm 0.08 Myr (Pointon et al., 2012), so a minimum age for *W. maryvonneae* is 313.70
3467 Ma.

3468 Soft maximum as for 75.3.

3469

3470 89.4. Discussion

3471

3472 *Srokalarva berthei* Haug et al., 2015 is a putative holometabolan larva, from the Mazon Creek
3473 and thus younger than *W. maryvonneae*. *S. berthei* has been interpreted as both an antliophoran
3474 (Labandeira, 2011) and a neuropterid (Haug et al., 2015), both positions within the crown group of
3475 Holometabola. *S. berthei*, however, remains informative about the evolutionary timing of insect
3476 metamorphosis.

3477

3478 90. Crown Hymenoptera

3479

3480 This clade comprises Symphyta (sawflies) and Apocrita (itself comprising Apoidea, Formicidae,
3481 and a paraphyletic group of wasps), their last common ancestor and all of its descendants (**Fig. 23**).
3482 Monophyly is supported by phylogenetic analysis of transcriptomes (Misof et al., 2014), morphology
3483 (Beutel et al., 2011), and morphology analysed together with molecular data (Ronquist et al., 2012).

3484

3485 90.1. Fossil specimens

3486
3487 *Triassoxyela foveolata* Rasnitsyn, 1964. PIN 2070/1, holotype (**Fig. 25a**).
3488

3489 90.2. Phylogenetic justification

3490
3491 In the total-evidence phylogenetic analysis of Ronquist et al. (2012), *T. foveolata* was found as
3492 a stem group member of the family Xyelidae. As Xyelidae is a crown group family of sawflies, it is thus
3493 crown Hymenoptera.
3494

3495 90.3. Age justification

3496
3497 *T. foveolata* was found in the Madygen Formation, south of the Fergana Valley, Kyrgyzstan.
3498 Key plant fossils *Scytophyllum* and *Neocalamites* correlate the Madygen to the *Scytophyllum* flora of
3499 the upper Keuper lithographic unit, of Ladinian-Carnian age (Dobruskina, 1995). The *Scytophyllum*
3500 flora is correlated with the Cortaderitian Stage of Gondwana due to the abundance of *Scytophyllum*
3501 (Morel et al., 2003). The Cortaderitian Stage is divided into 3 Biozones; a ⁴⁰Ar/³⁹Ar radiometric date
3502 for the middle biozone of the Cortaderitian Stage of 228.5 Ma ± 0.3 Myr was measured by Rogers et
3503 al. (1993), falling within the Carnian (O'Reilly et al., 2015). The Gondwanan Puesto Viejo Formation,
3504 part of the Barrealian Stage underlying the Cortaderitian Stage (and therefore the *Scytophyllum* flora)
3505 has been radiometrically dated to 232 Ma ± 4 Myr, also within the Carnian (Valencio et al., 1975).
3506 Recently calculated SHRIMP U-Pb dates dispute this age, instead constraining the Puesto Viejo
3507 Formation to 235.8 Ma ± 2.0 Myr (Ottone et al., 2014). This suggests the Cortaderitian Stage is no
3508 older than 237.8 Ma, and therefore the *Scytophyllum* flora and Madygen Formation can be no older
3509 than this age, still within the Carnian. Note that a GSSP for the Carnian-Norian boundary has not yet
3510 been identified; radioisotopic ages may suggest a younger boundary at ~220 Ma (Lucas et al., 2012).

3511 Nevertheless, a commonly accepted date for the Carnian upper boundary is estimated at 228.4 Ma \pm
3512 2 Myr based on cyclostratigraphy and a candidate GSSP (e.g. Ogg, 2012; Ogg et al., 2014), so this
3513 provides a minimum age at 226.4 Ma.

3514 Soft maximum as for 75.3.

3515

3516 90.1 Discussion

3517

3518 Previous work has suggested *Archexyela* ipswichensis Engel, 2005 from the Mt. Crosby
3519 Formation, Ipswich Coal Measures of Queensland, Australia may be the oldest hymenopteran (e.g.
3520 Nicholson et al., 2015). However, the stratigraphy of the Ipswich Basin also provides a minimum age
3521 of uppermost Carnian (Purdy and Cranfield, 2013), thus we calibrate crown Hymenoptera with the
3522 equally old *T. foveolata*, which has been included in landmark total-evidence phylogenies (O'Reilly et
3523 al., 2015; Ronquist et al., 2012).

3524

3525 91. Crown Aparaglossata

3526

3527 This clade comprises Neuropterida, Coleopterida and Mecopterida, their last common ancestor
3528 and all of its descendants (**Fig. 23**). The clade was first named by Peters et al. (2014) based on
3529 support from phylogenetic analysis of transcriptomes.

3530

3531 91.1. Fossil specimens

3532

3533 As for 89.1.

3534

3535 91.2. Phylogenetic justification

3536

3537 As for 89.2.

3538

3539 91.3. *Age justification*

3540

3541 As for 89.3.

3542

3543 **92. Crown Neuropterida**

3544

3545 This clade comprises Raphidioptera (snakeflies), Megaloptera (fishflies), Neuroptera (net-
3546 winged insects), their last common ancestor and all of its descendants (**Fig. 23**). Monophyly is
3547 established by phylogenetic analysis of transcriptomes (Misof et al., 2014; Peters et al., 2014), protein-
3548 coding genes (Wiegmann et al., 2009), morphology (Beutel et al., 2011), and combined molecular and
3549 morphological data (Winterton et al., 2010).

3550

3551 92.1. *Fossil specimens*

3552

3553 *Elmothone martynovae* Carpenter, 1976. MCZ 5585, holotype, a forewing (**Fig. 25b**). Figured
3554 by Prokop et al. (2015; Fig. 7A).

3555

3556 92.2. *Phylogenetic justification*

3557

3558 A morphological phylogenetic analysis placed the Permithonidae *sensu lato* as a stem group to
3559 the extant Neuroptera (Ren et al., 2009; shown in supplementary information therein). A position on
3560 the stem lineage of Neuroptera is thus part of the crown group of Neuropterida. As the coding was
3561 done at a family level, we note with caution that monophyly of the Permithonidae and the exact
3562 relationships of its member species with Neuroptera has not been examined in a phylogenetic context

3563 and remain obscure (Prokop et al., 2015). Nonetheless, most members of Permithonidae possess the
3564 character states coded by Ren et al. (2009), so we take the oldest well-described member, *E.*
3565 *martynovae*, as a calibration fossil.

3566

3567 92.3. Age justification

3568

3569 This fossil occurs in the Carlton Limestone Member of the Wellington Formation in the Sumner
3570 Group of Elmo, Dickinson County, central Kansas (Prokop et al., 2015; Zambito et al., 2012). The
3571 insect-bearing locality is correlated with the Leonardian regional Stage (Sawin et al., 2008; Zambito et
3572 al., 2012) on the basis of conchostracan biostratigraphy (Tasch, 1962). The Leonardian spans the
3573 Artinskian and the younger Kungurian Stage (Henderson et al., 2012). The upper boundary of the
3574 Kungurian is $272.3 \text{ Ma} \pm 0.5 \text{ Myr}$, thus providing a conservative minimum age estimate of 271.8 Ma.

3575 Soft maximum as for 75.3.

3576

3577 92.4. Discussion

3578

3579 A younger member of the Permithonidae, *Permithone belmontensis* Tillyard, 1922
3580 (Changhsingian or latest Permian of Belmont, Australia), was previously used as a calibration fossil for
3581 Neuropterida (Misof et al., 2014).

3582

3583 93. Crown Megaloptera

3584

3585 This clade comprises Sialidae and Corydalidae, their last common ancestor and all of its
3586 descendants (**Fig. 23**). Monophyly is established by phylogenetic analysis of full mitochondrial
3587 genomes (Wang et al., 2012), transcriptomes (Misof et al., 2014), and morphology of the wing base
3588 (Zhao et al., 2014).

3589

3590 93.1. *Fossil specimens*

3591

3592 *Eochauliodes striolatus* Liu et al., 2012. CNU-MEG-NN2011004 P/C, holotype part/counterpart,
3593 laterally preserving an adult including forewing and hindwing (**Fig. 25c**).

3594

3595 93.2. *Phylogenetic justification*

3596

3597 *E. striolatus* was included in a phylogenetic analysis of morphology, encompassing characters
3598 from wing venation, adult genitalia, and larval morphology where possible (Liu et al., 2012). *E.*
3599 *striolatus* was found within the crown Corydalidae, at the base of the 'Protochauliodes clade'
3600 (comprising extant species). This position is therefore within crown Megaloptera. The bifurcated
3601 anterior branch of the Rs vein is a relevant synapomorphy (Liu et al., 2012).

3602

3603 93.3. *Age justification*

3604

3605 As for 79.3.

3606

3607 93.4. *Discussion*

3608

3609 Another fossil from the Daohugou fauna, *Jurochauliodes ponomarenkoi* Wang and Zhang,
3610 2010 was found in a slightly more basal position within the Corydalidae (and thus Megaloptera) crown
3611 group (Liu et al., 2012). As it is of equal age to *E. striolatus*, it is also an acceptable calibration fossil
3612 for this clade.

3613

3614 **94. Crown Neuroptera**

3615

3616 This clade comprises Hemerobiiformia, Nevrothiformia and Myrmeleontiformia, their last
3617 common ancestor and all of its descendants (**Fig. 23**). Monophyly is supported by phylogenetic
3618 analysis of ribosomal and mitochondrial genes (Haring and Aspöck, 2004), housekeeping genes
3619 (Wiegmann et al., 2009), and morphology (Beutel et al., 2011; Zhao et al., 2014).

3620

3621 *94.1. Fossil specimens*

3622

3623 *Liassochrysa stigmatica* Ansorge and Schlüter, 1990. MBA.I 5046 (formerly from the Ansorge
3624 collection, Dobbertin, Germany: No. LDA301), holotype, preserving a forewing. Imaged in (Wedmann
3625 and Makarkin, 2007: Fig. 5a).

3626

3627 *94.2. Phylogenetic justification*

3628

3629 *L. stigmatica* was coded in the morphological matrix for the total evidence phylogeny of Liu et
3630 al. (2015). In that tree, it was a member of crown group Mantispidae, a family within Hemerobiiformia,
3631 and therefore crown Neuroptera (Liu et al., 2015). This fossil was also the oldest calibration used for
3632 Neuroptera in the divergence time analysis of Winterton et al. (2010).

3633

3634 *94.3. Age justification*

3635

3636 The fossil was recovered from the former clay pit of Schwinz, near Dobbertin, Mecklenburg,
3637 northeast Germany (Ansorge and Schlüter, 1990). Multiple associated ammonites (*Eleganticeras*
3638 *elegantulum*, *Lobolytoceras siemensii*, *Harpoceras capellatum*) indicate that the locality is correlated to
3639 the lower part of the *H. falciferum* ammonite Zone, early Toarcian (Ansorge and Schlüter, 1990;
3640 O'Reilly et al., 2015; Pálffy et al., 2002, 2000). The Boreal *falciferum* Zone is equivalent to the Tethyan

3641 *H. serpentinum* ammonoid Zone (Macchioni, 2002), and succeeded by the *Hildoceras bifrons*
3642 ammonoid Zone. The base of the *bifrons* Zone has been dated to 180.36 Ma \pm 0.7 Myr (Ogg et al.,
3643 2012b). From this, an upper boundary of the *falciferum* Zone can be derived, and thus a minimum age
3644 for Dobbertin, at 179.66 Ma.

3645 Soft maximum as for 75.3.

3646

3647 **95. Crown Coleoptera**

3648

3649 This clade comprises Strepsiptera (twisted wing parasites) and Coleoptera (beetles), their last
3650 common ancestor and all of its descendants (**Fig. 23**). Monophyly of this clade is an extremely well-
3651 examined question in systematics, often used to illustrate the principle of long branch attraction (e.g.
3652 Boussau et al., 2014; Carmean and Crespi, 1995; Huelsenbeck, 1998, 1997; Niehuis et al., 2012;
3653 Siddall and Whiting, 1999; Whiting et al., 1997; Wiegmann et al., 2009). However, recent analyses of
3654 genomes and transcriptomes have consistently converged on a sister group relationship between
3655 Strepsiptera and Coleoptera (Boussau et al., 2014; Misof et al., 2014; Niehuis et al., 2012).

3656

3657 *95.1. Fossil specimens*

3658

3659 *Adiphebia lacoana* Scudder, 1885. USNM 38140, holotype, preserving a forewing. Imaged in
3660 Béthoux (2009: Fig. 1(3-5)).

3661

3662 *95.2. Phylogenetic justification*

3663

3664 *A. lacoana* has not been included in formal cladistic analysis to test its phylogenetic position.
3665 Variation in forewing venation within species provides a challenge to homology statements (Béthoux,
3666 2009; Garwood and Sutton, 2010). However, *A. lacoana* shares a forewing character with the crown

3667 beetle suborder Archostemata, specifically: "the areas between ScP, RA, branches of RP, M, branches
3668 of CuA, and AA filled with a regular network of quadrangular to pentagonal cells forming intercalary
3669 longitudinal pseudo-veins" (Béthoux, 2009). Intercalary pseudo-veins are also observed in fossils
3670 throughout Pterygota, suggesting this is either a symplesiomorphic or homoplastic state. However,
3671 some of the wing regions exhibiting intercalary veins (ScP and RA) are restricted to fossil Coleoptera
3672 (Béthoux, 2009). *A. lacoana* has thus been designated as a sister group to all crown Coleoptera, i.e. a
3673 member of its stem lineage (Béthoux, 2009), and thus a crown group member of Coleopterida. This
3674 assignment is also supported by putative larval material (Labandeira, 2011).

3675 There has been debate, however, about the taphonomy of the network of wing veins,
3676 suggesting they are clumps of clay instead of morphological characters (Kukalova-Peck and Beutel,
3677 2012). Alternative placements were on the stem lineage of Neuroptera or Neuropterida (Kukalova-
3678 Peck and Beutel, 2012), or outside Holometabola altogether (Guan et al., 2016; Nel et al., 2013).

3679

3680 95.3. *Age justification*

3681

3682 Minimum as for 31.3. Soft maximum as for 75.3.

3683

3684 **96. Crown Coleoptera**

3685

3686 This clade comprises Archostemata, Myxophaga, Adephaga (ground beetles, tiger beetles,
3687 diving beetles, whirligig beetles) and Polyphaga (ladybugs, longhorn beetles, weevils, fireflies,
3688 scarabs, stag beetles, rove beetles), their last common ancestor and all of its descendants (**Fig. 23**).
3689 Monophyly is supported by phylogenetic analysis of nuclear protein-coding genes (McKenna et al.,
3690 2015) and morphology (Beutel et al., 2011).

3691

3692 96.1. *Fossil specimens*

3693

3694 *Triadogyrus sternalis* Ponomarenko, 1977. PIN 3320/13, holotype (**Fig. 25d**), an exoskeleton
3695 without head, prothorax, or legs (Arnol'di et al., 1992).

3696

3697 96.2. *Phylogenetic justification*

3698

3699 In the morphological phylogenetic analysis of Beutel et al. (2013), *T. sternalis* is a stem group
3700 member of the family Gyrinidae. As Gyrinidae is part of Adephaga, crown membership within both
3701 Adephaga and Coleoptera is justified.

3702

3703 96.3. *Age justification*

3704

3705 *T. sternalis* was recovered from the mouth of Bereni River near Garazhokva settlement,
3706 Khar'kov oblast, Izyum region, Ukraine (Arnol'di et al., 1992). Fossiliferous strata are lacustrine
3707 claystone, part of the Protopivka Formation, estimated as Late Carnian-Early Norian age within the
3708 late Triassic (Arnol'di et al., 1992; Rasnitsyn and Quicke, 2002; Shcherbakov, 2008). The upper Norian
3709 boundary is estimated at ~208.5 Ma, so this provides a conservative minimum age.

3710 Soft maximum as for 75.3.

3711

3712 96.4. *Discussion*

3713

3714 The Pennsylvanian (Mazon Creek) fossil *A. lacoana* is a member of the stem lineage of
3715 Coleoptera (Béthoux, 2009). Recent divergence time analyses (McKenna et al., 2015; Misof et al.,
3716 2014) have therefore elected not to calibrate the crown group of Coleoptera with *A. lacoana*. Resulting
3717 age estimates for crown Coleoptera ranged from 250-280 Ma, substantially younger than *A. lacoana*
3718 itself.

3719 The Permian *Coleopsis archaica* Kirejtshuk et al., 2014 was noted as a stem group fossil,
3720 potentially Protocoleoptera (stem Coleoptera) (McKenna et al., 2015). Thus it was not used as a
3721 calibration. However, using younger internal calibrations (the oldest from Madygen, 225 Ma in their
3722 dataset), the crown origin of Coleoptera was estimated around 250 Ma (McKenna et al., 2015).
3723 Accounting for error bars, the crown group may have originated shortly before (or shortly after) the
3724 end-Permian extinction, timing that is compatible with *C. archaica* as a very early representative.

3725

3726 **97. Crown Mecopterida**

3727

3728 This clade comprises Amphiesmenoptera and Antliophora, their last common ancestor and all
3729 of its descendants (**Fig. 24**). Phylogenetic support for monophyly of Mecopterida comes from
3730 genomes (Niehuis et al., 2012), transcriptomes (Misof et al., 2014) and morphology (Beutel et al.,
3731 2011). Note that the clade we refer to as Mecopterida was called Panorpida by Grimaldi and Engel
3732 (2005), because they used Mecopterida to refer to paraphyletic Mecoptera containing Siphonaptera
3733 (and excluding Diptera). Our clade Mecopterida was also referred to as Panorpoidea by several
3734 sources, including Ren et al. (2009). Analyses relying on molecular data alone do not support the
3735 paraphyly of Mecoptera (Misof et al., 2014; Peters et al., 2014; Wiegmann et al., 2009), and these
3736 tend to utilize our conception of Mecopterida.

3737

3738 *97.1. Fossil specimens*

3739

3740 *Permopanorpa inaequalis* Tillyard, 1926. YPM IP 005058, holotype, a wing (**Fig. 25e**).

3741

3742 *97.2. Phylogenetic justification*

3743

3744 *P. inaequalis* is the oldest member of the family Permopanorpidae, which was coded (at the

3745 family level) in the morphological matrix of Ren et al. (2009). In that tree, it was part of the total group
3746 of Antliophora (although the figure label indicated it was inside crown Antliophora, the topology clearly
3747 indicates it was on the stem lineage; Ren et al., 2009). As a stem group member of Antliophora, *P.*
3748 *inaequalis* is thus crown group Mecopterida.

3749

3750 97.3. Age justification

3751

3752 As for 92.3.

3753

3754 97.4. Discussion

3755

3756 *W. maryvonneae* (family Protomeropidae), from the Bashkirian of France, has been proposed
3757 as an “amphiesmenopteran or antliophoran”, which may mean it belongs on the stem lineage of one of
3758 those clades and thus in crown Mecopterida. It has also been drawn onto a phylogram as a stem
3759 member of Mecoptera (Nel et al., 2013). However, the evidence for any particular placement within
3760 Mecopterida is ambiguous, and thus it is possible the fossil is only stem Mecopterida. See 89.2 for
3761 greater detail.

3762 Conversely, the early to middle Permian family Kaltanidae has been included in a phylogenetic
3763 analysis, and shown to fall on the stem lineage of Amphiesmenoptera (Ren et al., 2009). Although
3764 Kaltanidae have been previously discussed as calibration fossils for Mecopterida (e.g. Benton and
3765 Donoghue, 2007), their oldest members are from the Kungurian Stage of Russia, the same age as
3766 Elmo (Bashkuev, 2008). Additionally, the family Belmontiidae is within crown Mecopterida in a
3767 phylogenetic analysis (Ren et al., 2009), but its oldest fossil is from the late Permian (Changhsingian)
3768 of Australia (Grimaldi and Engel, 2005).

3769

3770 98. Crown Amphiesmenoptera

3771

3772 This clade comprises Trichoptera (caddisflies) and Lepidoptera (butterflies, moths), their last
3773 common ancestor and all of its descendants (**Fig. 24**). Monophyly is supported by phylogenetic
3774 analysis of transcriptomes (Misof et al., 2014), nuclear protein-coding genes (Wiegmann et al., 2009),
3775 and morphology (Beutel et al., 2011; Kristensen, 1991).

3776

3777 *98.1. Fossil specimens*

3778

3779 *Archaeolepis mane* Whalley, 1985. BMNH In. 59397, holotype, preserving a hindwing (**Fig.**
3780 **25f**).

3781

3782 *98.2. Phylogenetic justification*

3783

3784 *A. mane* has been used to calibrate the lepidopteran root in previous molecular dating
3785 analyses (e.g. Wahlberg et al., 2013), where this relationship is based on two lines of evidence: wing
3786 scales and wing venation. The preservation of extremely rare scales completely covering the hindwing
3787 excludes *A. mane* from crown Trichoptera (Whalley, 1986, 1985) because Trichoptera only bear scales
3788 on the forewing. The presence of scales across the entirety of a wing with panorpoid venation can only
3789 signal amphiesmenopteran affinity.

3790 The Sc vein (with one visible branch) of *A. mane* is unlikely to represent the ancestral state for
3791 Lepidoptera, as the number of Sc vein branches varies in early-diverging moths, but is usually two
3792 branches, and this vein is multi-branched ancestrally in Amphiesmenoptera (Kukalova-Peck and
3793 Willmann, 1990; Minet et al., 2010; Sukatsheva and Vassilenko, 2011; Schachat and Brown, 2016).
3794 Although Trichoptera tend to have more wing veins than Lepidoptera, it is likely that fewer veins were
3795 lost by ancestral moths than is currently accepted in the literature, making distinctions between
3796 amphiesmenopteran branches difficult for Mesozoic fossils (Schachat and Brown, 2015, 2016). As

3797 reconstructed by Whalley (1986), the wing venation of *A. mane* differs markedly from the venation of
3798 crown Lepidoptera: there is a single, branched Cubitus vein, with CuP apparently absent, and all three
3799 branches of the anal vein reach the dorsum. In contrast, basal crown Lepidoptera nearly always have
3800 a CuP vein, and the anal vein becomes fused before reaching the dorsum (Common, 1973; Schachat
3801 and Brown, 2016). A position for *A. mane* within the crown group of Lepidoptera thus cannot be
3802 confirmed, but an identity as stem Lepidoptera is highly likely based on the wing scales in particular, in
3803 agreement with Whalley (1986). This fossil would therefore be within the crown group of
3804 Amphiesmenoptera.

3805

3806 98.3. Age justification

3807

3808 Whalley (1985) noted the locality as Black Ven, Charmouth, Dorset, on the Jurassic Coast of
3809 England. This was further specified as calcareous flatstone, probably from Bed 75a, of the *Caenisites*
3810 *turneri* ammonoid Zone (Sohn et al., 2012), or *Microderoceras birchi* Nodular of the “Shales with Beef”
3811 (Lang et al., 1923). Chemostratigraphy places the *C. turneri* (and *M. birchi*) Zones within the middle
3812 Sinemurian (Jenkyns et al., 2002). The upper boundary of the *C. turneri* Zone is thus dated to 195.31
3813 Ma (Ogg et al., 2012b), providing a minimum age.

3814 Soft maximum as for 75.3.

3815

3816 99. Crown Trichoptera

3817

3818 This clade comprises 'Spicipalpia', Annulipalpia and Integripalpia their last common ancestor
3819 and all of its descendants (**Fig. 24**). Monophyly is supported by phylogenetic analysis of
3820 transcriptomes (Misof et al., 2014), housekeeping genes (Kjer et al., 2002, 2001; Malm et al., 2013),
3821 and morphology (Beutel et al., 2011).

3822

3823 99.1. *Fossil specimens*

3824

3825 *Liadotaulius maior* Handlirsch, 1906. Handlirsch (1906) did not designate a holotype, thus we
3826 refer to three specimens figured by Ansorge (2002): (Ansorge collection, to be deposited at MBA: LGA
3827 1995; **Fig. 25g**), female forewing, (LGA 672), male forewing, and (LGA 1710), hindwing.

3828

3829 99.2. *Phylogenetic justification*

3830

3831 Taxonomic placement of *L. maior* requires apomorphies from the male wings, as female wings
3832 have many plesiomorphic venation characters (Ansorge, 2002). Further studies of a younger
3833 congeneric, *L. daohugouensis* Wu and Huang, 2012, reveal new characters shared with crown group
3834 Trichoptera. These include the apical part of Cu2 bending towards the wing margin, its
3835 desclerotisation, and complete anal veins (Ansorge, 2002; Wu and Huang, 2012). These apomorphies
3836 place the genus *Liadotaulius* in Philopotamidae, a family within crown group Annulipalpa, and thus
3837 Trichoptera (Wu and Huang, 2012).

3838

3839 99.3. *Age justification*

3840

3841 The fossils were recovered from Grimmen, northeast Germany (Ansorge, 2002). Further age
3842 information as for 94.3.

3843

3844 99.4. *Discussion*

3845

3846 Possible caddisfly larval cases were recently described from the early Permian of Brazil (Mouro
3847 et al., 2016). The cases are tubular in form, and particulate matter is stuck to some of the cases
3848 (Mouro et al., 2016). Of the two most basal extant trichopteran families that construct larval cases, the

Hydroptilidae construct tubular cases and the Glossosomatidae construct their cases from particulate matter (Malm et al., 2013). However, various types of larval cases, including tubular cases, are constructed by caddisflies belonging to distantly-related lineages (Malm et al., 2013); at present, it cannot be assumed that tubular larval cases have originated only once within the Trichoptera. Assuming the Permian fossils are indeed insect larval cases, therefore, does not confirm the phylogenetic position of their inhabitants within crown versus stem Trichoptera, as larval cases might have evolved in the stem group.

100. Crown Lepidoptera

This clade comprises Zeugloptera, Aglossata, Heterobathmiina and Glossata (itself comprising six infraorders, over 100 families, and over 160,000 species), their last common ancestor and all of its descendants (**Fig. 24**). The list of lepidopteran subclades comes from a recently published consensus (van Nieukerken et al., 2011), although some molecular analyses have not recovered these clades (Regier et al., 2013). Monophyly is supported by nuclear protein-coding genes (Regier et al., 2013), transcriptomes (Misof et al., 2014), and morphology (Beutel et al., 2011).

100.1. Fossil specimens

Parasabatinca aftimacrai Whalley, 1978. Although the holotype (the specimen to which we refer; **Fig. 25h**) and two paratypes were attributed to the NHMUK (Sohn et al., 2012), they are now housed as part of the Acra collection, curated by D. Azar, pending construction of a fossil museum at the Lebanese University in Fanar (Matn), Lebanon (D. Azar, pers. comm.).

100.2. Phylogenetic justification

3875 Although not included in formal phylogenetic analysis, morphological characters (morphology
3876 of the antennae with ascoids, number and shape of tibial spurs, mouthpart and maxillary palp
3877 morphology) support the position of *P. aftimacrai* in what was formerly known as the 'Sabatinca' group
3878 of genera within Micropterigidae (Kristensen and Skalski, 1998; D. Azar, pers. comm.). As *P. aftimacrai*
3879 has an unbranched R vein and because Rs_4 terminates below the apex, the wing venation of *P.*
3880 *aftimacrai* most closely resembles that of the extant species *Austromartyria porphyrodes*, which
3881 belongs to what is now known as the 'Southern sabatinoid' lineage of Micropterigidae (Gibbs, 2010).
3882 Based on the above morphological characters, *P. aftimacrai* is supported as the oldest crown group
3883 member in multiple summaries of the fossil record of Lepidoptera (Grimaldi and Engel, 2005, Fig.
3884 13.13; Sohn et al., 2015, Fig. 2). Membership either within the crown or stem of Micropterigidae places
3885 the fossil within crown Zeugloptera and crown Lepidoptera.

3886

3887 100.3. Age justification

3888

3889 As for 76.3.

3890

3891

3892 100.4. Discussion

3893

3894 A number of older fossils have been assigned to Lepidoptera, but their position within the
3895 crown is ambiguous. *A. mane*, from the Early Jurassic of Dorset, England, has been used to calibrate
3896 the lepidopteran root in previous molecular dating analyses (e.g. Wahlberg et al., 2013). See 98.2 for
3897 exclusion of *A. mane* from the lepidopteran crown.

3898 Sohn et al. (2015) suggested that two undescribed fossil species are members of the
3899 Micropterigidae stem lineage (and thus crown Zeugloptera and crown Lepidoptera). These are from
3900 the Toarcian (Early Jurassic) Grüne Series of Grimmen, Germany (Ansorge, 2002), but they are too

3901 poorly characterized to be confidently used as calibration fossils.

3902

3903 **101. Crown Antliophora**

3904

3905 This clade comprises Siphonaptera (fleas), Mecoptera (scorpionflies) and Diptera (flies), their
3906 last common ancestor and all of its descendants (**Fig. 24**). Support for monophyly comes from
3907 phylogenetic analysis of transcriptomes (Misof et al., 2014; Peters et al., 2014) and morphology
3908 (Beutel et al., 2011). A recent analysis of mitochondrial genomes finds Amphiesmenoptera within
3909 Antliophora under some analytical conditions, potentially challenging antliophoran monophyly (Song et
3910 al., 2016).

3911

3912 *101.1. Fossil specimens*

3913

3914 *Pseudonannochorista willmanni* Novokshonov, 1994. PIN 966/21, holotype, preserving a
3915 forewing (**Fig. 25i**).

3916

3917 *101.2. Phylogenetic justification*

3918

3919 Pseudonannochoristinae is a subfamily of the Permochoristidae (Bashkuev, 2011;
3920 Novokshonov, 1994), however, a morphological phylogenetic analysis indicates polyphyly of this family
3921 (Ren et al., 2009). While the Permochoristinae (the other subfamily of Permochoristidae) fall on the
3922 stem lineage of Antliophora, Pseudonannochoristinae are part of the stem lineage of Mecoptera (Ren
3923 et al., 2009). Therefore, *P. willmanni*, as a member of Pseudonannochoristinae, is part of the crown
3924 group of Antliophora.

3925

3926 *101.3. Age justification*

3927

3928 Minimum as for 77.3. Soft maximum as for 75.3.

3929

3930 *101.4. Discussion*

3931

3932 Other fossils from the families Permotanyderidae, Permotipulidae, and Nannochoristinae are
3933 all demonstrably within crown group Antliophora (Ren et al., 2009). However, the localities from which
3934 they are known are younger, of Changhsingian age (Belmont, Australia and Mooi River, South Africa).

3935 Fossils of Siphonaptera from the Jurassic (Gao et al., 2012) and Cretaceous (Gao et al., 2014;
3936 Huang, 2015), suggested to parasitise dinosaurs, have been excluded from the crown group in a
3937 recent molecular phylogenetic analysis (Zhu et al., 2015). The molecular clock analysis (which was
3938 calibrated with better established fossils from Dominican and Baltic amber, of Miocene and Eocene
3939 age, respectively) estimated the origins of crown Siphonaptera in the Valanginian to Aptian stages of
3940 the Early Cretaceous (Zhu et al., 2015). Furthermore, none of the Mesozoic fossils possess a
3941 diagnostic character combination for the crown group (Dittmar et al., 2016). As siphonapteran
3942 parasites of dinosaurs would require a strong assumption that piercing mouthparts must be used for
3943 blood-feeding (Dittmar et al., 2016), we do not include any crown fossil calibrations.

3944

3945 **102. Crown Mecoptera**

3946

3947 This clade comprises Apteropanorpidae, Bittacidae, Boreidae, Choristidae, Eomeropidae,
3948 Meropeidae, Nannochoristidae, Panorpidae, and Panorpididae, their last common ancestor and all of
3949 its descendants (**Fig. 24**). Paraphyly of the traditional concept of Mecoptera (i.e. inclusion of
3950 Siphonaptera) was proposed by Whiting (2002) on the basis of four nuclear genes. This was, however,
3951 contradicted by analysis of six nuclear genes (Wiegmann et al., 2009), transcriptomes (Misof et al.,
3952 2014; Peters et al., 2014), and morphology (Beutel et al., 2011). Each of the latter studies recovered a

3953 monophyletic Mecoptera as the sister group of Siphonaptera.

3954

3955 *102.1. Fossil specimens*

3956

3957 *Burmomerope eureka* Grimaldi and Engel, 2013 (collection of James Zigras, available for study
3958 at AMNH: JZC Bu-84), holotype in amber.

3959

3960 *102.2. Phylogenetic justification*

3961

3962 *B. eureka* was assigned to the stem group of the extant family Meropeidae, based on several
3963 wing venation characters, including loss of slanted portion of CuA in forewing and R-Rs fork basal
3964 (Grimaldi and Engel, 2013). A position on the stem lineage of Meropeidae is therefore within the crown
3965 group of Mecoptera.

3966

3967 *102.3. Age justification*

3968

3969 As for 87.3.

3970

3971 **103. Crown Diptera**

3972

3973 This clade comprises Tipulomorpha (crane flies), Psychodomorpha (moth flies, sand flies),
3974 Culicomorpha (mosquitoes, black flies), Bibionomorpha (march flies, fungus gnats) and Brachycera
3975 (horse flies, robber flies, fruit flies, house flies, blow flies, etc.), their last common ancestor and all of
3976 its descendants (**Fig. 24**). Monophyly of Diptera has been supported in many phylogenetic analyses,
3977 including those based on transcriptomes (Misof et al., 2014), mitochondrial genomes and microRNA
3978 presence (Wiegmann et al., 2011), and morphology (Beutel et al., 2011; Wiegmann et al., 2011).

3979

3980 103.1. *Fossil specimens*

3981

3982 *Grauvogelia arzvilleriana* Krzeminski et al., 1994 (part of the private Louis Grauvogel collection,
3983 Ringendorf, Bas-Rhin, France, No. 5514), holotype (**Fig. 25j**).

3984

3985 103.2. *Phylogenetic justification*

3986

3987 *G. arzvilleriana* was included in the morphological cladistic analysis of Blagoderov et al. (2007).

3988 In that analysis, it was supported on the stem group of Psychodomorpha (Blagoderov et al., 2007).

3989 Although the original description assigned *G. arzvilleriana* to its own family, several wing venation

3990 characters were noted as similarities with families of Psychodomorpha (Krzeminski et al., 1994). The

3991 stem group of Psychodomorpha is within crown Diptera.

3992

3993 103.3. *Age justification*

3994

3995 Minimum as for 72.3. Soft maximum as for 75.3.

3996

3997 103.4. *Discussion*

3998

3999 A number of other dipteran fossils have been described from Grès à Voltzia; of special interest
4000 is *Voltziapupa tentata* Lukashevich et al., 2010, known only from well-preserved pupae, while *G.*
4001 *arzvilleriana* is known only from adult wings. The venation of the wing sheath in *V. tentata* is not well
4002 preserved, preventing a clear link of characters with *G. arzvilleriana* (Lukashevich et al., 2010).

4003

4004 **104. Conclusions**

4005

4006 Based on this compilation, qualitative trends in the fossil record of arthropod crown group
4007 members can be described. Patchiness in our taxonomic coverage results from differential
4008 preservation potential, with a notable scarcity of taxa living in habitats with poorly preserved facies
4009 (e.g. intertidal barnacles or pelagic copepods). More completely preserved fossils representing ancient
4010 divergences are well represented in our list of calibrations, perhaps owing to the attention devoted to
4011 phylogenetic analysis of deep fossil relationships within arthropods (e.g. Garwood and Dunlop, 2014 ;
4012 Lee et al., 2013; Legg et al., 2013; Oakley et al., 2013; Rota-Stabelli et al., 2011). However because
4013 our review is focused on crown groups, about half of our calibrations are from mid-Palaeozoic
4014 localities, making them much more numerous than those from Cambrian Burgess Shale-type biotas.
4015 Throughout the dataset, there is less of a relationship between 'hard part' preservation (calcified body
4016 parts, such as ostracod carapaces) and phylogenetic accuracy than might be expected.

4017 Particular Konservat-Lagerstätten, such as Herefordshire (Silurian), Rhynie Chert (Devonian),
4018 Mazon Creek (Carboniferous), Crato (Cretaceous) and Burmese amber (Cretaceous), provide several
4019 calibrations representing different arthropod clades, presumably owing to their preservation of non-
4020 biomineralised tissues required to identify arthropods to the ordinal level. These sites are critically
4021 important for the arthropod fossil record because of their relatively low preservation potential of many
4022 groups, as is particularly the case for terrestrial arthropods, being less well mineralised than many of
4023 the marine groups. This is reflected in the low level of congruence between the order of appearance of
4024 lineages in the fossil record (stratigraphic appearance) and the order of phylogenetic branching (Wills,
4025 2001; O'Connor and Wills, 2016) in arthropods, as compared to more congruent datasets such as
4026 tetrapods (Benton et al., 1999, 2000; Norell and Novacek, 1992). Clustering of calibrations at
4027 Konservat-Lagerstätten localities may lead to highly variable lengths of ghost lineages for the different
4028 taxa that are preserved together at these sites, and indeed many of the clades in our database have
4029 soft maxima that are substantially older than their hard minimum date. Konservat-Lagerstätten
4030 localities are, however, fairly regularly spaced throughout the Middle to Late Palaeozoic and the

4031 Mesozoic, and interim periods of time are punctuated by numerous other fossil localities yielding fewer
4032 calibration points. This results in our database having good coverage throughout the Phanerozoic
4033 with fossil localities occurring on average every 4-10 million years. A notable exception is the 43.2
4034 million year gap in the Ordovician, during which no definite earliest appearances of any crown-group
4035 orders have been identified in our study, despite this period being known as the Ordovician
4036 biodiversification event (Servais et al., 2008, 2010). Numerous arthropod stem lineage taxa were
4037 abundant during the Ordovician (e.g. trilobites), while the possible crown group taxa that have been
4038 described, e.g. ostracods (Siveter et al., 2014; Williams et al., 2008), barnacles (Van Roy et al., 2010),
4039 pycnogonids (Rudkin et al., 2013), xiphosurans (Lamsdell, 2013; Rudkin et al., 2008; Van Roy et al.,
4040 2010), and acariform mites (Bernini et al., 2002) do not meet the rigorous standards employed herein
4041 for determining calibration points. From the Late Devonian through the Mississippian (382.7 to 323.2
4042 Ma) our dataset has another large gap during which we have only one calibration point, which
4043 interestingly corresponds with one of the largest mass extinctions events known in the fossil record
4044 (McGhee, 2013).

4045 The field of divergence time estimation itself is rapidly advancing. New methodologies to
4046 incorporate fossil morphology and stratigraphy into the model of diversification (Heath et al., 2014;
4047 Wilkinson et al., 2011) and the phylogenetic topology itself ('tip-dating'; Ronquist et al., 2012) are
4048 growing in popularity. Precision and accuracy of date estimates are improved with the inclusion of as
4049 many *a priori* justified fossils as possible in tip- (Lee et al., 2013; Ronquist et al., 2012; Zhang et al.,
4050 2016) or node-dating studies (Heath et al., 2014; Ho and Phillips, 2009; Warnock et al., 2012, 2015;
4051 Yang and Rannala, 2006). When examined in the context of geological and evolutionary history, the
4052 distribution of fossil calibrations in our dataset are comprehensive, and have been rigorously vetted to
4053 ensure they meet *a priori* requirements (Parham et al., 2012; Warnock et al., 2015). Following their
4054 use in molecular clock analyses, *a posteriori* methods such as cross-validation could be employed to
4055 explore the impact of calibrations on the resulting divergence time estimates (e.g. Battistuzzi et al.,
4056 2015; Dornburg et al., 2011; Marshall, 2008; Near et al., 2005), although these methods cannot justify

4057 removal of individual constraints (Warnock et al., 2015). Fossils mentioned in Discussion sections
4058 occupy key positions along clade stems, and should also be considered in divergence time
4059 applications. To this end, we have compiled a robust list of over 100 fossil calibrations covering much
4060 of the arthropod Tree of Life. We hope this summary will inspire further work clarifying the
4061 phylogenetic relationships of fossil arthropods, and morphological studies of characters linking them to
4062 their crown clades.

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4088 **REFERENCES**

4089

- 4090 Abele, L.G., Spears, T., Kim, W., Applegate, M., 1992. Phylogeny of Selected Maxillopodan and Other
4091 Crustacean Taxa Based on 18S Ribosomal Nucleotide Sequences: A Preliminary Analysis. *Acta*
4092 *Zool.* 73, 373–382.
- 4093 Ah Yong, S.T., 1997. Phylogenetic analysis of the Stomatopoda (Malacostraca). *J. Crustac. Biol.* 17,
4094 695–715.
- 4095 Ah Yong, S.T., Harling, C., 2000. The phylogeny of the stomatopod Crustacea. *Aust. J. Zool.* 48, 607–
4096 642.
- 4097 Aitkin, J.D., 1997. Stratigraphy of the Middle Cambrian platformal succession, southern Rocky
4098 Mountains, Geological Survey of Canada Bulletin, 322 pp.
- 4099 Akulov, N.I., Frolov, A.O., Mashchuk, I.M., Akulova, V.V., 2015. Jurassic deposits of the southern part
4100 of the Irkutsk sedimentary basin. *Stratigr. Geol. Correl.* 23, 387–409.
- 4101 Almeida, W.O., Christoffersen, M.L., 1999. A Cladistic Approach to Relationships in Pentastomida. *J.*
4102 *Parasitol.* 85, 695–704.
- 4103 Alonso, J., Arillo, A., Barrón, E., Corral, J.C., Grimalt, J., López, J.F., Lopez, R., Martínez-Delclòs, X.,
4104 Ortuño, V., Peñalver, E., Trincao, P.R., 2000. A new fossil resin with biological inclusions in
4105 Lower Cretaceous deposits from Álava (Northern Spain, Basque-Cantabrian Basin). *J.*
4106 *Paleontol.* 74, 158-178.
- 4107 Anderson, F.W., 1985. Ostracod faunas in the Purbeck and Wealden of England. *J.*
4108 *Micropalaeontology* 4, 1–67.
- 4109 Anderson, L.I., Trewin, N.H., 2003. An Early Devonian arthropod fauna from the Windyfield cherts,
4110 Aberdeenshire, Scotland. *Palaeontology* 46, 467–509.
- 4111 Anderson, L.I., Crighton, W.R., Hass, H., 2003. A new univalve crustacean from the Early Devonian
4112 Rhynie chert hot-spring complex. *Trans. R. Soc. Edinb. Earth Sci.* 94, 355–369.

- 4113 Andrew, D.R., 2011. A new view of insect–crustacean relationships II. Inferences from expressed
4114 sequence tags and comparisons with neural cladistics. *Arthropod Struct. Dev.* 40, 289–302.
- 4115 Ansorge, J., 2002. Upper Liassic Amphiesmenopterans (Trichoptera + Lepidoptera) from Germany—a
4116 review. *Acta Zool. Cracoviensia* 46, 285–290.
- 4117 Ansorge, J., Schlüter, T., 1990. The earliest chrysopid: *Liassochrysa stigmatica* n.g., n. sp. from the
4118 Lower Jurassic of Dobbertin, Germany. *Neuroptera Int.* 6, 87–93.
- 4119 Arabi, J., Cruaud, C., Couloux, A., Hassanin, A., 2010. Studying sources of incongruence in arthropod
4120 molecular phylogenies: Sea spiders (Pycnogonida) as a case study. *Comptes Rendus Biol.*
4121 333, 438–453.
- 4122 Arango, C.P., Wheeler, W.C., 2007. Phylogeny of the sea spiders (Arthropoda, Pycnogonida) based
4123 on direct optimization of six loci and morphology. *Cladistics* 23, 255–293.
- 4124 Arnol'di, L.V., Zherikhin, V.V., Nikritin, L.M., Ponomarenko, A.G., 1992. Mesozoic Coleoptera. Oxonian
4125 Press, New Delhi.
- 4126 Astrop, T.I., Hegna, T.A., 2015. Phylogenetic relationships between living and fossil spinicaudatan taxa
4127 (Branchiopoda Spinicaudata): reconsidering the evidence. *J. Crustac. Biol.* 35, 339–354.
- 4128 Avise, J.C., Nelson, W.S., Sugita, H., 1994. A speciation history of “living fossils”: molecular
4129 evolutionary patterns in horseshoe crabs. *Evolution* 1986–2001.
- 4130 Azar, D., Geze, R., Acra, F., 2010. Lebanese amber, in: Penney, D. (Ed.), *Biodiversity of Fossils in*
4131 *Amber from the Major World Deposits*. Siri Scientific Press, pp. 271–298.
- 4132 Babcock, L.E., Peng, S., Geyef, G., Shergold, J.H., 2005. Changing perspectives on Cambrian
4133 chronostratigraphy and progress toward subdivision of the Cambrian System. *Geosci. J.* 9,
4134 101–106.
- 4135 Baird, G.C., Sroka, S.D., Shabica, C.W., Beard, T.L., 1985. Mazon Creek-type fossil assemblages in
4136 the U.S. midcontinent Pennsylvanian: their recurrent character and palaeoenvironmental
4137 significance. *Philos. Trans. R. Soc. B Biol. Sci.* 311, 87–99.

- 4138 Bamber, R.N., 2007. A holistic re-interpretation of the phylogeny of the Pycnogonida Latreille, 1810
4139 (Arthropoda). Zootaxa 1668, 295–312.
- 4140 Baptista, C., Santiago-Blay, J.A., Soleglad, M.E., Fet, V., 2006. The Cretaceous Scorpion Genus,
4141 *Archaeobuthus*, Revisited (Scorpiones: Archaeobuthidae). Euscorpius 35, 1–28.
- 4142 Barrón, E., Elorza, L., Rengifo, M.J.C., 2001. Contribuciones al estudio palinológico del Cretácico
4143 Inferior de la Cuenca Vasco-Cantábrica: los afloramientos ambarígenos de Peñacerrada
4144 (España). Coloq. Paleontol. 135–156.
- 4145 Barrón, E., Peyrot, D., Rodríguez-López, J.P., Meléndez, N., López del Valle, R., Najarro, M., Rosales,
4146 I., Comas-Rengifo, M.J., 2015. Palynology of Aptian and upper Albian (Lower Cretaceous)
4147 amber-bearing outcrops of the southern margin of the Basque-Cantabrian basin (northern
4148 Spain). Cretac. Res. 52, 292–312.
- 4149 Barskov, I.S., Leonova, T.B., Shilovsky, O.P., 2014. Middle Permian cephalopods of the Volga-Ural
4150 Region. Paleontol. J. 48, 1331–1414.
- 4151 Bashkuev, A.S., 2008. The first record of Kaltanidae (Insecta: Mecoptera: Kaltanidae) from the
4152 Permian of European Russia. Paleontol. J. 42, 401–405.
- 4153 Bashkuev, A.S., 2011. Nedubroviidae, a new family of Mecoptera: the first Paleozoic long-proboscid
4154 scorpionflies. Zootaxa 2895, 47–57.
- 4155 Batten, D.J., 2007. Spores and pollen from the Crato Formation: biostratigraphic and
4156 palaeoenvironmental implications, in: The Crato Fossil Beds of Brazil: Window into an Ancient
4157 World. Cambridge University Press, Cambridge, pp. 566–573.
- 4158 Battistuzzi, F.U., Billing-Ross, P., Murillo, O., Filipinski, A., Kumar, S., 2015. A Protocol for Diagnosing
4159 the Effect of Calibration Priors on Posterior Time Estimates: A Case Study for the Cambrian
4160 Explosion of Animal Phyla. Mol. Biol. Evol. 32, 1907–1912.
- 4161 Bechly, G., 1997. New fossil Odonata from the Upper Triassic of Italy, with a redescription of
4162 *Italophlebia gervasutti*, and a reclassification of Triassic dragonflies. Riv. Mus. Civ. Sci. Nat. E
4163 Caffi 19, 31–70.

- 4164 Bechly, G., Stockar, R., 2011. The first Mesozoic record of the extinct apterygote insect genus
4165 *Dasyleptus* (Insecta: Archaeognatha: Monura: Dasyleptidae) from the Triassic of Monte San
4166 Giorgio (Switzerland). *Palaeodiversity* 4, 23–37.
- 4167 Becker, R.T., Gradstein, F.M., Hammer, O., 2012. The Devonian Period, in: *The Geologic Time Scale*.
4168 Elsevier, pp. 559–601.
- 4169 Bellec, L., Rabet, N., 2016. Dating of the Limnadiidae family suggests an American origin of
4170 *Eulimnadia*. *Hydrobiologia* 773, 149–161.
- 4171 Benner, J.S., Knecht, R.J., Engel, M.S., 2013. Comment on Marden (2013): “Reanalysis and
4172 experimental evidence indicate that the earliest trace fossil of a winged insect was a surface
4173 skimming neopteran.” *Evolution* 67, 2142–2149.
- 4174 Benton, M.J., Donoghue, P.C.J., 2007. Paleontological Evidence to Date the Tree of Life. *Mol. Biol.*
4175 *Evol.* 24, 26–53.
- 4176 Benton, M.J., Donoghue, P.C., Asher, R.J., Friedman, M., Near, T.J., Vinther, J., 2015. Constraints on
4177 the timescale of animal evolutionary history. *Palaeontol. Electron.* 18, 1–106.
- 4178 Benton, M.J., Hitchin, R., Wills, M.A., 1999. Assessing congruence between cladistics and
4179 stratigraphic data. *Syst. Biol.* 48, 581–596.
- 4180 Benton, M.J., Wills, M.A., Hitchin, R., 2000. Quality of the fossil record through time. *Nature* 403, 534–
4181 537.
- 4182 Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C., Dronov, A., 2009. The new chronostratigraphic
4183 classification of the Ordovician System and its relations to major regional series and stages
4184 and to $\delta^{13}\text{C}$ chemostratigraphy. *Lethaia* 42, 97–107.
- 4185 Bernini, F., 1986. Current ideas on the phylogeny and the adaptive radiations of Acarida. *Bolletino*
4186 *Zool.* 53, 279–313.
- 4187 Bernini, F., Carnevale, G., Bagnoli, G., Stouge, S., 2002. An early Ordovician oribatid mite (Acari:
4188 Oribatida) from the island of Öland, Sweden, in: *Acarid Phylogeny and Evolution: Adaptation in*
4189 *Mites and Ticks*. Springer, pp. 45–47.

- 4190 Béthoux, O., 2005. Wing venation pattern of Plecoptera (Insecta: Neoptera). *Illiesia* 1, 52–81.
- 4191 Béthoux, O., 2009. The Earliest Beetle Identified. *J. Paleontol.* 83, 931–937.
- 4192 Béthoux, O., Beckemeyer, R.J., Engel, M.S., Hall, J.D., 2010. New data on *Homocladus grandis*, a
4193 Permian stem-mantodean (Polyneoptera: Dictyoptera). *J. Paleontol.* 84, 746–753.
- 4194 Béthoux, O., Cui, Y., Kondratieff, B., Stark, B., Ren, D., 2011. At last, a Pennsylvanian stem-stonefly
4195 (Plecoptera) discovered. *BMC Evol. Biol.* 11, 248.
- 4196 Béthoux, O., Nel, A., 2002. Venation pattern and revision of Orthoptera *sensu nov.* and sister groups.
4197 Phylogeny of Palaeozoic and Mesozoic Orthoptera *sensu nov.* *Zootaxa* 96, 1–88.
- 4198 Béthoux, O., Nel, A., 2005. Some Palaeozoic “Protorthoptera” are “ancestral” orthopteroids: Major
4199 wing braces as clues to a new split among the “Protorthoptera” (Insecta). *J. Syst. Palaeontol.*
4200 2, 285–309.
- 4201 Béthoux, O., Nel, A., 2010. Description of a new grylloblattidan insect from Montceau-les-Mines (Late
4202 Carboniferous; France) and definition of *Phenopterum* Carpenter, 1950. *Syst. Entomol.* 35,
4203 546–553.
- 4204
- 4205 Béthoux, O., Nel, A., Lapeyrie, J., Gand, G., Galtier, J., 2002. *Raphogla rubra* gen. n., sp. n., the oldest
4206 representative of the clade of modern Ensifera (Orthoptera: Tettigoniidea, Gryllidea). *Eur. J.*
4207 *Entomol.* 99, 111–116.
- 4208 Béthoux, O., Wieland, F., 2009. Evidence for Carboniferous origin of the order Mantodea (Insecta:
4209 Dictyoptera) gained from forewing morphology. *Zool. J. Linn. Soc.* 156, 79–113.
- 4210 Beutel, R.G., Friedrich, F., Hörnschemeyer, T., Pohl, H., Hünefeld, F., Beckmann, F., Meier, R., Misof,
4211 B., Whiting, M.F., Vilhelmsen, L., 2011. Morphological and molecular evidence converge upon
4212 a robust phylogeny of the megadiverse Holometabola. *Cladistics* 27, 341–355.
- 4213 Beutel, R.G., Wang, B., Tan, J.-J., Ge, S.-Q., Ren, D., Yang, X.-K., 2013. On the phylogeny and
4214 evolution of Mesozoic and extant lineages of Adephaga (Coleoptera, Insecta). *Cladistics* 29,
4215 147–165.

- 4216 Bill, P.C., 1914. Über crustaceen aus dem Voltziensandstein des Elasses. Mitteilungen der
4217 Geologischen Landesanstalt von Elsaß-Lothringen, Strassburg. 8, 289-338.
- 4218 Bird, T.L., Wharton, R.A., Prendini, L., 2015. Chelicerel Morphology in Solifugae (Arachnida): Primary
4219 Homology, Terminology, and Character Survey. Bull. Am. Mus. Nat. Hist. 394, 1–355.
- 4220 Blagoderov, V., Grimaldi, D.A., Fraser, N.C., 2007. How Time Flies for Flies: Diverse Diptera from the
4221 Triassic of Virginia and Early Radiation of the Order. Am. Mus. Novit. 3572, 1–39.
- 4222 Blanke, A., Greve, C., Wipfler, B., Beutel, R.G., Holland, B.R., Misof, B., 2013. The Identification of
4223 Concerted Convergence in Insect Heads Corroborates Palaeoptera. Syst. Biol. 62, 250–263.
- 4224 Blanke, A., Koch, M., Wipfler, B., Wilde, F., Misof, B., 2014. Head morphology of *Tricholepidion*
4225 *gertschi* indicates monophyletic Zygentoma. Front. Zool. 11, 1.
- 4226 Blanke, A., Machida, R., Szucsich, N.U., Wilde, F., Misof, B., 2015. Mandibles with two joints evolved
4227 much earlier in the history of insects: dicondily is a synapomorphy of bristletails, silverfish and
4228 winged insects. Syst. Entomol. 40, 357–364.
- 4229 Blanke, A., Wesener, T., 2014. Revival of forgotten characters and modern imaging techniques help to
4230 produce a robust phylogeny of the Diplopoda (Arthropoda, Myriapoda). Arthropod Struct. Dev.
4231 43, 63–75.
- 4232 Blanke, A., Wipfler, B., Letsch, H., Koch, M., Beckmann, F., Beutel, R., Misof, B., 2012. Revival of
4233 Palaeoptera-head characters support a monophyletic origin of Odonata and Ephemeroptera
4234 (Insecta) Cladistics 28, 560–581.
- 4235 Bonato, L., Drago, L., Murienne, J., 2014a. Phylogeny of Geophilomorpha (Chilopoda) inferred from
4236 new morphological and molecular evidence. Cladistics 30, 485–507.
- 4237 Bonato, L., Edgecombe, G.D., Minelli, A., 2014b. Geophilomorph centipedes from the Cretaceous
4238 amber of Burma. Palaeontology 57, 97–110.
- 4239 Bond, J.E., Garrison, N.L., Hamilton, C.A., Godwin, R.L., Hedin, M., Agnarsson, I., 2014.
4240 Phylogenomics Resolves a Spider Backbone Phylogeny and Rejects a Prevailing Paradigm for
4241 Orb Web Evolution. Curr. Biol. 24, 1765–1771.

- 4242 Bourquin, S., Durand, M., Diez, J.B., Broutin, J., Fluteau, F., 2007. El limite Permico-Triasico y la
4243 sedimentacion durante el Triasico inferior en las cuencas de Europa occidental: una vision
4244 general. *J. Iber. Geol.* 221–237.
- 4245 Bourquin, S., Peron, S., Durand, M., 2006. Lower Triassic sequence stratigraphy of the western part of
4246 the Germanic Basin (west of Black Forest): Fluvial system evolution through time and space.
4247 *Sediment. Geol.* 186, 187–211.
- 4248 Boussau, B., Walton, Z., Delgado, J.A., Collantes, F., Beani, L., Stewart, I.J., Cameron, S.A., Whitfield,
4249 J.B., Johnston, J.S., Holland, P.W.H., Bachtrog, D., Kathirithamby, J., Huelsenbeck, J.P., 2014.
4250 Strepsiptera, Phylogenomics and the Long Branch Attraction Problem. *PLoS ONE* 9, e107709.
- 4251 Boyko, C.B., Bruce, N.L., Merrin, K.L., Ota, Y., Poore, G.C.B., Taiti, S., Schotte, M., Wilson, G.D.F.,
4252 2008. World marine, freshwater and terrestrial isopod crustaceans database.
4253 <http://www.marinespecies.org/isopoda> (accessed 23.03.16).
- 4254 Bracken, H.D., Toon, A., Felder, D.L., Martin, J.W., Finley, M., Rasmussen, J., Palero, F., Crandall,
4255 K.A., 2009. The decapod tree of life: compiling the data and moving toward a consensus of
4256 decapod evolution. *Arthropod Syst. Phylogeny* 67, 99–116.
- 4257 Bracken-Grissom, H.D., Ah Yong, S.T., Wilkinson, R.D., Feldmann, R.M., Schweitzer, C.E., Breinholt,
4258 J.W., Bendall, M., Palero, F., Chan, T.-Y., Felder, D.L., Robles, R., Chu, K.-H., Tsang, L.-M.,
4259 Kim, D., Martin, J.W., Crandall, K.A., 2014. The Emergence of Lobsters: Phylogenetic
4260 Relationships, Morphological Evolution and Divergence Time Comparisons of an Ancient
4261 Group (Decapoda: Achelata, Astacidea, Glypheidea, Polychelida). *Syst. Biol.* 63, 457–479.
- 4262 Bracken-Grissom, H.D., Cannon, M.E., Cabezas, P., Feldmann, R.M., Schweitzer, C.E., Ah Yong, S.T.,
4263 Felder, D.L., Lemaitre, R., Crandall, K.A., 2013. A comprehensive and integrative
4264 reconstruction of evolutionary history for Anomura (Crustacea: Decapoda). *BMC Evol. Biol.* 13,
4265 128.

- 4266 Bradler, S., Buckley, T.R., 2011. Stick insect on unsafe ground: does a fossil from the early Eocene of
4267 France really link Mesozoic taxa with the extant crown group of Phasmatodea? Syst. Entomol.
4268 36, 218–222.
- 4269 Brauckmann, C., Brauckmann, B., Groning, E., 1994. The stratigraphical position of the oldest known
4270 Pterygota (Insecta. Carboniferous, Namurian). Ann. Société Géologique Belg. 117, 47–56.
- 4271 Brauckmann, C., Koch, L., 1983. *Prothelyphonus naufragus* n. sp., a new whip scorpion (Arachnida:
4272 Thelyphonida: Thelyphonidae) from the Namurian (lower Upper Carboniferous) of West
4273 Germany. Entomol. Gen. 9, 63–73.
- 4274 Brauckmann, C., Schneider, J., 1996. Ein unter-karbonisches Insekt aus dem Raum
4275 Bitterfeld/Delitzsch (Pterygota, Arnsbergium, Deutschland). Neues Jahrb. Geol. Palaontologie-
4276 Monatshefte 17–30.
- 4277 Brewer, M.S., Swafford, L., Spruill, C.L., Bond, J.E., 2013. Arthropod phylogenetics in light of three
4278 novel millipede (Myriapoda: Diplopoda) mitochondrial genomes with comments on the
4279 appropriateness of mitochondrial genome sequence data for inferring deep level relationships.
4280 PLoS ONE 8, e68005.
- 4281 Briggs, D.E.G., Collins, D., 1988. A Middle Cambrian chelicerate from Mount Stephen, British
4282 Columbia. Palaeontology 31, 779–798.
- 4283 Briggs, D.E.G., Liu, H.P., McKay, R.M., Witzke, B.J., 2015. Bivalved arthropods from the Middle
4284 Ordovician Winneshiek Lagerstätte, Iowa, USA. J. Paleontol. 89, 991–1006.
- 4285 Briggs, D.E.G., Siveter, D.J., Siveter, D.J., Sutton, M.D., Garwood, R.J., Legg, D., 2012. Silurian
4286 horseshoe crab illuminates the evolution of arthropod limbs. Proc. Natl. Acad. Sci. 109, 15702–
4287 15705.
- 4288 Briggs, D.E.G., Sutton, M.D., Siveter, D.J., Siveter, D.J., 2004. A new phyllocarid (Crustacea:
4289 Malacostraca) from the Silurian Fossil-Lagerstatte of Herefordshire, UK. Proc. R. Soc. B Biol.
4290 Sci. 271, 131–138.

- 4291 Briggs, D.E., Sutton, M.D., Siveter, D.J., Siveter, D.J., 2005. Metamorphosis in a Silurian barnacle.
4292 Proc. R. Soc. B Biol. Sci. 272, 2365–2369.
- 4293 Brongniart, C., 1883. Recherches pour servir à l'histoire des insectes fossiles des temps primaires
4294 précédées d'une étude sur la nervation des ailes des insectes. Bull. Société d'Industrie Min.
4295 Saint-Etienne, 7, 1–491.
- 4296 Brongniart, C., 1885. Les Insectes fossiles des terrains primaires. Coup d'oeil rapide sur la faune
4297 entomologique des terrains paléozoïques. Bull. Société Amis Sci. Nat. Rouen 1885, 50–68.
- 4298 Brydone, R.M., 1912. The stratigraphy of the chalk of Hampshire, with map and palaeontological
4299 notes. Dulau, London.
- 4300 Buckeridge, J.S., 1983. Fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia. N.Z.
4301 Geol. Surv. Paleontol. Bull. 50, 1–151.
- 4302 Buckeridge, J.S., 1979. The fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia.
4303 (PhD). University of Auckland, Auckland.
- 4304 Buckeridge, J.S., Newman, W.A., 2006. A revision of the Iblidae and the stalked barnacles (Crustacea:
4305 Cirripedia: Thoracica), including new ordinal, familial and generic taxa, and two new species
4306 from New Zealand and Tasmanian waters. Zootaxa 1136, 1–38.
- 4307 Buckman, R.S., Mound, L.A., Whiting, M.F., 2013. Phylogeny of thrips (Insecta: Thysanoptera) based
4308 on five molecular loci. Syst. Entomol. 38, 123–133.
- 4309 Budd, G.E., Jensen, S., 2000. A critical reappraisal of the fossil record of the bilaterian phyla. Biol. Rev.
4310 75, 253–295.
- 4311 Bull, E.E., Loydell, D.K., 1995. Uppermost Telychian graptolites from the North Esk Inlier, Pentland
4312 Hills, near Edinburgh. Scottish Journal of Geology 31, 163–170.
- 4313 Bybee, S.M., Bracken-Grissom, H., Haynes, B.D., Hermansen, R.A., Byers, R.L., Clement, M.J., Udall,
4314 J.A., Wilcox, E.R., Crandall, K.A., 2011. Targeted Amplicon Sequencing (TAS): A Scalable
4315 Next-Gen Approach to Multilocus, Multitaxa Phylogenetics. Genome Biol. Evol. 3, 1312–1323.

- 4316 Bybee, S.M., Ogden, T.H., Branham, M.A., Whiting, M.F., 2008. Molecules, morphology and fossils: a
4317 comprehensive approach to odonate phylogeny and the evolution of the odonate wing.
4318 Cladistics 24, 477–514.
- 4319 Calvet, F., Tucker, M.E., 1995. Mud-mounds with reefal caps in the upper Muschelkalk (Triassic),
4320 eastern Spain, in: Monty, C.L.V., Bosence, D.W.J., Bridges, P.H., Pratt, B.R. (Eds.), Carbonate
4321 Mud-Mounds: Their Origin and Evolution, Int. Assoc. Sediment. Spec. Publ. Blackwell Science,
4322 pp. 311–333.
- 4323 Camacho, A.I., Rey, I., Dorda, B.A., Machordom, A., Valdecasas, A.G., 2002. A note on the systematic
4324 position of the Bathynellacea (Crustacea, Malacostraca) using molecular evidence. Contrib.
4325 Zool. 71, 123–129.
- 4326 Campbell, L.I., Rota-Stabelli, O., Edgecombe, G.D., Marchioro, T., Longhorn, S.J., Telford, M.J.,
4327 Philippe, H., Rebecchi, L., Peterson, K.J., Pisani, D., 2011. MicroRNAs and phylogenomics
4328 resolve the relationships of Tardigrada and suggest that velvet worms are the sister group of
4329 Arthropoda. Proc. Natl. Acad. Sci. 108, 15920–15924.
- 4330 Campos, D.R.B., 1986. Primeiro registro fóssil de Scorpionoidea na chapada do Araripe (Cretáceo
4331 Inferior), Brasil. An. Acad. Bras. Ciênc. 58, 135–137.
- 4332 Cao, Z., Yu, Y., Wu, Y., Hao, P., Di, Z., He, Y., Chen, Z., Yang, W., Shen, Z., He, X., Sheng, J., Xu, X.,
4333 Pan, B., Feng, J., Yang, X., Hong, W., Zhao, W., Li, Z., Huang, K., Li, T., Kong, Y., Liu, H.,
4334 Jiang, D., Zhang, B., Hu, J., Hu, Y., Wang, B., Dai, J., Yuan, B., Feng, Y., Huang, W., Xing, X.,
4335 Zhao, G., Li, X., Li, Y., Li, W., 2013. The genome of *Mesobuthus martensii* reveals a unique
4336 adaptation model of arthropods. Nat. Commun. 4, 2602.
- 4337 Carapelli, A., Liò, P., Nardi, F., van der Wath, E., Frati, F., 2007. Phylogenetic analysis of mitochondrial
4338 protein coding genes confirms the reciprocal paraphyly of Hexapoda and Crustacea. BMC
4339 Evol. Biol. 7, S8.
- 4340 Carmean, D., Crespi, B.J., 1995. Do long branches attract flies? Nature 373, 666.

- 4341 Caron, J.-B., Gaines, R.R., Mángano, M.G., Streng, M., Daley, A.C., 2010. A new Burgess Shale–type
 4342 assemblage from the “thin” Stephen Formation of the southern Canadian Rockies. *Geology* 38,
 4343 811–814.
- 4344 Carpenter, F.M., 1938. Two Carboniferous insects from the vicinity of Mazon Creek, Illinois. *Am. J. Sci.*
 4345 216, 445–452.
- 4346 Carpenter, F.M., 1960. A Triassic odonate from Argentina. *Psyche* 67, 71–75.
- 4347 Carpenter, F.M., 1966. The Lower Permian insects of Kansas. Part II. The orders Protorthoptera and
 4348 Orthoptera. *Psyche* 73, 46–88.
- 4349 Carpenter, F.M., 1976. Lower Permian insects of Kansas. 12. Protorthoptera (continued), Neuroptera,
 4350 additional Palaeodictyoptera, and families of uncertain position. *Psyche* 83, 336–376.
- 4351 Carvalho, M. d. G.P., Lourenço, W.R., 2001. A new family of fossil scorpions from the Early Cretaceous
 4352 of Brazil. *Comptes Rendus Académie Sci.-Ser. IIA-Earth Planet. Sci.* 332, 711–716.
- 4353 Castellani, C., Maas, A., Waloszek, D., Haug, J.T., 2011. New pentastomids from the Late Cambrian of
 4354 Sweden - deeper insight of the ontogeny of fossil tongue worms. *Palaeontogr. Abt. A* 95–145.
- 4355 Catuneanu, O., Wopfner, H., Eriksson, P.G., Cairncross, B., Rubidge, B.S., Smith, R.M.H., Hancox,
 4356 P.J., 2005. The Karoo basins of south-central Africa. *J. Afr. Earth Sci.* 43, 211–253.
- 4357 Chang, S., Zhang, H., Renne, P.R., Fang, Y., 2009a. High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ age for the Jehol Biota.
 4358 *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 280, 94–104.
- 4359 Chang, S., Zhang, H., Renne, P.R., Fang, Y., 2009b. High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ age constraints on the
 4360 basal Lanqi Formation and its implications for the origin of angiosperm plants. *Earth Planet.*
 4361 *Sci. Lett.* 279, 212–221.
- 4362 Chen, P.J., Hudson, J.D., 1991. The conchostracan fauna of the Great Estuarine Group, Middle
 4363 Jurassic, Scotland. *Palaeontology* 34, 515–545.
- 4364 Chen, P., Li, G., Batten, D.J., 2007. Evolution, migration and radiation of late Mesozoic
 4365 conchostracans in East Asia. *Geol. J.* 42, 391–413.

- 4366 Chen, W.-J., Koch, M., Mallatt, J.M., Luan, Y.-X., 2014. Comparative Analysis of Mitochondrial
4367 Genomes in Diplura (Hexapoda, Arthropoda): Taxon Sampling Is Crucial for Phylogenetic
4368 Inferences. *Genome Biol. Evol.* 6, 105–120.
- 4369 Chernyshev, B.I., 1930. Cirripeden aus den Basin des Donetz und von Kusnetsk. *Zool. Anz.* 92, 26–
4370 28.
- 4371 Chilton, C., 1929. Note on a fossil shrimp from Hawkesbury sandstones. *J. R. Soc. New South Wales*
4372 62, 366–368.
- 4373 Collette, J.H., Hagadorn, J.W., 2010a. Three-dimensionally preserved arthropods from Cambrian
4374 Lagerstätten of Quebec and Wisconsin. *J. Paleontol.* 84, 646–667.
- 4375 Collette, J.H., Hagadorn, J.W., 2010b. Early evolution of phyllocarid arthropods: phylogeny and
4376 systematics of Cambrian-Devonian archaeostracans. *J. Paleontol.* 84, 795–820.
- 4377 Common, I.F.B., 1973. A new family of Dacnonypha (Lepidoptera) based on three new species from
4378 southern Australia, with notes on the Agathiphaeidae. *Aust. J. Entomol.* 12, 11–73.
- 4379 Condon, D.J., Zhu, M., Bowring, S., Wang, W., Yang, A., Jin, Y., 2005. U-Pb Ages from the
4380 Neoproterozoic Doushantuo Formation, China. *Science* 308, 92–95.
- 4381 Cressey, R., Boxshall, G., 1989. *Kabatarina pattersoni*, a fossil parasitic copepod (Dichelesthidae)
4382 from a Lower Cretaceous fish. *Micropaleontology* 35, 150–167.
- 4383 Crimes, T.P., 1987. Trace fossils and correlation of late Precambrian and early Cambrian strata. *Geol.*
4384 *Mag.* 124, 97–119.
- 4385 Crimes, T.P., Jiang, Z., 1986. Trace fossils from the Precambrian–Cambrian boundary candidate at
4386 Meishucun, Jinning, Yunnan, China. *Geol. Mag.* 123, 641–649.
- 4387 Crowson, R.A., 1985. Comments on Insecta of the Rhynie Chert. *Entomol. Gen.* 97–98.
- 4388 Cryan, J.R., Urban, J.M., 2012. Higher-level phylogeny of the insect order Hemiptera: is
4389 Auchenorrhyncha really paraphyletic? *Syst. Entomol.* 37, 7–21.

- 4390 Cui, Y., Xie, Q., Hua, J., Dang, K., Zhou, J., Liu, X., Wang, G., Yu, X., Bu, W., 2013. Phylogenomics of
4391 Hemiptera (Insecta: Paraneoptera) based on mitochondrial genomes. *Syst. Entomol.* 38, 233–
4392 245.
- 4393 Dahms, H.-U., 2004. Postembryonic apomorphies proving the monophyletic status of the Copepoda.
4394 *Zool. Stud.* 43, 446–453.
- 4395 Darwin, C., 1851. A Monograph on the Fossil Lepadidae, Or, Pedunculated Cirripedes of Great Britain.
4396 Palaeontographical Society.
- 4397 Davis, R.B., Nicholson, D.B., Saunders, E.L., Mayhew, P.J., 2011. Fossil gaps inferred from
4398 phylogenies alter the apparent nature of diversification in dragonflies and their relatives. *BMC*
4399 *Evol. Biol.* 11, 252.
- 4400 Davydov, V.I., Korn, D., Schmitz, M.D., Gradstein, F.M., Hammer, O., 2012. The Carboniferous Period,
4401 in: *The Geologic Time Scale*. Elsevier, pp. 603–651.
- 4402 De Grave, S., Chan, T.-Y., Chu, K.H., Yang, C.-H., Landeira, J.M., 2015. Phylogenetics reveals the
4403 crustacean order Amphionidacea to be larval shrimps (Decapoda: Caridea). *Sci. Rep.* 5,
4404 17464.
- 4405 Delclòs, X., Peñalver, E., Arillo, A., Engel, M.S., Nel, A., Azar, D., Ross, A., 2016. New mantises
4406 (Insecta: Mantodea) in Cretaceous ambers from Lebanon, Spain, and Myanmar. *Cretac. Res.*
4407 60, 91–108.
- 4408 Dell'Ampio, E., Meusemann, K., Szucsich, N.U., Peters, R.S., Meyer, B., Borner, J., Petersen, M.,
4409 Aberer, A.J., Stamatakis, A., Walz, M.G., Minh, B.Q., von Haeseler, A., Ebersberger, I., Pass,
4410 G., Misof, B., 2014. Decisive Data Sets in Phylogenomics: Lessons from Studies on the
4411 Phylogenetic Relationships of Primarily Wingless Insects. *Mol. Biol. Evol.* 31, 239–249.
- 4412 Demoulin, G., 1970. Remarques critiques sur des larves “éphéméromorphes” du Permien. *Bull. Inst.*
4413 *R. Sci. Nat. Belg.* 46, 1–10.
- 4414 Dettmann, M.E., Thomson, M.R.A., 1987. Cretaceous palynomorphs from the James Ross Island
4415 area, Antarctica. A pilot study. *Bull.-Br. Antarct. Surv.* 13–59.

- 4416 D'Haese, C.A., 2003. Morphological appraisal of Collembola phylogeny with special emphasis on
4417 Poduromorpha and a test of the aquatic origin hypothesis. *Zool. Scr.* 32, 563–586.
- 4418 Diedrich, C.G., 2011. Middle Triassic horseshoe crab reproduction areas on intertidal flats of Europe
4419 with evidence of predation by archosaurs. *Biol. J. Linn. Soc.* 103, 76–105.
- 4420 Dittmar, K., Zhu, Q., Hastriter, M.W., Whiting, M.F., 2016. On the probability of dinosaur fleas. *BMC*
4421 *Evol. Biol.* 16.
- 4422 Dixon, C.J., Ah Yong, S.T., Schram, F.R., 2003. A new hypothesis of decapod phylogeny. *Crustaceana*
4423 76, 935–975.
- 4424 Djernæs, M., Klass, K.-D., Eggleton, P., 2015. Identifying possible sister groups of Cryptocercidae +
4425 Isoptera: A combined molecular and morphological phylogeny of Dictyoptera. *Mol. Phylogenet.*
4426 *Evol.* 84, 284–303.
- 4427 Djernæs, M., Klass, K.-D., Picker, M.D., Damgaard, J., 2012. Phylogeny of cockroaches (Insecta,
4428 Dictyoptera, Blattodea), with placement of aberrant taxa and exploration of out-group sampling.
4429 *Syst. Entomol.* 37, 65–83.
- 4430 Dobruskina, I.A., 1995. Keuper (Triassic) Flora from Middle Asia (Madygen, Southern Fergana):
4431 Bulletin 5. New Mexico Museum of Natural History and Science, Albuquerque.
- 4432 Dohle, W., 2001. Are the insects terrestrial crustaceans? A discussion of some new facts and
4433 arguments and the proposal of the proper name “Tetraconata” for the monophyletic unit
4434 Crustacea + Hexapoda, in: *Annales de La Société Entomologique de France*. Presented at the
4435 Symposium on the Origin of the Hexapoda, Société entomologique de France, pp. 85–103.
- 4436 Dornburg, A., Beaulieu, J.M., Oliver, J.C., Near, T.J., 2011. Integrating Fossil Preservation Biases in
4437 the Selection of Calibrations for Molecular Divergence Time Estimation. *Syst. Biol.* 60, 519-
4438 527.
- 4439 Doyle, J.A., Endress, P.K., 2014. Integrating Early Cretaceous Fossils into the Phylogeny of Living
4440 Angiosperms: ANITA Lines and Relatives of Chloranthaceae. *Int. J. Plant Sci.* 175, 555–600.
- 4441 Drumm, D.T., 2010. Phylogenetic Relationships of Tanaidacea (Eumalacostraca: Peracarida) Inferred

- 4442 from Three Molecular Loci. J. Crustac. Biol. 30, 692–698.
- 4443 Drygant, D., Szaniawski, H., 2012. Lochkovian conodonts from Podolia, Ukraine, and their
4444 stratigraphic significance. Acta Palaeontol. Pol. 57, 833-861.
- 4445 Dubinin, V.B., 1962. Class Acaromorpha: mites or gnathosomic chelicerate arthropods. Fundam.
4446 Palaeontol. 447–473.
- 4447 Dunlop, J.A., 2010. Geological history and phylogeny of Chelicerata. Arthropod Struct. Dev. 39, 124–
4448 142.
- 4449 Dunlop, J.A., Anderson, L.I., Braddy, S.J., 2004. A redescription of *Chasmataspis laurencii* Caster and
4450 Brooks, 1956 (Chelicerata: Chasmataspidida) from the Middle Ordovician of Tennessee, USA,
4451 with remarks on chasmataspid phylogeny. Trans. R. Soc. Edinb. Earth Sci. 94, 207-225.
- 4452 Dunlop, J.A., Anderson, L.I., Kerp, H., Hass, H., 2003. A harvestman (Arachnida: Opiliones) from the
4453 Early Devonian Rhynie cherts, Aberdeenshire, Scotland. Trans. R. Soc. Edinb. Earth Sci. 94,
4454 341–354.
- 4455 Dunlop, J.A., Selden, P.A., 2009. Calibrating the chelicerate clock: a paleontological reply to
4456 Jeyaprakash and Hoy. Exp. Appl. Acarol. 48, 183–197.
- 4457 Dunlop, J.A., Zhou, G.R.S., Braddy, S.J., 2007. The affinities of the Carboniferous whip spider
4458 *Graeophonus anglicus* Pocock, 1911 (Arachnida: Amblypygi). Earth Environ. Sci. Trans. R.
4459 Soc. Edinb. 98, 165–178.
- 4460 Edgecombe, G.D., 2004. Morphological data, extant Myriapoda, and the myriapod stem-group.
4461 Contrib. Zool. 73, 267–252.
- 4462 Edgecombe, G.D., 2010. Palaeomorphology: fossils and the inference of cladistic relationships. Acta
4463 Zool. 91, 72–80.
- 4464 Edgecombe, G.D., 2011. Chilopoda—the fossil history, in: Treatise on Zoology-Anatomy, Taxonomy,
4465 Biology. The Myriapoda. pp. 355–361.

- 4466 Edgecombe, G.D., Giribet, G., 2004. Adding mitochondrial sequence data (16S rRNA and cytochrome
4467 c oxidase subunit I) to the phylogeny of centipedes (Myriapoda: Chilopoda): an analysis of
4468 morphology and four molecular loci. *J. Zool. Syst. Evol. Res.* 42, 89–134.
- 4469 Eklund, H., Doyle, J.A., Herendeen, P.S., 2004. Morphological phylogenetic analysis of living and
4470 fossil Chloranthaceae. *Int. J. Plant Sci.* 165, 107–151.
- 4471 Engel, M.S., 2005. A new sawfly from the Triassic of Queensland (Hymenoptera: Xyelidae). *Mem.*
4472 *Queensl. Mus.* 51.2, 558.
- 4473 Engel, M.S., Barden, P., Riccio, M.L., Grimaldi, D.A., 2016a. Morphologically Specialized Termite
4474 Castes and Advanced Sociality in the Early Cretaceous. *Curr. Biol.* 26, 522-530.
- 4475 Engel, M.S., Breitkreuz, L.C.V., Cai, C., Alvarado, M., Azar, D., Huang, D., 2016b. The first Mesozoic
4476 microwhip scorpion (Palpigradi): a new genus and species in mid-Cretaceous amber from
4477 Myanmar. *Sci. Nat.* 103, 1-7.
- 4478 Engel, M.S., Grimaldi, D.A., 2004. New light shed on the oldest insect. *Nature* 427, 624–627.
- 4479 Engel, M.S., Grimaldi, D., Krishna, K., 2007. Primitive termites from the Early Cretaceous of Asia
4480 (Isoptera). *Stuttg. Beitr. Naturk. Ser. B* 371.
- 4481 Engel, M.S., Grimaldi, D.A., Krishna, K., 2009. Termites (Isoptera): their phylogeny, classification, and
4482 rise to ecological dominance. *Am. Mus. Novit.* 3650, 1–27.
- 4483 Engel, M.S., Ortega-Blanco, J., Azar, D., 2011. The earliest earwigs in amber (Dermaptera): A new
4484 genus and species from the Early Cretaceous of Lebanon. *Insect Syst. Evol.* 42, 139-148.
- 4485 Engel, M.S., Wang, B., Alqarni, A.S. 2016c. A thorny, ‘anareolate’ stick-insect (Phasmatidae s.l.) in
4486 Upper Cretaceous amber from Myanmar, with remarks on diversification times among
4487 Phasmatodea. *Cretac. Res.* 63, 45-53.
- 4488 Enghoff, H., 1984. Phylogeny of millipedes—a cladistic analysis. *J. Zool. Syst. Evol. Res.* 22, 8–26.
- 4489 Enghoff, H., Short, M., Stoev, P., Wesener, T., 2015. Diplopoda—Taxonomic Overview, in: *Treatise on*
4490 *Zoology-Anatomy, Taxonomy, Biology. The Myriapoda.* p. 363.

- 4491 Farrell, Ú.C., Briggs, D.E.G., Gaines, R.R., 2011. Paleoecology of the Olenid Trilobite *Triarthrus*: New
4492 Evidence from Beecher's Trilobite Bed and Other Sites of Pyritization. *Palaios* 26, 730–742.
- 4493 Farrell, Ú.C., Martin, M.J., Hagadorn, J.W., Whiteley, T., Briggs, D.E., 2009. Beyond Beecher's
4494 Trilobite Bed: Widespread pyritization of soft tissues in the Late Ordovician Taconic foreland
4495 basin. *Geology* 37, 907–910.
- 4496 Fayers, S.R., Trewin, N.H., 2005. A hexapod from the early Devonian Windyfield chert, Rhynie,
4497 Scotland. *Palaeontology* 48, 1117–1130.
- 4498 Feldmann, R.M., Osgood Jr, R.G., Szmuc, E.J., Meinke, D.W., 1978. *Chagrinichnites brooksi*, a new
4499 trace fossil of arthropod origin. *J. Paleontol.* 287–294.
- 4500 Feldmann, R.M., Schweitzer, C.E, Hu, S., Huang, J., Zhou, C., Zhang, Q., Wen, W., Xie, T., Maguire,
4501 E., 2015. Spatial distribution of Crustacea and associated organisms in the Luoping Biota
4502 (Anisian, Middle Triassic), Yunnan Province, China: evidence of periodic mass kills. *J.*
4503 *Paleontol.* 89, 1022-1037.
- 4504 Fernández, R., Edgecombe, G.D., Giribet, G., 2016 (in press). Exploring phylogenetic relationships
4505 within Myriapoda and the effects of matrix composition and occupancy on phylogenomic
4506 reconstruction. *Syst. Biol.*
- 4507 Fernández, R., Giribet, G., 2015. Unnoticed in the tropics: phylogenomic resolution of the poorly
4508 known arachnid order Ricinulei (Arachnida). *R. Soc. Open Sci.* 2, 150065.
- 4509 Fernández, R., Hormiga, G., Giribet, G., 2014a. Phylogenomic Analysis of Spiders Reveals
4510 Nonmonophyly of Orb Weavers. *Curr. Biol.* 24, 1772–1777.
- 4511 Fernández, R., Laumer, C.E., Vahtera, V., Libro, S., Kaluziak, S., Sharma, P.P., Pérez-Porro, A.R.,
4512 Edgecombe, G.D., Giribet, G., 2014b. Evaluating Topological Conflict in Centipede Phylogeny
4513 Using Transcriptomic Data Sets. *Mol. Biol. Evol.* 31, 1500–1513.
- 4514 Filipiak, P., Zatoń, M., Szaniawski, H., Wrona, R., Racki, G., 2012. Palynology and Microfacies of
4515 Lower Devonian Mixed Carbonate-Siliciclastic Deposits in Podolia, Ukraine. *Acta Palaeontol.*
4516 *Pol.* 57, 863–877.

- 4517 Fletcher, T.P., Collins, D.H., 1998. The middle Cambrian Burgess Shale and its relationship to the
4518 Stephen Formation in the southern Canadian Rocky Mountains. *Can. J. Earth Sci.* 35, 413–
4519 436.
- 4520 Fletcher, T.P., Collins, D.H., 2003. The Burgess Shale and associated Cambrian formations west of the
4521 Fossil Gully Fault Zone on Mount Stephen, British Columbia. *Can. J. Earth Sci.* 40, 1823–1838.
- 4522 Friedemann, K., Wipfler, B., Bradler, S., Beutel, R.G., 2012. On the head morphology of *Phyllium* and
4523 the phylogenetic relationships of Phasmatodea (Insecta). *Acta Zool.* 93, 184–199.
- 4524 Friis, E.M., Pedersen, K.R., Crane, P.R., 1999. Early angiosperm diversification: the diversity of pollen
4525 associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal.
4526 *Ann. Mo. Bot. Gard.* 259–296.
- 4527 Friis, E.M., Pedersen, K.R., Crane, P.R., 2005. When Earth started blooming: insights from the fossil
4528 record. *Curr. Opin. Plant Biol.* 8, 5–12.
- 4529 Gaju-Ricart, M., Baltanás, R.M., Bach de Roca, C., 2015. Forward without wings: Current progress
4530 and future perspectives in the study of Microcoryphia and Zygentoma. *Soil Org.* 87, 183–195.
- 4531 Gale, A.S., 1996. Turonian correlation and sequence stratigraphy of the Chalk in southern England.
4532 *Geol. Soc. Lond. Spec. Publ.* 103, 177–195.
- 4533 Gale, A.S., 2015. Origin and phylogeny of verruciform barnacles (Crustacea, Cirripedia, Thoracica).
4534 *J. Syst. Palaeontol.* 13, 753–789.
- 4535 Gale, A.S., Sørensen, A.M., 2015. Origin of the balanomorph barnacles (Crustacea, Cirripedia,
4536 Thoracica): new evidence from the Late Cretaceous (Campanian) of Sweden. *J. Syst.*
4537 *Palaeontol.* 13, 791–824.
- 4538 Gallego, O.F., 2010. A new crustacean clam shrimp (Spinicaudata: Eosestheriidae) from the Upper
4539 Triassic of Argentina and its importance for “conchostracan” taxonomy. *Alcheringa* 34, 179–
4540 195.

- 4541 Gall, J.-C., 1985. Fluvial depositional environment evolving into deltaic setting with marine influences
4542 in the Buntsandstein of Northern Vosges (France), in: *Aspects of Fluvial Sedimentation in the*
4543 *Lower Triassic Buntsandstein of Europe*. Springer, pp. 449–477.
- 4544 Gall, J.-C., Grauvogel-Stamm, L., 1993. Buntsandstein (lower Triassic) of Eastern France. *Nonmarine*
4545 *Triassic Bull.* 33, 141.
- 4546 Gao, K., Ren, D., 2006. Radiometric Dating of Ignimbrite from Inner Mongolia Provides no Indication
4547 of a Post-Middle Jurassic Age for the Daohugou Beds. *Acta Geol. Sin.* 80, 42–45.
- 4548 Gao, T., Shih, C., Rasnitsyn, A.P., Xu, X., Wang, S., Ren, D., 2014. The first flea with fully distended
4549 abdomen from the Early Cretaceous of China. *BMC Evol. Biol.* 14, 168.
- 4550 Gao, T., Shih, C., Xu, X., Wang, S., Ren, D., 2012. Mid-Mesozoic Flea-like Ectoparasites of Feathered
4551 or Haired Vertebrates. *Curr. Biol.* 22, 732–735.
- 4552 Gao, Y., Bu, Y., Luan, Y.-X., 2008. Phylogenetic Relationships of Basal Hexapods Reconstructed from
4553 Nearly Complete 18S and 28S rRNA Gene Sequences. *Zoolog. Sci.* 25, 1139–1145.
- 4554 Garrison, N.L., Rodriguez, J., Agnarsson, I., Coddington, J.A., Griswold, C.E., Hamilton, C.A., Hedin,
4555 M., Kocot, K.M., Ledford, J.M., Bond, J.E., 2016. Spider phylogenomics: untangling the Spider
4556 Tree of Life. *PeerJ* 4, e1719.
- 4557 Garrouste, R., Clément, G., Nel, P., Engel, M.S., Grandcolas, P., D'Haese, C., Lagebro, L., Denayer,
4558 J., Gueriau, P., Lafaite, P., Olive, S., Prestianni, C., Nel, A., 2012. A complete insect from the
4559 Late Devonian period. *Nature* 488, 82–85.
- 4560 Garwood, R.J., Dunlop, J., 2014. Three-dimensional reconstruction and the phylogeny of extinct
4561 chelicerate orders. *PeerJ* 2, e641.
- 4562 Garwood, R.J., Dunlop, J.A., Giribet, G., Sutton, M.D., 2011. Anatomically modern Carboniferous
4563 harvestmen demonstrate early cladogenesis and stasis in Opiliones. *Nat. Commun.* 2, 444.
- 4564 Garwood, R.J., Sharma, P.P., Dunlop, J.A., Giribet, G., 2014. A Paleozoic Stem Group to Mite
4565 Harvestmen Revealed through Integration of Phylogenetics and Development. *Curr. Biol.* 24,
4566 1017–1023.

- 4567 Garwood, R., Sutton, M., 2010. X-ray micro-tomography of Carboniferous stem-Dictyoptera: new
4568 insights into early insects. *Biol. Lett.* 6, 699–702.
- 4569 Gehling, J.G., Jago, J.B., Paterson, J.R., García-Bellido, D.C., Edgecombe, G.D., 2011. The geological
4570 context of the lower Cambrian (Series 2) Emu Bay Shale Lagerstätte and adjacent
4571 stratigraphic units, Kangaroo Island, South Australia. *Aust. J. Earth Sci.* 58, 243–257.
- 4572 Getty, P.R., Sproule, R., Wagner, D.L., Bush, A.M., 2013. Variation in Wingless Insect Trace Fossils:
4573 Insights from Neoichnology and the Pennsylvanian of Massachusetts. *Palaios* 28, 243–258.
- 4574 Gibbs, G., 2010. Micropterigidae (Lepidoptera) of the Southwestern Pacific: a revision with the
4575 establishment of five new genera from Australia, New Caledonia and New Zealand. *Zootaxa*
4576 2520, 1–48.
- 4577 Giles, P.S., Naylor, R.D., Ténière, P.J., 2002. A synthesis of Carboniferous stratigraphy—Cape Breton
4578 Island, Nova Scotia, with new data from southwestern Cape Breton Island. *Atlantic Geology*
4579 38, 83.
- 4580 Giribet, G., Edgecombe, G.D., 2006. Conflict between datasets and phylogeny of centipedes: an
4581 analysis based on seven genes and morphology. *Proc. R. Soc. B Biol. Sci.* 273, 531–538.
- 4582 Giribet, G., Edgecombe, G.D., 2013. Stable phylogenetic patterns in scutigeromorph centipedes
4583 (Myriapoda : Chilopoda : Scutigeromorpha): dating the diversification of an ancient lineage of
4584 terrestrial arthropods. *Invertebr. Syst.* 27, 485–501.
- 4585 Giribet, G., Edgecombe, G.D., Wheeler, W.C., 2001. Arthropod phylogeny based on eight molecular
4586 loci and morphology. *Nature* 413, 157–161.
- 4587 Giribet, G., Edgecombe, G.D., Wheeler, W.C., Babbitt, C., 2002. Phylogeny and Systematic Position of
4588 Opiliones: A Combined Analysis of Chelicerate Relationships Using Morphological and
4589 Molecular Data. *Cladistics* 18, 5–70.

- 4590 Giribet, G., McIntyre, E., Christian, E., Espinasa, L., Ferreira, R.L., Francke, Ó.F., Harvey, M.S., Isaia,
4591 M., Kováč, Ľ., McCutchen, L., Souza, M.F., Zagamajster, M., 2014. The first phylogenetic
4592 analysis of Palpigradi (Arachnida)—the most enigmatic arthropod order. *Invertebr. Syst.* 28,
4593 350–360.
- 4594 Giribet, G., Ribera, C., 2000. A Review of Arthropod Phylogeny: New Data Based on Ribosomal DNA
4595 Sequences and Direct Character Optimization. *Cladistics* 16, 204–231.
- 4596 Glenner, H., Grygier, M.J., Høeg, J.T., Jensen, P.G., Schram, F.R., 1995. Cladistic analysis of the
4597 Cirripedia Thoracica. *Zool. J. Linn. Soc.* 114, 365–404.
- 4598 Goldring, R., Jensen, S., 1996. Trace fossils and biofabrics at the Precambrian–Cambrian boundary
4599 interval in western Mongolia. *Geol. Mag.* 133, 403–415.
- 4600 Gomez, B., Martin-Closas, C., Barale, G., Sole de porta, N., Thevenard, F., Guignard, G., 2002.
4601 *Frenelopsis* (Coniferales: Cheirolepidiaceae) and related male organ genera from the Lower
4602 Cretaceous of Spain. *Palaeontology* 45, 997–1036.
- 4603 Gorochov, A.V., 2013. No evidence for Paleozoic origin of mantises (Dictyoptera: Mantina).
4604 *Zoosystematica Ross.* 22, 6–14.
- 4605 Gratshev, V.G., Zherikhin, V.V., 2000. New Early Cretaceous weevil taxa from Spain (Coleoptera,
4606 Curculionoidea). *Acta Geológica Hispánica* 35, 37–46.
- 4607 Greenslade, P.J.M., 1988. Reply to R. A. Crowson's "Comments on Insecta of the Rhynie Chert."
4608 *Entomol. Gen.* 13, 115–117.
- 4609 Greenslade, P., Whalley, P.E.S., 1986. The systematic position of *Rhyniella praecursor* Hirst & Maulik
4610 (Collembola), the earliest known hexapod, in: *Second International Seminar on Apterygota*.
4611 University of Siena., pp. 319–323.
- 4612 Grimaldi, D., 2003. A Revision of Cretaceous Mantises and Their Relationships, Including New Taxa
4613 (Insecta: Dictyoptera: Mantodea). *Am. Mus. Novit.* 3412, 1–47.
- 4614 Grimaldi, D., Engel, M.S., 2005. *Evolution of the Insects*. Cambridge University Press, Cambridge.
- 4615 Grimaldi, D., Engel, M.S., 2006. Fossil Liposcelididae and the lice ages (Insecta: Psocodea). *Proc. R.*

- 4616 Soc. B Biol. Sci. 273, 625–633.
- 4617 Grimaldi, D.A., Engel, M.S., 2013. The Relict Scorpionfly Family Meropeidae (Mecoptera) in
4618 Cretaceous Amber. J. Kans. Entomol. Soc. 86, 253–263.
- 4619 Grimaldi, D., Shmakov, A., Fraser, N., 2004. Mesozoic Thrips and Early Evolution of the Order
4620 Thysanoptera (Insecta). J. Paleontol. 78, 941–952.
- 4621 Guan, Z., Prokop, J., Roques, P., Lapeyrie, J., Nel, A., 2016. Revision of the enigmatic insect family
4622 Anthracoptilidae enlightens the evolution of Palaeozoic stem-dictyopterans. Acta Palaeontol.
4623 Pol. 61, 71–87.
- 4624 Gueriau, P., Charbonnier, S., Clément, G., 2014. First decapod crustaceans in a Late Devonian
4625 continental ecosystem. Palaeontology 57, 1203–1213.
- 4626 Gueriau, P., Rabet, N., Clément, G., Lagebro, L., Vannier, J., Briggs, D.E.G., Charbonnier, S., Olive, S.,
4627 Béthoux, O., 2016. A 365-Million-Year-Old Freshwater Community Reveals Morphological and
4628 Ecological Stasis in Branchiopod Crustaceans. Curr. Biol. 26, 383–390.
- 4629 Guo, Y., Béthoux, O., Gu, J., Ren, D., 2013. Wing venation homologies in Pennsylvanian
4630 “cockroachoids” (Insecta) clarified thanks to a remarkable specimen from the Pennsylvanian of
4631 Ningxia (China). J. Syst. Palaeontol. 11, 41–46.
- 4632 Gutiérrez, P.R., Muzón, J., Limarino, C.O., 2000. The earliest late Carboniferous winged insect
4633 (Insecta, Protodonata) from Argentina: geographical and stratigraphical location. Ameghiniana
4634 37, 375–378.
- 4635 Handlirsch, A., 1906. Die Fossilen Insekten und die Phylogenie der Rezenten Formen, parts I–IV. Ein
4636 Handbuch für Palaontologen und Zoologen. Engelmann, Leipzig.
- 4637 Handlirsch, A., 1911. New Paleozoic insects from the vicinity of Mazon Creek, Illinois. Am. J. Sci. 297–
4638 326.
- 4639 Haring, E., Aspöck, U., 2004. Phylogeny of the Neuropterida: a first molecular approach. Syst.
4640 Entomol. 29, 415–430.
- 4641 Harvey, M.S., 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata:

- 4642 Arachnida). Invertebr. Taxon. 6, 1373-1435.
- 4643 Harvey, T.H.P., 2008. Organic-walled microfossils from the Early Cambrian of Canada (PhD).
4644 University of Cambridge, Cambridge, UK.
- 4645 Harvey, T.H.P., Butterfield, N.J., 2008. Sophisticated particle-feeding in a large Early Cambrian
4646 crustacean. Nature 452, 868–871.
- 4647 Harvey, T.H.P., Pedder, B.E., 2013. Copepod Mandible Palynomorphs from the Nolichucky Shale
4648 (Cambrian, Tennessee): Implications for the Taphonomy and Recovery of Small Carbonaceous
4649 Fossils. Palaios 28, 278–284.
- 4650 Harvey, T.H.P., Vélez, M.I., Butterfield, N.J., 2012. Exceptionally preserved crustaceans from western
4651 Canada reveal a cryptic Cambrian radiation. Proc. Natl. Acad. Sci. 109, 1589–1594.
- 4652 Haug, C., Briggs, D.E., Mikulic, D.G., Kluessendorf, J., Haug, J.T., 2014. The implications of a Silurian
4653 and other thylacocephalan crustaceans for the functional morphology and systematic affinities
4654 of the group. BMC Evol. Biol. 14, 159.
- 4655 Haug, C., Haug, J.T., 2015. The ambiguous use of the prefix “Pan” in arthropod systematics. J. Zool.
4656 Sci. 3, 19–24.
- 4657 Haug, C., Kutschera, V., Ahyong, S.T., Vega, F.J., Maas, A., Waloszek, D., Haug, J.T., 2013. Re-
4658 evaluation of the Mesozoic mantis shrimp *Ursquilla yehoachi* based on new material and the
4659 virtual peel technique. Palaeontol. Electron. 16, 1-14.
- 4660 Haug, J.T., Haug, C., Garwood, R.J., 2016. Evolution of insect wings and development - new details
4661 from Palaeozoic nymphs. Biol. Rev. 91, 53–69.
- 4662 Haug, J.T., Haug, C., Maas, A., Kutschera, V., Waloszek, D., 2010. Evolution of mantis shrimps
4663 (Stomatopoda, Malacostraca) in the light of new Mesozoic fossils. BMC Evol. Biol. 10, 290.
- 4664 Haug, J.T., Haug, C., Schweigert, G., Sombke, A., 2014. The evolution of centipede venom claws –
4665 Open questions and possible answers. Arthropod Struct. Dev. 43, 5–16.
- 4666 Haug, J.T., Labandeira, C.C., Santiago-Blay, J.A., Haug, C., Brown, S., 2015. Life habits, hox genes,
4667 and affinities of a 311 million-year-old holometabolan larva. BMC Evol. Biol. 15.

- 4668 He, H.Y., Wang, X.L., Zhou, Z.H., Zhu, R.X., Jin, F., Wang, F., Ding, X., Boven, A., 2004. $^{40}\text{Ar}/^{39}\text{Ar}$
 4669 dating of ignimbrite from Inner Mongolia, northeastern China, indicates a post-Middle Jurassic
 4670 age for the overlying Daohugou Bed. *Geophys. Res. Lett.* 31, L20609.
- 4671 Heath, T.A., Huelsenbeck, J.P., Stadler, T., 2014. The fossilized birth-death process for coherent
 4672 calibration of divergence-time estimates. *Proc. Natl. Acad. Sci.* 111, E2957–E2966.
- 4673 Hegna, T.A., 2012. Phylogeny and fossil record of branchiopod crustaceans: an integrative approach
 4674 (PhD). Yale University, New Haven.
- 4675 Hegna, T.A., Ren, D., 2010. Two new “notostracans”, *Chenops* gen. nov. and *Jeholops* gen. nov.
 4676 (Crustacea: Branchiopoda: ?Notostraca) from the Yixian Formation, Northeastern China. *Acta*
 4677 *Geol. Sin.* 84, 886–894.
- 4678 Helby, R., 1973. Review of Late Permian and Triassic palynology of New South Wales. *Geol. Soc.*
 4679 *Aust. Spec. Publ.* 4, 141–155.
- 4680 Henderickx, H., Boone, M., 2016. The basal pseudoscorpion family Feaellidae Ellingsen , 1906 walks
 4681 the Earth for 98.000.000 years: a new fossil genus has been found in Cretaceous Burmese
 4682 amber (Pseudoscorpiones: Feaellidae). *Entomo-Info* 27, 1-12.
- 4683 Henderson, C.M., Davydov and, V.I., Wardlaw, B.R., Gradstein, F.M., Hammer, O., 2012. The Permian
 4684 Period, in: *The Geologic Time Scale*. Elsevier, pp. 653–679.
- 4685 Hennig, W., 1981. *Insect Phylogeny*. John Wiley & Sons, Chichester, New York.
- 4686 Herbert, G., 1997. Sequence stratigraphic analysis of early and middle Triassic alluvial and estuarine
 4687 fades in the Sydney Basin, Australia. *Aust. J. Earth Sci.* 44, 125–143.
- 4688 Herrera, S., Watanabe, H., Shank, T.M., 2015. Evolutionary and biogeographical patterns of barnacles
 4689 from deep-sea hydrothermal vents. *Mol. Ecol.* 24, 673–689.
- 4690 Hirst, S., 1923. On some Arachnid remains from the Old Red Sandstone (Rhynie Chert Bed,
 4691 Aberdeenshire). *Ann. Mag. Nat. Hist.* 12, 455–474.
- 4692 Hirst, S., Maulik, S., 1926. On some arthropod remains from the Rhynie chert (Old Red Sandstone).
 4693 *Geol. Mag.* 63, 69–71.

- 4694 Ho, J., 1994. Copepod phylogeny: a reconsideration of Huys & Boxshall's "parsimony versus
4695 homology." *Hydrobiologia* 292, 31–39.
- 4696 Ho, S.Y.W., Phillips, M.J., 2009. Accounting for Calibration Uncertainty in Phylogenetic Estimation of
4697 Evolutionary Divergence Times. *Syst. Biol.* 58, 367–380.
- 4698 Høeg, J.T., Achituv, Y., Chan, B.K.K., Chan, K., Jensen, P.G., Pérez-Losada, M., 2009a. Cypris
4699 morphology in the barnacles *Ibla* and *Paralepas* (Crustacea: Cirripedia Thoracica) implications
4700 for cirripede evolution. *J. Morphol.* 270, 241–255.
- 4701 Høeg, J.T., Lagersson, N.C., Glenner, H., 2004. The complete cypris larva and its significance in
4702 thecostracan phylogeny, in: Scholtz, G. (Ed.), *Evolutionary and Developmental Biology of*
4703 *Crustacea*, Crustacean Issues. AA Balkema Publishers, Lisse, Netherlands, pp. 197-215.
- 4704 Høeg, J.T., Pérez-Losada, M., Glenner, H., Kolbasov, G.A., Crandall, K.A., 2009b. Evolution of
4705 morphology, ontogeny and life cycles within the Crustacea Thecostraca. *Arthropod Syst.*
4706 *Phylogeny* 67, 199–217.
- 4707 Hof, C.H., 1998. Late Cretaceous stomatopods (Crustacea, Malacostraca) from Israel and Jordan.
4708 *Contrib. Zool.* 67, 257–266.
- 4709 Horne, D.J., 1995. A revised ostracod biostratigraphy for the Purbeck-Wealden of England. *Cretac.*
4710 *Res.* 16, 639–663.
- 4711 Horne, D.J., Schon, I., Smith, R.J., Martens, K., 2005. What are Ostracoda? A cladistic analysis of the
4712 extant superfamilies of the subclasses Myodocopa and Podocopa (Crustacea: Ostracoda), in:
4713 Koenemann, S., Jenner, R.A. (Eds.), *Crustacea and Arthropod Relationships*, Crustacean
4714 Issues. CRC Press, Boca Raton, pp. 249–273.
- 4715 Hörnschemeyer, T., Haug, J.T., Béthoux, O., Beutel, R.G., Charbonnier, S., Hegna, T.A., Koch, M.,
4716 Rust, J., Wedmann, S., Bradler, S., Willmann, R., 2013. Is *Strudiella* a Devonian insect? *Nature*
4717 494, E3–E4.

- 4718 Hou, X., Williams, M., Siveter, D.J., Siveter, D.J., Aldridge, R.J., Sansom, R.S., 2010. Soft-part
4719 anatomy of the Early Cambrian bivalved arthropods *Kunyangella* and *Kunmingella*:
4720 significance for the phylogenetic relationships of Bradiriida. Proc. R. Soc. B Biol. Sci. 277,
4721 1835–1841.
- 4722 Hu, S., Zhang, Q., Chen, Z., Zhou, C., Lü, T., Xie, T., Wen, W., Huang, J., Benton, M.J., 2010. The
4723 Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-
4724 Permian mass extinction. Proc. R. Soc. B Biol. Sci. 278, 2274-2282.
- 4725 Huang, D., 2015. *Tarwinia australis* (Siphonaptera: Tarwiniidae) from the Lower Cretaceous
4726 Koonwarra fossil bed: Morphological revision and analysis of its evolutionary relationship.
4727 Cretac. Res. 52, 507–515.
- 4728 Huang, D., Nel, A., Shen, Y., Selden, P.A., Lin, Q., 2006. Discussions on the age of the Daohugou
4729 fauna--evidence from invertebrates. Prog. Nat. Sci. 16, 309–312.
- 4730 Huang, D., Nel, A., Zompro, O., Waller, A., 2008. Mantophasmatodea now in the Jurassic.
4731 Naturwissenschaften 95, 947–952.
- 4732 Huang, J.-D., Ren, D., Sinitshenkova, N.D., Shih, C.-K., 2008. New fossil mayflies (Insecta:
4733 Ephemeroptera) from the Middle Jurassic of Daohugou, Inner Mongolia, China. Insect Sci. 15,
4734 193–198.
- 4735 Huelsenbeck, J.P., 1997. Is the Felsenstein Zone a fly trap? Syst. Biol. 46, 69–74.
- 4736 Huelsenbeck, J.P., 1998. Systematic Bias in Phylogenetic Analysis: Is the Strepsiptera Problem
4737 Solved? Syst. Biol. 47, 519–537.
- 4738 Huys, R., Boxshall, G.A., 1991. Copepod Evolution. Ray Society, London.
- 4739 Huys, R., Llewellyn-Hughes, J., Conroy-Dalton, S., Olson, P.D., Spinks, J.N., Johnston, D.A., 2007.
4740 Extraordinary host switching in siphonostomatoid copepods and the demise of the
4741 Monstrilloida: Integrating molecular data, ontogeny and antennular morphology. Mol.
4742 Phylogenet. Evol. 43, 368–378.

- 4743 Ibarra-Cerdeña, C.N., Zaldívar-Riverón, A., Peterson, A.T., Sánchez-Cordero, V., Ramsey, J.M., 2014.
4744 Phylogeny and Niche Conservatism in North and Central American Triatomine Bugs
4745 (Hemiptera: Reduviidae: Triatominae), Vectors of Chagas' Disease. PLoS Negl. Trop. Dis. 8,
4746 e3266.
- 4747 Ignatov, M.S., 1992. *Bryokhutuliinia jurassica*, gen. et spec. nova, a remarkable fossil moss from
4748 Mongolia. J. Hattori Bot. Lab. p377–388.
- 4749 Ignatov, M.S., Karasev, E.V., Sinitsa, S.M., 2011. Upper Jurassic mosses from Baigul (Transbaikalia,
4750 South Siberia). Arctoa 20, 43–64.
- 4751 Inward, D., Beccaloni, G., Eggleton, P., 2007. Death of an order: a comprehensive molecular
4752 phylogenetic study confirms that termites are eusocial cockroaches. Biol. Lett. 3, 331–335.
- 4753 Isachsen, C.E., Bowring, S.A., Landing, E., Samson, S.D., 1994. New constraint on the division of
4754 Cambrian time. Geology 22, 496–498.
- 4755 Ishiwata, K., Sasaki, G., Ogawa, J., Miyata, T., Su, Z.-H., 2011. Phylogenetic relationships among
4756 insect orders based on three nuclear protein-coding gene sequences. Mol. Phylogenet. Evol.
4757 58, 169–180.
- 4758 Jaeckel, O., 1921. Einen neuen Phyllocariden aus dem Unterdevon der Bundenbacher Dachschiefer.
4759 Z. Dtsch. Geol. Ges. Monatsbericht 72, 290–292.
- 4760 Jago, J.B., García-Bellido, D.C., Gehling, J.G., 2016 (in press). An early Cambrian chelicerate from the
4761 Emu Bay Shale, South Australia. Palaeontology.
- 4762 Jago, J.B., Gehling, J.G., Paterson, J.R., Brock, G.A., Zang, W., 2012. Cambrian stratigraphy and
4763 biostratigraphy of the Flinders Range and the north coast of Kangaroo Island, South Australia.
4764 Episodes 35, 247–255.
- 4765 Jagt, J.W., Buckeridge, J.S., 2005. A case of homonymy in fossil verrucid barnacles: *Verruca withersi*
4766 (Crustacea, Thoracica). Scr. Geol. 130, 187–189.

- 4767 Jarvis, K.J., Haas, F., Whiting, M.F., 2005. Phylogeny of earwigs (Insecta: Dermaptera) based on
4768 molecular and morphological evidence: reconsidering the classification of Dermaptera. Syst.
4769 Entomol. 30, 442–453.
- 4770 Jarzembowski, E.A., 1981. An early Cretaceous termite from southern England (Isoptera:
4771 Hodotermitidae). Syst. Entomol. 6, 91–96.
- 4772 Jaume, D., Pinardo-Moya, E., Boxshall, G.A., 2013. A presumed spelaegriphacean crustacean from
4773 an upper Barremian wetland (Las Hoyas; Lower Cretaceous; Central Spain). Palaeontology 56,
4774 15-28.
- 4775 Jenkyns, H.C., Jones, C.E., Gröcke, D.R., Hesselbo, S.P., Parkinson, D.N., 2002. Chemostratigraphy
4776 of the Jurassic System: applications, limitations and implications for palaeoceanography. J.
4777 Geol. Soc. 159, 351–378.
- 4778 Jenner, R.A., Dhubhghaill, C., Ferla, M.P., Wills, M.A., 2009. Eumalacostracan phylogeny and total
4779 evidence: limitations of the usual suspects. BMC Evol. Biol. 9, 21.
- 4780 Jeram, A.J., Selden, P., Edwards, D., 1990. Land animals in the Silurian: arachnids and myriapods
4781 from Shropshire, England. Science 250, 658–661.
- 4782 Jirikowski, G.J., Richter, S., Wolff, C., 2013. Myogenesis of Malacostraca-the “egg-nauplius” concept
4783 revisited. Front. Zool. 10, 9994–10.
- 4784 Jones, W.T., Feldmann, R.M., Mikulic, D.G., 2015. Archaeostracan (Phyllocarida: Archaeostraca)
4785 antennulae and antennae: sexual dimorphism in early malacostracans and *Ceratiocaris* M'Coy,
4786 1849 as a possible stem eumalacostracan. J. Crustac. Biol. 35, 191–201.
- 4787 Jones, W.T., Feldmann, R.M., Schram, F.R., Schweitzer, C.E., Maguire, E.P., 2016. The proof is in the
4788 pouch: *Tealliocaris* is a peracarid. Palaeodiversity 9, 75-88.
- 4789 Judson, M.L., 2009. Cheliferoid pseudoscorpions (Arachnida, Chelonethi) from the Lower Cretaceous
4790 of France. Geodiversitas 31, 61–71.
- 4791 Judson, M.L., 2012. Reinterpretation of *Dracochela deprehendor* (Arachnida: Pseudoscorpiones) as a
4792 stem-group pseudoscorpion. Palaeontology 55, 261–283.

4793 Kakui, K., Katoh, T., Hiruta, S.F., Kobayashi, N., Kajihara, H., 2011. Molecular systematics of
4794 Tanaidacea (Crustacea: Peracarida) based on 18S sequence data, with an amendment of
4795 suborder/superfamily-level classification. *Zoolog. Sci.* 28, 749–757.

4796 Kaltenpoth, M., Roeser-Mueller, K., Koehler, S., Peterson, A., Nechitaylo, T.Y., Stubblefield, J.W.,
4797 Herzner, G., Seger, J., Strohm, E., 2014. Partner choice and fidelity stabilize coevolution in a
4798 Cretaceous-age defensive symbiosis. *Proc. Natl. Acad. Sci.* 111, 6359–6364.

4799 Kin, A., Blazejowski, B., 2014. The horseshoe crab of the genus *Limulus*: living fossil or stabilomorph?
4800 *PLoS ONE* 9, e108036.

4801 Kirejtshuk, A.G., Poschmann, M., Prokop, J., Garrouste, R., Nel, A., 2014. Evolution of the elytral
4802 venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera:
4803 Tshekardocoleidae). *J. Syst. Palaeontol.* 12, 575–600.

4804 Kjellesvig-Waering, E.N., 1986. A restudy of the fossil Scorpionida of the world. *Palaeontographica*
4805 *Americana* 55, 1–287.

4806 Kjer, K.M., Blahnik, R.J., Holzenthal, R.W., 2001. Phylogeny of Trichoptera (Caddisflies):
4807 Characterization of Signal and Noise Within Multiple Datasets. *Syst. Biol.* 50, 781–816.

4808 Kjer, K.M., Blahnik, R.J., Holzenthal, R.W., 2002. Phylogeny of caddisflies (Insecta, Trichoptera). *Zool.*
4809 *Scr.* 31, 83–91.

4810 Kjer, K.M., Carle, F.L., Litman, J., Ware, J.L., 2006. A molecular phylogeny of Hexapoda. *Arthropod*
4811 *Syst. Phylogeny* 64, 35–44.

4812 Kjer, K.M., Ware, J.L., Rust, J., Wappler, T., Lanfear, R., Jermiin, L.S., Zhou, X., Aspöck, H., Aspöck,
4813 U., Beutel, R.G., Blanke, A., Donath, A., Flouri, T., Frandsen, P.B., Kapli, P., Kawahara, A.Y.,
4814 Letsch, H., Mayer, C., McKenna, D.D., Meusemann, K., Niehuis, O., Peters, R.S., Wiegmann,
4815 B.M., Yeates, D.K., von Reumont, B.M., Stamatakis, A., Misof, B., 2015. Response to
4816 Comment on “Phylogenomics resolves the timing and pattern of insect evolution.” *Science* 349,
4817 487–c.

- 4818 Klopstein, S., Vilhelmsen, L., Ronquist, F., 2015. A Nonstationary Markov Model Detects Directional
4819 Evolution in Hymenopteran Morphology. *Syst. Biol.* 64, 1089–1103.
- 4820 Kluge, N.J., 1998. Phylogeny and higher classification of Ephemeroptera. *Zoosystematica Ross.* 7,
4821 255–269.
- 4822 Kluge, N.J., 2004. The Phylogenetic System of Ephemeroptera (the first experience in consistently
4823 non-ranking taxonomy) Volume 1. Ephemeroptera except for Turbanoculata and Leptophlebia.
4824 Kluwer Academic Publishers, Dordrecht-Hardbound.
- 4825 Knecht, R.J., Engel, M.S., Benner, J.S., 2011. Late Carboniferous paleoichnology reveals the oldest
4826 full-body impression of a flying insect. *Proc. Natl. Acad. Sci.* 108, 6515–6519.
- 4827 Kocarek, P., John, V., Hulva, P., 2013. When the Body Hides the Ancestry: Phylogeny of
4828 Morphologically Modified Epizoic Earwigs Based on Molecular Evidence. *PLoS ONE* 8,
4829 e66900.
- 4830 Koch, M., 1997. Monophyly and phylogenetic position of the Diplura (Hexapoda). *Pedobiologia* 41, 9–
4831 12.
- 4832 Koch, M., 2003. Character evolution in the Archaeognatha: consensus and conflict. *Entomol. Abh.* 61,
4833 120–122.
- 4834 Koch, M., 2009. Diplura, in: Resh, V.H., Carde, R.T. (Eds.), *Encyclopedia of Insects*. Academic Press,
4835 London, pp. 281–283.
- 4836 Kohli, M.K., Ware, J.L., Bechly, G., 2016. How to date a dragonfly: Fossil calibrations for odonates.
4837 *Palaeontol. Electron.* 19, 1-14.
- 4838 Kornicker, L.S., 1981. Revision, distribution, ecology, and ontogeny of the Ostrocode subfamily
4839 Cyclasteropinae (Myodocopina, Cylindroleberididae). *Smithson. Contrib. Zool.* 319, 1–548.
- 4840 Kotov, A.A., 2007. Jurassic Cladocera (Crustacea, Branchiopoda) with a description of an extinct
4841 Mesozoic order. *J. Nat. Hist.* 41, 13–37.
- 4842 Kotov, A.A., 2009. A revision of the extinct Mesozoic family Prochydoridae Smirnov, 1992 (Crustacea:
4843 Cladocera) with a discussion of its phylogenetic position. *Zool. J. Linn. Soc.* 155, 253–265.

- 4844 Kotov, A.A., 2013. Morphology and phylogeny of the Anomopoda (Crustacea: Cladocera). Scientific
4845 press Ltd KMK, Moscow.
- 4846 Krandijevsky, V.S., 1963. The ostracod fauna of Silurian localities of Podolia. AN. URSR, Inst. Geol.
4847 Nauk, Kiev, 1–176.
- 4848 Kristensen, N.P., 1981. Phylogeny of insect orders. Annu. Rev. Entomol. 26, 135–157.
- 4849 Kristensen, N.P., 1991. Phylogeny of extant hexapods. Insects Aust. 1, 125–140.
- 4850 Kristensen, N.P., Skalski, A.W., 1998. Palaeontology and phylogeny, in: Lepidoptera, Moths and
4851 Butterflies. pp. 7–25.
- 4852 Krzemiński, W., Krzeminska, E., Papier, F., 1994. *Grauvogelia arzvilleriana* sp. n.-the oldest Diptera
4853 species [Lower-Middle Triassic of France]. Acta Zool. Cracoviensia 2, 267-274.
- 4854 Kühne, W.G., Schlüter, T., 1985. A fair deal for the Devonian Arthropoda fauna of Rhynie. Entomol.
4855 Gen. 91–96.
- 4856 Kukalová-Peck, J., 1985. Ephemeroïd wing venation based upon new gigantic Carboniferous mayflies
4857 and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta,
4858 Ephemera). Can. J. Zool. 63, 933–955.
- 4859 Kukalová-Peck, J., 1991. Fossil history and the evolution of hexapod structures. Insects Aust. 1, 141–
4860 179.
- 4861 Kukalová-Peck, J., Beutel, R.G., 2012. Is the Carboniferous †*Adiphebia lacoana* really the “oldest
4862 beetle”? Critical reassessment and description of a new Permian beetle family. Eur. J. Entomol.
4863 109, 633–645.
- 4864 Kukalová-Peck, J., Willmann, R., 1990. Lower Permian “mecopteroid-like” insects from central Europe
4865 (Insecta, Endopterygota). Can. J. Earth Sci. 27, 459–468.
- 4866 Labandeira, C.C., 2011. Evidence for an Earliest Late Carboniferous Divergence Time and the Early
4867 Larval Ecology and Diversification of Major Holometabola Lineages. Entomol. Am. 117, 9–21.
- 4868 Lagebro, L., Gueriau, P., Hegna, T.A., Rabet, N., Butler, A.D., Budd, G.E., 2015. The oldest
4869 notostracan (Upper Devonian Strud locality, Belgium). Palaeontology 58, 497–509.

- 4870 Lamsdell, J.C., 2013. Revised systematics of Palaeozoic “horseshoe crabs” and the myth of
4871 monophyletic Xiphosura: Re-evaluating the Monophyly of Xiphosura. Zool. J. Linn. Soc. 167,
4872 1–27.
- 4873 Lamsdell, J.C., Briggs, D.E.G., Liu, H.P., Witzke, B.J., McKay, R.M., 2015. A new Ordovician arthropod
4874 from the Winneshiek Lagerstätte of Iowa (USA) reveals the ground plan of eurypterids and
4875 chasmataspids. Sci. Nat. 102.
- 4876 Lamsdell, J.C., McKenzie, S.C., 2015. *Tachypleus syriacus* (Woodward)—a sexually dimorphic
4877 Cretaceous crown limulid reveals underestimated horseshoe crab divergence times. Org.
4878 Divers. Evol. 15, 681–693.
- 4879 Lang, W.D., Spath, L.F., Richardson, W.A., 1923. Shales-with-“beef,” a Sequence in the Lower Lias of
4880 the Dorset Coast. Q. J. Geol. Soc. 79, 47–66.
- 4881 Larink, O., 1997. Apomorphic and plesiomorphic characteristics in Archaeognatha, Monura and
4882 Zygentoma. Pedobiologia 41, 3–8.
- 4883 Laurentiaux, D., 1952. Découverte d'un homoptère prosboloïde dans le namurien belge. Publications
4884 de l'Association pour l'Etude de la Paléontologie Bruxelles. 14, 16 pp.
- 4885 Laurie, M., 1899. On a Silurian Scorpion and some additional Eurypterid Remains from the Pentland
4886 Hills. Trans. R. Soc. Edinb. 39, 575–590.
- 4887 Lauterbach, K.E., 1989. The pan-monophylum—a practical help in phylogenetic systematics. Zool. Anz.
4888 223, 139–156.
- 4889 Lee, M.S.Y., Soubrier, J., Edgecombe, G.D., 2013. Rates of Phenotypic and Genomic Evolution during
4890 the Cambrian Explosion. Curr. Biol. 23, 1889–1895.
- 4891 Lee, S.-W., 2014. New Lower Cretaceous basal mantodean (Insecta) from the Crato Formation (NE
4892 Brazil). Geol. Carpathica 65, 285–292.
- 4893 Legalov, A.A., 2010. Checklist of Mesozoic Curculionoidea (Coleoptera) with description of new taxa.
4894 Balt. J. Coleopterol. 10, 71–101.

- 4895 Legendre, F., Nel, A., Svenson, G.J., Robillard, T., Pellens, R., Grandcolas, P., 2015. Phylogeny of
4896 Dictyoptera: Dating the Origin of Cockroaches, Praying Mantises and Termites with Molecular
4897 Data and Controlled Fossil Evidence. PLoS ONE 10, e0130127.
- 4898 Legg, D.A., 2014. *Sanctacaris uncata*: the oldest chelicerate (Arthropoda). Naturwissenschaften 101,
4899 1065–1073.
- 4900 Legg, D.A., Sutton, M.D., Edgecombe, G.D., 2013. Arthropod fossil data increase congruence of
4901 morphological and molecular phylogenies. Nat. Commun. 4.
- 4902 Lehmann, J., Murphy, M.A., 2001. A new placenticeratid ammonite from the Albian (Lower Cretaceous)
4903 of California and the inferred history of some placenticeratid and engonoceratid ammonites.
4904 Neues Jahrb. Geol. Palaontologie Monatshefte 343–358.
- 4905 Lehmann, W.M., 1944. *Palaeoscorpius devonicus* n.g., n. sp., ein Skorpion aus dem rheinischen
4906 Unterdevon. Neues Jahrbuch für Paläontologie, Monatshefte B 7, 177–185.
- 4907 Leonova, T.B., 2007. Correlation of the Kazanian of the Volga–Urals with the Roadian of the global
4908 Permian scale. Palaeoworld 16, 246–253.
- 4909 Leonova, T.B., Shilovsky, O.P., 2007. Evolution of the Permian family Spirolegoceratidae (Goniatitida,
4910 Ammonoidea). Paleontol. J. 41, 28–38.
- 4911 Letsch, H., Gottsberger, B., Ware, J.L., 2016. Not going with the flow: a comprehensive time-calibrated
4912 phylogeny of dragonflies (Anisoptera: Odonata: Insecta) provides evidence for the role of lentic
4913 habitats on diversification. Mol. Ecol. 25, 1340–1353.
- 4914 Letsch, H., Simon, S., 2013. Insect phylogenomics: new insights on the relationships of lower
4915 neopteran orders (Polyneoptera): Phylogenomics of Polyneoptera. Syst. Entomol. 38, 783–
4916 793.
- 4917 Li, G., Ando, H., Hasegawa, H., Yamamoto, M., Hasegawa, T., Ohta, T., Hasebe, N., Ichinnorov, N.,
4918 2014. Confirmation of a Middle Jurassic age for the Eedemt Formation in Dundgobi Province,
4919 southeast Mongolia: constraints from the discovery of new spinicaudatans (clam shrimps).
4920 Alcheringa 38, 305–316.

- 4921 Li, G., Matsuoka, A., 2012. Jurassic clam shrimp ("conchostracan") faunas in China. *Sci. Rep.*, Niigata
 4922 Univ. (Geology) 27, 73–88.
- 4923 Li, Y., Béthoux, O., Pang, H., Ren, D., 2013a. Early Pennsylvanian Odonatoptera from the Xiaheyuan
 4924 locality (Ningxia, China): new material, taxa, and perspectives. *Foss. Rec.* 16, 117–139.
- 4925 Li, Y., Ren, D., Pecharová, M., Prokop, J., 2013b. A new palaeodictyopterid (Insecta:
 4926 Palaeodictyoptera: Spilapteridae) from the Upper Carboniferous of China supports a close
 4927 relationship between insect faunas of Quilianshan (northern China) and Laurussia. *Alcheringa*
 4928 37, 487–495.
- 4929 Liao, W., Ruan, Y., 2003. Devonian biostratigraphy of China, in: Zhang, W., Palmer, A.R. (Eds.),
 4930 Biostratigraphy of China. Science Press, Beijing, p. 237.
- 4931 Lins, L.S.F., Ho, S.Y.W., Wilson, G.D.F., Lo, N., 2012. Evidence for Permo-Triassic colonization of the
 4932 deep sea by isopods. *Biol. Lett.* 8, 979–982.
- 4933 Linse, K., Jackson, J.A., Fitzcharles, E., Sands, C.J., Buckeridge, J.S., 2013. Phylogenetic position of
 4934 Antarctic Scalpelliformes (Crustacea: Cirripedia: Thoracica). *Deep Sea Res. Part Oceanogr.*
 4935 Res. Pap. 73, 99–116.
- 4936 Liu, Q., Zheng, D., Zhang, Q., Wang, B., Fang, Y., Zhang, H., 2014. Two new kalligrammatids (Insecta,
 4937 Neuroptera) from the Middle Jurassic of Daohugou, Inner Mongolia, China. *Alcheringa* 38, 65–
 4938 69.
- 4939 Liu, S., Gao, L., 1985. Conchostracans and spores of upper Devonian Huangjiadeng Formation in
 4940 Hubei Province. *Acta Geosci. Sin.* 7, 113–127.
- 4941 Liu, X., Wang, Y., Shih, C., Ren, D., Yang, D., 2012. Early Evolution and Historical Biogeography of
 4942 Fishflies (Megaloptera: Chauliiodinae): Implications from a Phylogeny Combining Fossil and
 4943 Extant Taxa. *PLoS ONE* 7, e40345.

- 4944 Liu, X., Winterton, S.L., Wu, C., Piper, R., Ohl, M., 2015. A new genus of mantidflies discovered in the
4945 Oriental region, with a higher-level phylogeny of Mantispidae (Neuroptera) using DNA
4946 sequences and morphology: New genus and higher phylogeny of Mantispidae. *Syst. Entomol.*
4947 40, 183–206.
- 4948 Liu, Y., Ren, D., Prokop, J., 2009a. Discovery of a new Namurian archaeorthopterid from Ningxia,
4949 China (Insecta: Archaeorthoptera). *Zootaxa* 2032, 63–68.
- 4950 Liu, Y., Sinitshenkova, N.D., Ren, D., 2009b. A revision of the Jurassic Stonefly Genera
4951 *Dobbertiniopteryx* Ansorge and *Karanemoura* Sinitshenkova (Insecta: Plecoptera), with the
4952 description of new species from the Daohugou locality, China. *Paleontol. J.* 43, 183–190.
- 4953 Liu, Y., Sinitshenkova, N.D., Ren, D., Shih, C., 2011. Pronemouridae fam. nov. (Insecta: Plecoptera),
4954 the stem group of Nemouridae and Notonemouridae, from the Middle Jurassic of Inner
4955 Mongolia, China. *Palaeontology* 54, 923–933.
- 4956 Lourenço, W.R., Gall, J.-C., 2004. Fossil scorpions from the Buntsandstein (Early Triassic) of France.
4957 *Comptes Rendus Palevol* 3, 369–378.
- 4958 Lozovsky, V.R., Minikh, M.G., Grunt, T.A., Kukhtinov, D.A., Ponomarenko, A.G., Sukacheva, I.D., 2009.
4959 The Ufimian Stage of the East European scale: Status, validity, and correlation potential.
4960 *Stratigr. Geol. Correl.* 17, 602–614.
- 4961 Lucas, S.G., Tanner, L.H., Kozur, H.W., Weems, R.E., Heckert, A.B., 2012. The Late Triassic
4962 timescale: Age and correlation of the Carnian–Norian boundary. *Earth-Sci. Rev.* 114, 1–18.
- 4963 Lukashevich, E.D., Przhiboro, A.A., Marchal-Papier, F., Grauvogel-Stamm, L., 2010. The oldest
4964 occurrence of immature Diptera (Insecta), Middle Triassic, France. *Ann. Société Entomol. Fr.*
4965 46, 4–22.
- 4966 Lyal, C.H.C., 1985. Phylogeny and classification of the Psocodea, with particular reference to the lice
4967 (Psocodea: Phthiraptera). *Syst. Entomol.* 10, 145–165.

- 4968 Macchioni, F., 2002. Myths and legends in the correlation between the Boreal and Tethyan Realms.
4969 Implications on the dating of the Early Toarcian mass extinctions and the Oceanic Anoxic
4970 Event. *Geobios* 35, 150–164.
- 4971 MacNaughton, R.B., Narbonne, G.M., 1999. Evolution and ecology of Neoproterozoic-Lower Cambrian
4972 trace fossils, NW Canada. *Palaios* 97–115.
- 4973 Maksoud, S., Azar, D., Granier, B., Gèze, R., 2016 (in press). New data on the age of the Lower
4974 Cretaceous amber outcrops of Lebanon. *Palaeoworld*.
- 4975 Maksoud, S., Granier, B., Azar, D., Gèze, R., Paicheler, J.-C., Moreno-Bedmar, J.A., 2014. Revision
4976 of “Falaise de Blanche” (Lower Cretaceous) in Lebanon, with the definition of a Jezzinian
4977 Regional Stage. *Carnets Geol.-Noteb. Geol.* 14, 401–427.
- 4978 Małkowski, K., Racki, G., Drygant, D., Szaniawski, H., 2009. Carbon isotope stratigraphy across the
4979 Silurian–Devonian transition in Podolia, Ukraine: evidence for a global biogeochemical
4980 perturbation. *Geol. Mag.* 146, 674.
- 4981 Malm, T., Johanson, K.A., Wahlberg, N., 2013. The evolutionary history of Trichoptera (Insecta): A
4982 case of successful adaptation to life in freshwater. *Syst. Entomol.* 38, 459–473.
- 4983 Marden, J.H., 2013a. Reply to “Comment on Marden (2013) regarding the interpretation of the earliest
4984 trace fossil of a winged insect.” *Evolution* 67, 2150–2153.
- 4985 Marden, J.H., 2013b. Reanalysis and experimental evidence indicate that the earliest trace fossil of a
4986 winged insect was a surface-skimming neopteran: trace fossil of a Carboniferous neopteran
4987 insect. *Evolution* 67, 274–280.
- 4988 Mark, D.F., Rice, C.M., Fallick, A.E., Trewin, N.H., Lee, M.R., Boyce, A., Lee, J.K.W., 2011. $^{40}\text{Ar}/^{39}\text{Ar}$
4989 dating of hydrothermal activity, biota and gold mineralization in the Rhynie hot-spring system,
4990 Aberdeenshire, Scotland. *Geochim. Cosmochim. Acta* 75, 555–569.
- 4991 Mark, D.F., Rice, C.M., Trewin, N.H., 2013. Discussion on “A high-precision U–Pb age constraint on
4992 the Rhynie Chert Konservat-Lagerstätte: time scale and other implications”. *J. Geol. Soc.* 170,
4993 701–703.

- 4994 Marshall, J.E.A., 1991. Palynology of the Stonehaven Group, Scotland: evidence for a Mid Silurian
4995 age and its geological implications. *Geol. Mag.* 128, 283–286.
- 4996 Marshall, C.R., 2008. A simple method for bracketing absolute divergence times on molecular
4997 phylogenies using multiple fossil calibration points. *Am. Nat.* 171, 726–742.
- 4998 Martill, D.M., 2007. The age of the Cretaceous Santana Formation fossil Konservat Lagerstätte of
4999 north-east Brazil: a historical review and an appraisal of the biochronostratigraphic utility of its
5000 palaeobiota. *Cretac. Res.* 28, 895–920.
- 5001 Martill, D.M., Bechly, G., Loveridge, R.F., 2007. The Crato fossil beds of Brazil: Window into an ancient
5002 world. Cambridge University Press, Cambridge.
- 5003 Martín-Closas, C., Clavel, B., Schroeder, R., Charollais, J., Conrad, M.-A., 2009. Charophytes from
5004 the Barremian-lower Aptian of the Northern Subalpine Chains and Jura Mountains, France:
5005 correlation with associated marine assemblages. *Cretac. Res.* 30, 49–62.
- 5006 Martín-Closas, C., López-Morón, N., 1995. The charophyte flora, in: Montsec and Montral-Alcover.
5007 Two Konservat Lagerstätten, Catalonia, Spain. II International Symposium on Lithographic
5008 Limestones Field Trip Book. pp. 29–31.
- 5009 Martínez, C., Madriñán, S., Zavada, M., Alberto Jaramillo, C., 2013. Tracing the fossil pollen record of
5010 *Hedyosmum* (Chloranthaceae), an old lineage with recent Neotropical diversification. *Grana*
5011 52, 161–180.
- 5012 Martins-Neto, R.G., Gallego, O.F., Zavattieri, A.M., 2008. The Triassic insect fauna from Argentina:
5013 Coleoptera, Hemiptera and Orthoptera from the Potrerillos Formation, south of cerro Cacheuta,
5014 Cuyana basin. *Alavesia* 2, 47–58.
- 5015 Martynov, A.V., 1927. Jurassic fossil insects from Turkestan. 7. Some Odonata, Neuroptera,
5016 Thysanoptera. *Ezhegodnik Russkogo Paleontologicheskogo Obshchestva* 21, 757–768.
- 5017 Massoud, Z., 1967. Contribution à l'étude de *Rhyniella praecursor* Hirst et Maulik 1926, Collembola
5018 fossile du Dévonien. *Rev. Ecol. Biol. Sol.* 4, 497–505.

- 5019 Mathers, T.C., Hammond, R.L., Jenner, R.A., Hänfling, B., Gómez, A., 2013. Multiple global radiations
5020 in tadpole shrimps challenge the concept of “living fossils.” *PeerJ* 1, e62.
- 5021 Ma, X., Liao, W., Wang, D., 2009. The Devonian System of China, with a discussion on sea-level
5022 change in South China. *Geol. Soc. Lond. Spec. Publ.* 314, 241–262.
- 5023 McCafferty, W.P., 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta): a
5024 commentary on systematics. *Ann. Entomol. Soc. Am.* 84, 343–360.
- 5025 McGhee, G.R., 2013. When the invasion of land failed: the legacy of the Devonian extinctions.
5026 Columbia University Press, New York.
- 5027 McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W.,
5028 Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., Mchugh, J.V.,
5029 Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Słipiński, A.,
5030 Maddison, D.R., Farrell, B.D., 2015. The beetle tree of life reveals that Coleoptera survived
5031 end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution:
5032 Phylogeny and evolution of Coleoptera (beetles). *Syst. Entomol.* 40, 835–880.
- 5033 Meland, K., Mees, J., Porter, M.L., Wittmann, K.J., 2015. Taxonomic review of the orders Mysida and
5034 Stygiomysida (Crustacea, Peracarida). *PLoS ONE* 10, e0124656.
- 5035 Meland, K., Willassen, E., 2007. The disunity of “Mysidacea” (Crustacea). *Mol. Phylogenet. Evol.* 44,
5036 1083–1104.
- 5037 Melchin, M.J., Sadler, P.M., Cramer, B.D., Cooper, R.A., Gradstein, F.M., Hammer, O., 2012. The
5038 Silurian Period, in: *The Geologic Time Scale*. Elsevier, pp. 525–558.
- 5039 Mendes, L.F., Poinar, G.O., 2008. A new fossil silverfish (*Zygentoma*: Insecta) in Mesozoic Burmese
5040 amber. *Eur. J. Soil Biol.* 44, 491–494.
- 5041 Mendes, L.F., Wunderlich, J., 2013. New data on thysanurans preserved in Burmese amber
5042 (*Microcoryphia* and *Zygentoma* Insecta). *Soil Org.* 85, 11–22.

- 5043 Menning, M., Alekseev, A.S., Chuvashov, B.I., Davydov, V.I., Devuyst, F.-X., Forke, H.C., Grunt, T.A.,
 5044 Hance, L., Heckel, P.H., Izokh, N.G., Jin, Y.-G., Jones, P.J., Kotlyar, G.V., Kozur, H.W.,
 5045 Nemyrovska, T.I., Schneider, J.W., Wang, X.-D., Weddige, K., Weyer, D., Work, D.M., 2006.
 5046 Global time scale and regional stratigraphic reference scales of Central and West Europe, East
 5047 Europe, Tethys, South China, and North America as used in the Devonian–Carboniferous–
 5048 Permian Correlation Chart 2003 (DCP 2003). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 240,
 5049 318–372.
- 5050 Menon, F., 2007. Higher systematics of scorpions from the Crato Formation, Lower Cretaceous of
 5051 Brazil. *Palaeontology* 50, 185–195.
- 5052 Meusemann, K., von Reumont, B.M., Simon, S., Roeding, F., Strauss, S., Kuck, P., Ebersberger, I.,
 5053 Walz, M., Pass, G., Breuers, S., Achter, V., von Haeseler, A., Burmester, T., Hadrys, H.,
 5054 Wagele, J.W., Misof, B., 2010. A Phylogenomic Approach to Resolve the Arthropod Tree of
 5055 Life. *Mol. Biol. Evol.* 27, 2451–2464.
- 5056 Michel, L.A., Tabor, N.J., Montañez, I.P., Schmitz, M.D., Davydov, V.I., 2015. Chronostratigraphy and
 5057 Paleoclimatology of the Lodève Basin, France: Evidence for a pan-tropical aridification event
 5058 across the Carboniferous–Permian boundary. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 430,
 5059 118–131.
- 5060 Michels, J., Schnack-Schiel, S.B., 2005. Feeding in dominant Antarctic copepods? Does the
 5061 morphology of the mandibular gnathobases relate to diet? *Mar. Biol.* 146, 483–495.
- 5062 Miller, J.F., Loch, J.D., Taylor, J.F., 2012. Biostratigraphy of Cambrian and Lower Ordovician strata in
 5063 the Llano uplift, central Texas, in: Derby, J.R., Fritz, R.D., Longacre, S.A., Morgan, W.A.,
 5064 Sternbach, C.A. (Eds.), *The Great American Carbonate Bank: The Geology and Economic
 5065 Resources of the Cambrian – Ordovician Sauk Megasequence of Laurentia*, AAPG Memoir.
 5066 pp. 187–202.
- 5067 Minet, J., Huang, D.-Y., Wu, H., Nel, A., 2010. Early Mecoptera and the systematic position of the
 5068 Microptysmatidae (Insecta: Endopterygota). *Ann. Société Entomol. Fr.* 46, 262–270.

5069 Minxiao, W., Song, S., Chaolun, L., Xin, S., 2011. Distinctive mitochondrial genome of Calanoid
 5070 copepod *Calanus sinicus* with multiple large non-coding regions and reshuffled gene order:
 5071 Useful molecular markers for phylogenetic and population studies. BMC Genomics 12, 73.
 5072 Misof, B., Liu, S., Meusemann, K., Peters, R.S., Donath, A., Mayer, C., Frandsen, P.B., Ware, J.,
 5073 Flouri, T., Beutel, R.G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J.,
 5074 Aberer, A.J., Aspöck, U., Aspöck, H., Bartel, D., Blanke, A., Berger, S., Böhm, A., Buckley, T.R.,
 5075 Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang,
 5076 Y., Jermini, L.S., Kawahara, A.Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li,
 5077 Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D.D., Meng, G., Nakagaki, Y.,
 5078 Navarrete-Heredia, J.L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont,
 5079 B.M., Schütte, K., Sekiya, K., Shimizu, S., Slipinski, A., Stamatakis, A., Song, W., Su, X.,
 5080 Szucsich, N.U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein,
 5081 M., Tong, X., Uchifune, T., Walz, M.G., Wiegmann, B.M., Wilbrandt, J., Wipfler, B., Wong,
 5082 T.K.F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D.K., Yoshizawa, K., Zhang, Q.,
 5083 Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Li, Y., Xu,
 5084 X., Zhang, Y., Yang, H., Wang, J., Wang, J., Kjer, K.M., Zhou, X., 2014. Phylogenomics
 5085 resolves the timing and pattern of insect evolution. Science 346, 763–767.
 5086 Miyazawa, H., Ueda, C., Yahata, K., Su, Z.-H., 2014. Molecular phylogeny of Myriapoda provides
 5087 insights into evolutionary patterns of the mode in post-embryonic development. Sci. Rep. 4,
 5088 4127.
 5089 Moisan, P., Labandeira, C.C., Matushkina, N.A., Wappler, T., Voigt, S., Kerp, H., 2012. Lycopsid–
 5090 arthropod associations and odonatopteran oviposition on Triassic herbaceous *Isoetites*.
 5091 Palaeogeogr. Palaeoclimatol. Palaeoecol. 344–345, 6–15.

- 5092 Møller, O.S., Olesen, J., Avenant-Oldewage, A., Thomsen, P.F., Glenner, H., 2008. First maxillae
5093 suction discs in Branchiura (Crustacea): Development and evolution in light of the first
5094 molecular phylogeny of Branchiura, Pentastomida, and other “Maxillopoda.” *Arthropod Struct.*
5095 *Dev.* 37, 333–346.
- 5096 Morel, E.M., Artabe, A.E., Spalletti, L.A., 2003. Triassic floras of Argentina: biostratigraphy, floristic
5097 events and comparison with other areas of Gondwana and Laurasia. *Alcheringa* 27, 231–243.
- 5098 Morse, J.C., 1997. Phylogeny of Trichoptera. *Annu. Rev. Entomol.* 42, 427–450.
- 5099 Mortimore, R., 2011. A chalk revolution: what have we done to the Chalk of England? *Proc. Geol.*
5100 *Assoc.* 122, 232–297.
- 5101 Mound, L.A., Morris, D.C., 2007. The insect order Thysanoptera: Classification versus systematics.
5102 *Zootaxa* 1668, 395–411.
- 5103 Mouro, L.D., Zatoń, M., Fernandes, A.C.S., Waichel, B.L., 2016. Larval cases of caddisfly (Insecta:
5104 Trichoptera) affinity in Early Permian marine environments of Gondwana. *Sci. Rep.* 6, 19215.
- 5105 Müller, K.J., 1983. Crustacea with preserved soft parts from the Upper Cambrian of Sweden. *Lethaia*
5106 16, 93–109.
- 5107 Mundel, P., 1979. The centipedes (Chilopoda) of the Mazon Creek, in: *Mazon Creek Fossils.*
5108 Academic Press, New York, pp. 361–378.
- 5109 Murienne, J., Edgecombe, G.D., Giribet, G., 2010. Including secondary structure, fossils and molecular
5110 dating in the centipede tree of life. *Mol. Phylogenet. Evol.* 57, 301–313.
- 5111 Murienne, J., Harvey, M.S., Giribet, G., 2008. First molecular phylogeny of the major clades of
5112 Pseudoscorpiones (Arthropoda: Chelicerata). *Mol. Phylogenet. Evol.* 49, 170–184.
- 5113 Murphy, J.L., 1973. Protosalvinia (*Foerstia*) Zone in the Upper Devonian sequence of eastern Ohio,
5114 northwestern Pennsylvania, and western New York. *Geol. Soc. Am. Bull.* 84, 3405–3410.
- 5115 Narbonne, G.M., Myrow, P.M., Landing, E., Anderson, M.M., 1987. A candidate stratotype for the
5116 Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern
5117 Newfoundland. *Can. J. Earth Sci.* 24, 1277–1293.

- 5118 Near T.J., Meylan, P.A., Shaffer, H.B., 2005. Assessing concordance of fossil calibration points in
5119 molecular clock studies: an example using turtles. *Am. Nat.* 165, 137-146.
- 5120 Nel, A., Delfosse, E., 2011. A New Chinese Mesozoic Stick Insect. *Acta Palaeontol. Pol.* 56, 429–432.
- 5121 Nel, A., Gand, G., Garric, J., Lapeyrie, J., 1999. The first recorded protozygopteran insects from the
5122 Upper Permian of France. *Palaeontology* 42, 83–97.
- 5123 Nel, A., Marie, V., Schmeibner, S., 2002. Revision of the Lower Mesozoic dragonfly family
5124 Triasolestidae Tillyard, 1918 (Odonata: Epiproctophora). *Ann. Paléontol.* 88, 189-214.
- 5125 Nel, A., Prokop, J., Nel, P., Grandcolas, P., Huang, D.-Y., Roques, P., Guilbert, E., Dostál, O., Szwedo,
5126 J., 2012. Traits and evolution of wing venation pattern in paraneopteran insects. *J. Morphol.*
5127 273, 480–506.
- 5128 Nel, A., Roques, P., Nel, P., Prokin, A.A., Bourgoin, T., Prokop, J., Szwedo, J., Azar, D., Desutter-
5129 Grandcolas, L., Wappler, T., Garrouste, R., Coty, D., Huang, D., Engel, M.S., Kirejtshuk, A.G.,
5130 2013. The earliest known holometabolous insects. *Nature* 503, 257–261.
- 5131 Nel, A., Roques, P., Nel, P., Prokop, J., Steyer, J.S., 2007. The earliest holometabolous insect from the
5132 Carboniferous: a “crucial” innovation with delayed success (Insecta Protomeropina
5133 Protomeropidae). *Ann. Société Entomol. Fr.* 43, 349–355.
- 5134 Nel, P., Azar, D., Prokop, J., Roques, P., Hodebert, G., Nel, A., 2012. From Carboniferous to Recent:
5135 wing venation enlightens evolution of thysanopteran lineage. *J. Syst. Palaeontol.* 10, 385–399.
- 5136 Nguyen Duy-Jacquemin, M.N., Azar, D., 2004. The oldest records of Polyxenida (Myriapoda,
5137 Diplopoda): new discoveries from the Cretaceous ambers of Lebanon and France.
5138 *Geodiversitas* 26, 631–641.
- 5139 Nicholson, D.B., Mayhew, P.J., Ross, A.J., 2015. Changes to the Fossil Record of Insects through
5140 Fifteen Years of Discovery. *PLoS ONE* 10, e0128554.

5141 Niehuis, O., Hartig, G., Grath, S., Pohl, H., Lehmann, J., Tafer, H., Donath, A., Krauss, V., Eisenhardt,
 5142 C., Hertel, J., Petersen, M., Mayer, C., Meusemann, K., Peters, R.S., Stadler, P.F., Beutel, R.G.,
 5143 Bornberg-Bauer, E., McKenna, D.D., Misof, B., 2012. Genomic and Morphological Evidence
 5144 Converge to Resolve the Enigma of Strepsiptera. *Curr. Biol.* 22, 1309–1313.

5145 Nielsen, A.T., Weidner, T., Terfelt, F., Høyberget, M., 2014. Upper Cambrian (Furongian)
 5146 biostratigraphy in Scandinavia revisited: definition of superzones. *GFF* 136, 193–197.

5147 Nielsen, C., 1995. *Animal evolution: Interrelationships of living Phyla*. Oxford University Press, Oxford.

5148 Norell, M.A., Novacek, M.J., 1992. Congruence between superpositional and phylogenetic patterns:
 5149 Comparing cladistics patterns with fossil records. *Cladistics* 8, 319–337.

5150 Novojilov, N.I., 1970. *Vymershie limnadioidei (Conchostraca-Limnadioidea)*. Nauka, Moscow.

5151 Novokshonov, V.G., 1994. Permian Scorpionflies (Insecta, Panorpidia) of the Families Kaltanidae,
 5152 Permochoristidae and Robinjohniidae. *Paleontol. Zhurnal* 65–76.

5153 Oakley, T.H., 2003. On homology of arthropod compound eyes. *Integr. Comp. Biol.* 43, 522–530.

5154 Oakley, T.H., Wolfe, J.M., Lindgren, A.R., Zaharoff, A.K., 2013. Phylotranscriptomics to Bring the
 5155 Understudied into the Fold: Monophyletic Ostracoda, Fossil Placement, and Pancrustacean
 5156 Phylogeny. *Mol. Biol. Evol.* 30, 215–233.

5157 Obst, M., Faurby, S., Bussarawit, S., Funch, P., 2012. Molecular phylogeny of extant horseshoe crabs
 5158 (Xiphosura, Limulidae) indicates Paleogene diversification of Asian species. *Mol. Phylogenet.*
 5159 *Evol.* 62, 21–26.

5160 O'Connor, A., Wills, M.A., 2016 (in press). Measuring stratigraphic congruence across trees, higher
 5161 taxa and time. *Syst. Biol.*

5162 Ogden, T.H., Gattolliat, J.L., Sartori, M., Staniczek, A.H., Soldán, T., Whiting, M.F., 2009. Towards a
 5163 new paradigm in mayfly phylogeny (Ephemeroptera): combined analysis of morphological and
 5164 molecular data. *Syst. Entomol.* 34, 616–634.

5165 Ogden, T.H., Whiting, M.F., 2005. Phylogeny of Ephemeroptera (mayflies) based on molecular
 5166 evidence. *Mol. Phylogenet. Evol.* 37, 625–643.

- 5167 Ogg, J.G., 2012. Triassic, in: The Geologic Time Scale. Elsevier, pp. 681–730.
- 5168 Ogg, J.G., Hinnov, L.A., Huang, C., 2012a. Cretaceous, in: The Geologic Time Scale. Elsevier, pp.
5169 793–853.
- 5170 Ogg, J.G., Hinnov, L.A., Huang, C., 2012b. Jurassic, in: The Geologic Time Scale. Elsevier, pp. 731–
5171 791.
- 5172 Ogg, J.G., Huang, C., Hinnov, L.A., 2014. Triassic timescale status: A brief overview. *Albertiana* 41, 3–
5173 30.
- 5174 Olempska, E., Horne, D.J., Szaniawski, H., 2012. First record of preserved soft parts in a Palaeozoic
5175 podocopid (Metacopina) ostracod, *Cytherellina submagna*: phylogenetic implications. *Proc. R.*
5176 *Soc. B Biol. Sci.* 279, 564–570.
- 5177 Olesen, J., 1998. A phylogenetic analysis of the Conchostraca and Cladocera (Crustacea,
5178 Branchiopoda, Diplostraca). *Zool. J. Linn. Soc.* 122, 491–536.
- 5179 Olesen, J., 2007. Monophyly and phylogeny of Branchiopoda, with focus on morphology and
5180 homologies of branchiopod phyllopodous limbs. *J. Crustac. Biol.* 27, 165–183.
- 5181 Olesen, J., 2009. Phylogeny of Branchiopoda (Crustacea)—character evolution and contribution of
5182 uniquely preserved fossils. *Arthropod Syst. Phylogeny* 67, 3–39.
- 5183 O'Reilly, J.E., dos Reis, M., Donoghue, P.C.J., 2015. Dating tips for divergence-time estimation.
5184 *Trends Genet.* 31, 637–650.
- 5185 Orr, P.J., Briggs, D.E.G., 1999. Exceptionally preserved conchostracans and other crustaceans from
5186 the Upper Carboniferous of Ireland. *Spec. Pap. Palaeontol.* 62, 1–68.
- 5187 Ortega-Hernández, J., 2016. Making sense of “lower” and “upper” stem-group Euarthropoda, with
5188 comments on the strict use of the name Arthropoda von Siebold, 1848: Upper and lower stem-
5189 Euarthropoda. *Biol. Rev.* 91, 255–273.

- 5190 Ottone, E.G., Monti, M., Marsicano, C.A., de la Fuente, M.S., Naipauer, M., Armstrong, R., Mancuso,
5191 A.C., 2014. A new Late Triassic age for the Puesto Viejo Group (San Rafael depocenter,
5192 Argentina): SHRIMP U–Pb zircon dating and biostratigraphic correlations across southern
5193 Gondwana. *J. South Am. Earth Sci.* 56, 186–199.
- 5194 Owen, C.L., Bracken-Grissom, H., Stern, D., Crandall, K.A., 2015. A synthetic phylogeny of freshwater
5195 crayfish: insights for conservation. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 20140009.
- 5196 Pálffy, J., Smith, P.L., Mortensen, J.K., 2000. A U–Pb and $^{40}\text{Ar}/^{39}\text{Ar}$ time scale for the Jurassic. *Can. J.*
5197 *Earth Sci.* 37, 923–944.
- 5198 Pálffy, J., Smith, P.L., Mortensen, J.K., 2002. Dating the end-Triassic and Early Jurassic mass
5199 extinctions, correlative large igneous provinces, and isotopic events. *Spec. Pap.-Geol. Soc.*
5200 *Am.* 523–532.
- 5201 Palmer, A.R., 1954. The faunas of the Riley Formation in central Texas. *J. Paleontol.* 709–786.
- 5202 Palopoli, M.F., Minot, S., Pei, D., Satterly, A., Endrizzi, J., 2014. Complete mitochondrial genomes of
5203 the human follicle mites *Demodex brevis* and *D. folliculorum*: novel gene arrangement,
5204 truncated tRNA genes, and ancient divergence between species. *BMC Genomics* 15, 1124.
- 5205 Parham, J.F., Donoghue, P.C.J., Bell, C.J., Calway, T.D., Head, J.J., Holroyd, P.A., Inoue, J.G., Irmis,
5206 R.B., Joyce, W.G., Ksepka, D.T., Patane, J.S.L., Smith, N.D., Tarver, J.E., van Tuinen, M.,
5207 Yang, Z., Angielczyk, K.D., Greenwood, J.M., Hipsley, C.A., Jacobs, L., Makovicky, P.J., Müller,
5208 J., Smith, K.T., Theodor, J.M., Warnock, R.C.M., Benton, M.J., 2012. Best Practices for
5209 Justifying Fossil Calibrations. *Syst. Biol.* 61, 346–359.
- 5210 Parry, S.F., Noble, S.R., Crowley, Q.G., Wellman, C.H., 2011. A high-precision U–Pb age constraint on
5211 the Rhynie Chert Konservat-Lagerstätte: time scale and other implications. *J. Geol. Soc.* 168,
5212 863–872.
- 5213 Parry, S.F., Noble, S.R., Crowley, Q.G., Wellman, C.H., 2013. Reply to Discussion on “A high-precision
5214 U–Pb age constraint on the Rhynie Chert Konservat-Lagerstätte: time scale and other
5215 implications” *Journal*, 168, 863–872. *J. Geol. Soc.* 170, 703–706.

- 5216 Peñalver, E., Delclòs, X., 2010. Spanish amber, in: Penney, D. (Ed.), Biodiversity of Fossils in Amber
5217 from the Major World Deposits. pp. 236–270.
- 5218 Peng, N., Liu, Y., Kuang, H., Jiang, X., Xu, H., 2012. Stratigraphy and Geochronology of Vertebrate
5219 Fossil-Bearing Jurassic Strata from Linglongta, Jianchang County, Western Liaoning,
5220 Northeastern China. *Acta Geol. Sin.* 86, 1326–1339.
- 5221 Peng, S., 2003. Chronostratigraphic subdivision of the Cambrian of China. *Geol. Acta* 1, 135-144.
- 5222 Peng, S., 2009. The newly-developed Cambrian biostratigraphic succession and chronostratigraphic
5223 scheme for South China. *Chin. Sci. Bull.* 54, 4161–4170.
- 5224 Peng, S., Babcock, L.E., 2008. Cambrian Period, in: *The Concise Geologic Time Scale*. Cambridge
5225 University Press, Cambridge, pp. 37–46.
- 5226 Peng, S., Babcock, L.E., Cooper, R.A., 2012. The Cambrian Period, in: *The Geologic Time Scale*.
5227 Elsevier, pp. 437–488.
- 5228 Pepato, A.R., da Rocha, C.E., Dunlop, J.A., 2010. Phylogenetic position of the acariform mites:
5229 sensitivity to homology assessment under total evidence. *BMC Evol. Biol.* 10, 235.
- 5230 Pepato, A.R., Klimov, P.B., 2015. Origin and higher-level diversification of acariform mites – evidence
5231 from nuclear ribosomal genes, extensive taxon sampling, and secondary structure alignment.
5232 *BMC Evol. Biol.* 15.
- 5233 Pérez-Losada, M., Harp, M., Høeg, J.T., Achituv, Y., Jones, D., Watanabe, H., Crandall, K.A., 2008.
5234 The tempo and mode of barnacle evolution. *Mol. Phylogenet. Evol.* 46, 328–346.
- 5235 Pérez-Losada, M., Høeg, J.T., Crandall, K.A., 2009a. Remarkable convergent evolution in specialized
5236 parasitic Thecostraca (Crustacea). *BMC Biol.* 7, 15.
- 5237 Pérez-Losada, M., Høeg, J.T., Crandall, K.A., 2009b. Stalked and acorn barnacles (Thoracica), in:
5238 Hedges, B.S., Kumar, S. (Eds.), *The Timetree of Life*. Oxford University Press, Oxford, pp. 298-
5239 301.

- 5240 Pérez-Losada, M., Høeg, J.T., Simon-Blecher, N., Achituv, Y., Jones, D., Crandall, K.A., 2014.
5241 Molecular phylogeny, systematics and morphological evolution of the acorn barnacles
5242 (Thoracica: Sessilia: Balanomorpha). *Mol. Phylogenet. Evol.* 81, 147–158.
- 5243 Perrier, V., Charbonnier, S., 2014. The Montceau-les-Mines Lagerstätte (Late Carboniferous, France).
5244 *Comptes Rendus Palevol* 13, 353–367.
- 5245 Peters, R.S., Meusemann, K., Petersen, M., Mayer, C., Wilbrandt, J., Ziesmann, T., Donath, A., Kjer,
5246 K.M., Aspöck, U., Aspöck, H., Aberer, A., Stamatakis, A., Friedrich, F., Hunefeld, F. Niehuis, O.,
5247 Beutel, R.G., Misof, B., 2014. The evolutionary history of holometabolous insects inferred from
5248 transcriptome-based phylogeny and comprehensive morphological data. *BMC Evol. Biol.* 14,
5249 52.
- 5250 Petrunina, A.S., Neretina, T.V., Mugue, N.S., Kolbasov, G.A., 2014. Tantulocarida versus Thecostraca:
5251 inside or outside? First attempts to resolve phylogenetic position of Tantulocarida using gene
5252 sequences. *J. Zool. Syst. Evol. Res.* 52, 100–108.
- 5253 Petrunkevitch, A., 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. Yale
5254 University Press, New Haven.
- 5255 Petrunkevitch, A., 1949. A study of the structure classification and relationships of the Palaeozoic
5256 Arachnida based on the collections of the British Museum. *Transactions of the Connecticut*
5257 *Academy of Arts and Sciences* 37, 69–315.
- 5258 Plotnick, R.E., 1999. Habitat of Llandoveryan-Lockhovian eurypterids, in: Boucot, A.J., Lawson, J.D.
5259 (Eds.), *Paleocommunities - a Case Study from the Silurian and Lower Devonian*. Cambridge
5260 University Press, Cambridge, pp. 106–136.
- 5261 Pocock, R.I., 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain.
5262 Palaeontographical Society, London.
- 5263 Poinar, G., 2015. Rickettsial-like cells in the Cretaceous tick, *Cornupalpatum burmanicum* (Ixodida:
5264 Ixodidae). *Cretac. Res.* 52, 623–627.

- 5265 Poinar, G., Brown, A.E., 2003. A new genus of hard ticks in Cretaceous Burmese amber (Acari:
5266 Ixodida: Ixodidae). *Syst. Parasitol.* 54, 199–205.
- 5267 Pointon, M.A., Chew, D.M., Ovtcharova, M., Sevastopulo, G.D., Crowley, Q.G., 2012. New high-
5268 precision U–Pb dates from western European Carboniferous tuffs; implications for time scale
5269 calibration, the periodicity of late Carboniferous cycles and stratigraphical correlation. *J. Geol.*
5270 *Soc. Lond.* 169, 713–721.
- 5271 Polly, P.D., Ksepka, D.T., Parham, J.F., 2015. Announcing the Fossil Calibration Series and Database.
5272 *Palaeontol. Electron.* 18, 1–5.
- 5273 Ponomarenko, A.G., 1977. Suborder Adephaga, Polyphaga Incertae Sedis, Infraorder Staphyliniformia,
5274 in *Mezozoiskie zhestkokryiye [Mesozoic Coleoptera]*. *Akad. Nauk SSSR Tr. Paleontol. Instituta*
5275 161, 17–119.
- 5276 Pons, D., Berthou, P.Y., Campos, D. de A., 1990. Quelques observations sur la palynologie de l'Aptien
5277 Supérieur et de l'Albien du bassin d'Araripe (NE du Brésil). *Atas Do* 1, 241–252.
- 5278 Poore, G.C.B., 2005. Peracarida: monophyly, relationships and evolutionary success. *Nauplius* 13, 1–
5279 27.
- 5280 Pritykina, L.N., 1981. *Noviye Triasoviye Strekozy Sredney Azii [New Triassic dragonflies from Central*
5281 *Asia]*. *Trudy Paleontologicheskogo Instituta* 183, 5–42.
- 5282 Prokop, J., Krzeminski, W., Krzeminska, E., Hörschemeyer, T., Ilger, J.-M., Brauckmann, C.,
5283 Grandcolas, P., Nel, A., 2014. Late Palaeozoic Paoliida is the sister group of Dictyoptera
5284 (Insecta: Neoptera). *J. Syst. Palaeontol.* 12, 601–622.
- 5285 Prokop, J., Krzemiński, W., Krzemińska, E., Wojciechowski, D., 2012. Paoliida, a Putative Stem-Group
5286 of Winged Insects: Morphology of New Taxa from the Upper Carboniferous of Poland. *Acta*
5287 *Palaeontol. Pol.* 57, 161–173.
- 5288 Prokop, J., Nel, A., 2007. An enigmatic Palaeozoic stem-group: Paoliida, designation of new taxa from
5289 the Upper Carboniferous of the Czech Republic (Insecta: Paoliidae, Katerinkidae fam. n.). *Afr.*
5290 *Invertebr.* 48, 77–86.

- 5291 Prokop, J., Nel, A., 2009. Systematic position of *Triplosoba*, hitherto the oldest mayfly, from Upper
5292 Carboniferous of Commeny in Central France (Insecta: Palaeodictyoptera). Syst. Entomol.
5293 34, 610-615.
- 5294 Prokop, J., Nel, A., Hoch, I., 2005. Discovery of the oldest known Pterygota in the Lower
5295 Carboniferous of the Upper Silesian Basin in the Czech Republic (Insecta: Archaeorthoptera).
5296 Geobios 38, 383–387.
- 5297 Prokop, J., Nel, A., Tenny, A., 2010. On the phylogenetic position of the palaeopteran
5298 Syntonopteroidea (Insecta: Ephemeroptera), with a new species from the Upper Carboniferous
5299 of England. Org. Divers. Evol. 10, 331–340.
- 5300 Prokop, J., Rodrigues Fernandes, F., Lapeyrie, J., Nel, A., 2015. Discovery of the first lacewings
5301 (Neuroptera: Permithonidae) from the Guadalupian of the Lodève Basin (Southern France).
5302 Geobios 48, 263–270.
- 5303 Purdy, D.J., Cranfield, L.C., 2013. Ipswich Basin, in: Jell, P.A. (Ed.), Geology of Queensland.
5304 Geological Survey of Queensland, Brisbane, pp. 391-396.
- 5305 Raasch, G.O., 1951. Revision of Croixian dikelocephalids. III. Acad. Sci. Trans. 44, 137–151.
- 5306 Racheboeuf, P.R., Vannier, J., Anderson, L.I., 2002. A New Three-Dimensionally Preserved
5307 Xiphosuran Chelicerate from the Montceau-Les-Mines Lagerstätte (Carboniferous, France).
5308 Palaeontology 45, 125–147.
- 5309 Rainford, J.L., Hofreiter, M., Nicholson, D.B., Mayhew, P.J., 2014. Phylogenetic Distribution of Extant
5310 Richness Suggests Metamorphosis Is a Key Innovation Driving Diversification in Insects. PLoS
5311 ONE 9, e109085.
- 5312 Rasnitsyn, A.P., 1964. New Triassic Hymenoptera of the Middle Asia. Paleontol. Zhurnal 1, 88–96.
- 5313 Rasnitsyn, A.P., Quicke, D.L.J., 2002. History of Insects. Kluwer Academic Publishers, Dordrecht;
5314 Boston.
- 5315 Rees, D.J., Noever, C., Høeg, J.T., Ommundsen, A., Glenner, H., 2014. On the Origin of a Novel
5316 Parasitic-Feeding Mode within Suspension-Feeding Barnacles. Curr. Biol. 24, 1429–1434.

5317 Regier, J.C., Mitter, C., Zwick, A., Bazinet, A.L., Cummings, M.P., Kawahara, A.Y., Sohn, J.-C., Zwickl,
 5318 D.J., Cho, S., Davis, D.R., Baixeras, J., Parr, C., Weller, S., Lees, D.C., Mitter, K.T., 2013. A
 5319 large-scale, higher-level, molecular phylogenetic study of the insect order Lepidoptera (moths
 5320 and butterflies). PLoS ONE 8, e58568.

5321 Regier, J.C., Shultz, J.W., Kambic, R.E., 2005. Pancrustacean phylogeny: hexapods are terrestrial
 5322 crustaceans and maxillopods are not monophyletic. Proc. R. Soc. B Biol. Sci. 272, 395–401.

5323 Regier, J.C., Shultz, J.W., Zwick, A., Hussey, A., Ball, B., Wetzler, R., Martin, J.W., Cunningham, C.W.,
 5324 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding
 5325 sequences. Nature 463, 1079–1083.

5326 Rehm, P., Borner, J., Meusemann, K., von Reumont, B.M., Simon, S., Hadrys, H., Misof, B.,
 5327 Burmester, T., 2011. Dating the arthropod tree based on large-scale transcriptome data. Mol.
 5328 Phylogenet. Evol. 61, 880–887.

5329 Rehm, P., Meusemann, K., Borner, J., Misof, B., Burmester, T., 2014. Phylogenetic position of
 5330 Myriapoda revealed by 454 transcriptome sequencing. Mol. Phylogenet. Evol. 77, 25–33.

5331 Reiss, Z., Almogi-Labin, A., Lewy, Z., Moshkovitz, S., 1986. Biostratigraphic datums in the Senonian of
 5332 Israel. Proc. K. Ned. Akad. Van Wet. Ser. B Palaeontol. Geol. Phys. Chem. Anthropol. 89, 95–
 5333 104.

5334 Remy, J.M., Avnimelech, M., 1955. *Eryon yehoachi* nov. sp. et *Cenomanocarcinus* cf. *vanstraeleni*
 5335 Stenzel Crustacés décapodes du Crétacé supérieur de l'état de l'Israël. Bull. Société
 5336 Géologique Fr. 5, 311–314.

5337 Ren, D., Labandeira, C.C., Santiago-Blay, J.A., Rasnitsyn, A.P., Shih, C., Bashkuev, A., Logan, M.A.V.,
 5338 Hotton, C.L., Dilcher, D.L., 2009. A Probable Pollination Mode Before Angiosperms: Eurasian,
 5339 Long-Proboscis Scorpionflies. Science 326, 840–846.

5340 Ren, D., Nel, A., Prokop, J., 2008. New early griffenfly, *Sinomeganeura huangheensis* from the Late
 5341 Carboniferous of northern China (Meganisoptera: Meganeuridae). Insect Syst. Evol. 39, 223–
 5342 229.

- 5343 Richards, B.C., 2013. Current status of the International Carboniferous time scale. Carbonif.-Permian
5344 Transit. NM Mus. Nat. Hist. Sci Bull 60, 348–353.
- 5345 Richardson, J.B., Bonamo, P.M., McGregor, D.C., 1993. The spores of *Leclercqia* and the dispersed
5346 spore morphon *Acinosporites lindlarensis* Riegel: a case of gradualistic evolution. Bull. Nat.
5347 Hist. Mus. Geol. Ser. 49, 121–155.
- 5348 Richter, S., Olesen, J., Wheeler, W.C., 2007. Phylogeny of Branchiopoda (Crustacea) based on a
5349 combined analysis of morphological data and six molecular loci. Cladistics 23, 301–336.
- 5350 Richter, S., Scholtz, G., 2001. Phylogenetic analysis of the Malacostraca (Crustacea). J. Zool. Syst.
5351 Evol. Res. 39, 113–136.
- 5352 Riek, E.F., 1976. New Upper Permian insects from Natal, South Africa. Ann. Natal Mus. 22, 755–789.
- 5353 Riek, E.F., Kukalová-Peck, J., 1984. A new interpretation of dragonfly wing venation based upon Early
5354 Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states
5355 in pterygote wings. Can. J. Zool. 62, 1150–1166.
- 5356 Rogers, D.C., 2013. Anostraca catalogus (Crustacea: Branchiopoda). Raffles Bull Zool 61, 525–546.
- 5357 Rogers, R.R., Swisher III, C.C., Sereno, P.C., Monetta, A.M., Forster, C.A., Martínez, R.N., 1993. The
5358 Ischigualasto Tetrapod assemblage (Late Triassic, Argentina) and ⁴⁰Ar/³⁹Ar dating of dinosaur
5359 origins. Science 260, 794–797.
- 5360 Ronquist, F., Klopstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D.L., Rasnitsyn, A.P., 2012. A
5361 Total-Evidence Approach to Dating with Fossils, Applied to the Early Radiation of the
5362 Hymenoptera. Syst. Biol. 61, 973–999.
- 5363 Ross, A.J., Cook, E., 1995. The stratigraphy and palaeontology of the Upper Weald Clay (Barremian)
5364 at Smokejacks Brickworks, Ockley, Surrey, England. Cretac. Res. 16, 705–716.
- 5365 Ross, A.J., York, P.V., 2003. A catalogue of the type and figured specimens of Hexapoda from the
5366 Rhynie chert (early Devonian) at The Natural History Museum, London, UK. Trans. R. Soc.
5367 Edinb. Earth Sci. 94.

- 5368 Rota-Stabelli, O., Campbell, L., Brinkmann, H., Edgecombe, G.D., Longhorn, S.J., Peterson, K.J.,
5369 Pisani, D., Philippe, H., Telford, M.J., 2011. A congruent solution to arthropod phylogeny:
5370 phylogenomics, microRNAs and morphology support monophyletic Mandibulata. *Proc. R. Soc.*
5371 *B Biol. Sci.* 278, 298–306.
- 5372 Rota-Stabelli, O., Daley, A.C., Pisani, D., 2013a. Molecular timetrees reveal a Cambrian colonization of
5373 land and a new scenario for ecdysozoan evolution. *Curr. Biol.* 23, 392–398.
- 5374 Rota-Stabelli, O., Lartillot, N., Philippe, H., Pisani, D., 2013b. Serine codon-usage bias in deep
5375 phylogenomics: Pancrustacean relationships as a case study. *Syst. Biol.* 62, 121–133.
- 5376 Rudkin, D.M., Cuggy, M.B., Young, G.A., Thompson, D.P., 2013. An Ordovician pycnogonid (sea
5377 spider) with serially subdivided 'head' region. *J. Paleontol.* 87, 395–405.
- 5378 Rudkin, D.M., Young, G.A., Nowlan, G.S., 2008. The Oldest Horseshoe Crab: A New Xiphosurid from
5379 Late Ordovician Konservat-Lagerstätten Deposits, Manitoba, Canada: The Oldest Horseshoe
5380 Crab. *Palaeontology* 51, 1–9.
- 5381 Sánchez-García, A., Peñalver, E., Pérez-de la Fuente, R., Delclòs, X., 2015. A rich and diverse
5382 tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-
5383 producing forests in North Iberia: palaeobiological implications. *J. Syst. Palaeontol.* 13, 645–
5384 676.
- 5385 Sanders, H.L., 1963. Significance of the Cephalocarida, in: Whittington, H.B., Rolfe, W.D.I. (Eds.),
5386 *Phylogeny and Evolution of Crustacea*. Museum of Comparative Zoology, Cambridge, MA, pp.
5387 163–175.
- 5388 Sanders, K.L., Lee, M.S.Y., 2010. Arthropod molecular divergence times and the Cambrian origin of
5389 pentastomids. *Syst. Biodivers.* 8, 63–74.

5390 Sanggaard, K.W., Bechsgaard, J.S., Fang, X., Duan, J., Dyrland, T.F., Gupta, V., Jiang, X., Cheng, L.,
 5391 Fan, D., Feng, Y., Han, L., Huang, Z., Wu, Z., Liao, L., Settepani, V., Thøgersen, I.B.,
 5392 Vanthournout, B., Wang, T., Zhu, Y., Funch, P., Enghild, J.J., Schauser, L., Andersen, S.U.,
 5393 Villesen, P., Schierup, M.H., Bilde, T., Wang, J., 2014. Spider genomes provide insight into
 5394 composition and evolution of venom and silk. *Nat. Commun.* 5, 3765.
 5395 Sano, M., Nishibe, Y., Tanaka, Y., Nishida, S., 2015. Temporally sustained dietary niche partitioning in
 5396 two mesopelagic copepod species and their mouthpart morphology. *Mar. Ecol. Prog. Ser.* 518,
 5397 51–67.
 5398 Sasaki, G., Ishiwata, K., Machida, R., Miyata, T., Su, Z.-H., 2013. Molecular phylogenetic analyses
 5399 support the monophyly of Hexapoda and suggest the paraphyly of Entognatha. *BMC Evol.*
 5400 *Biol.* 13, 236.
 5401 Sawin, R.S., Franseen, E.K., West, R.R., Ludvigson, G.A., Watney, W.L., 2008. Clarification and
 5402 changes in Permian stratigraphic nomenclature in Kansas. Kansas Geological Survey.
 5403 Schachat, S.R., Brown, R.L., 2015. Color Pattern on the Forewing of *Micropterix* (Lepidoptera:
 5404 Micropterigidae): Insights into the Evolution of Wing Pattern and Wing Venation in Moths. *PLoS*
 5405 *ONE* 10, e0139972.
 5406 Schachat, S.R., Brown, R.L., 2016. Forewing color pattern in Micropterigidae (Insecta: Lepidoptera):
 5407 homologies between contrast boundaries, and a revised hypothesis for the origin of symmetry
 5408 systems. *BMC Evol. Biol.* 16, 116.
 5409 Schawaller, W., Shear, W.A., Bonamo, P.M., 1991. The first Paleozoic pseudoscorpions (Arachnida,
 5410 Pseudoscorpionida). *Am. Mus. Novit.* 3009, 1-17.
 5411 Schneider, J.W., Körner, F., Roscher, M., Kroner, U., 2006. Permian climate development in the
 5412 northern peri-Tethys area — The Lodève basin, French Massif Central, compared in a
 5413 European and global context. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 240, 161–183.
 5414 Scholtz, G., 2000. Evolution of the nauplius stage in malacostracan crustaceans. *J. Zool. Syst. Evol.*
 5415 *Res.* 38, 175–187.

- 5416 Schram, F.R., 1970. Isopod from the Pennsylvanian of Illinois. *Science* 169, 854–855.
- 5417 Schram, F.R., 1975. A Pennsylvanian Lepadomorph Barnacle from the Mazon Creek Area, Illinois. *J.*
5418 *Paleontol.* 49, 928–930.
- 5419 Schram, F.R., 1984. Fossil Syncarida. *Trans. San Diego Soc. Nat. Hist.* 20, 189–246.
- 5420 Schram, F.R., 1986. *Crustacea*. Oxford University Press, New York.
- 5421 Schram, F.R., 2014. Family level classification within Thylacocephala, with comments on their
5422 evolution and possible relationships. *Crustaceana* 87, 340–363.
- 5423
- 5424 Schram, F.R., Dixon, C.J., 2004. Decapod phylogeny: addition of fossil evidence to a robust
5425 morphological cladistic data set. *Bull. Mizunami Foss. Mus.* 31, 1–19.
- 5426 Schram, F.R., Feldmann, R.M., Copeland, M.J., 1978. The Late Devonian Palaeopalaemonidae and
5427 the earliest decapod crustaceans. *J. Paleontol.* 1375–1387.
- 5428 Schram, F.R., Hof, C.H., 1998. Fossils and the interrelationships of major crustacean groups, in:
5429 Edgecombe, G.D. (Ed.), *Arthropod Fossils and Phylogeny*. Columbia University Press, New
5430 York, pp. 233–302.
- 5431 Schram, F.R., Hof, C.H., Steeman, F.A., 1999. Thylacocephala (Arthropoda: Crustacea?) from the
5432 Cretaceous of Lebanon and implications for thylacocephalan systematics. *Palaeontology* 42,
5433 769–797.
- 5434 Schram, F.R., Koenemann, S., 2004. Are the crustaceans monophyletic?, in: Cracraft, J., Donoghue,
5435 M.J. (Eds.), *Assembling the Tree of Life*. Oxford University Press, New York. pp. 319–329.
- 5436 Schram, F.R., Newman, W.A., 1980. *Verruca withersi* n. sp. (Crustacea: Cirripedia) from the middle of
5437 the Cretaceous of Colombia. *J. Paleontol.* 229–233.
- 5438 Schwarz, A., Cabezas-Cruz, A., Kopecký, J., Valdés, J.J., 2014. Understanding the evolutionary
5439 structural variability and target specificity of tick salivary Kunitz peptides using next generation
5440 transcriptome data. *BMC Evol. Biol.* 14, 1.

- 5441 Schweigert, G., Dietl, G., 1997. Ein fossiler Hundertfüßler (Chilopoda, Geophilida) aus dem
5442 Nusplinger Plattenkalk (Oberjura, Südwestdeutschland). Stuttg. Beitrage Naturkunde B Geol.
5443 Palaontologie 254, 1–111.
- 5444 Schwentner, M., Clavier, S., Fritsch, M., Olesen, J., Padhye, S., Timms, B.V., Richter, S., 2013.
5445 *Cyclestheria hislopi* (Crustacea: Branchiopoda): A group of morphologically cryptic species with
5446 origins in the Cretaceous. Mol. Phylogenet. Evol. 66, 800–810.
- 5447 Schwentner, M., Timms, B.V., Bastrop, R., Richter, S., 2009. Phylogeny of Spinicaudata
5448 (Branchiopoda, Crustacea) based on three molecular markers – An Australian origin for
5449 *Limnadopsis*. Mol. Phylogenet. Evol. 53, 716–725.
- 5450 Scourfield, D.J., 1926. On a New Type of Crustacean from the Old Red Sandstone (Rhynie Chert Bed,
5451 Aberdeenshire)-*Lepidocaris rhyniensis*, gen. et sp. nov. Philos. Trans. R. Soc. Lond. Ser. B
5452 Contain. Pap. Biol. Character 214, 153–187.
- 5453 Scourfield, D.J., 1940a. Two New and Nearly Complete Specimens of Young Stages of the Devonian
5454 Fossil Crustacean *Lepidocaris rhyniensis*. Proc. Linn. Soc. London 152, 290–298.
- 5455 Scourfield, D.J., 1940b. The oldest known fossil insect. Nature 3682, 799–801.
- 5456 Scudder, S.H., 1885. Palaeodictyoptera; Or the Affinities and Classification of Paleozoic Hexapoda.
5457 Mem. Boston Soc. Nat. Hist. 3, 319–351.
- 5458 Scudder, S.H., 1890a. Illustrations of the Carboniferous Arachnida of North America, of the orders
5459 Anthracomarti and Pedipalpi. Mem. Boston Soc. Nat. Hist. 4, 443–456.
- 5460 Scudder, S.H., 1890b. New Carboniferous Myriapoda from Illinois. Mem. Boston Soc. Nat. Hist. 4,
5461 417–442.
- 5462 Secrétan, S., Riou, B., 1983. Un groupe énigmatique de crustacés, ses représentants du Callovien de
5463 La Voulte- sur- Rhône. Ann. Paléontol. 69, 59–97.
- 5464 Secrétan, S., Riou, B., 1986. Les Mysidacés (Crustacea, Peracarida) du Callovien de La Voulte- sur-
5465 Rhône. Ann. Paléontol. 72, 295–323.

- 5466 Selden, P.A., 1996. First fossil mesothele spider, from the Carboniferous of France. *Rev. Suisse Zool.*
5467 2, 585–96.
- 5468 Selden, P.A., 2000. *Palaeothele*, replacement name for the fossil mesothele spider *Eothele* Selden
5469 non Rowell. *Bull.-Br. Arachnol. Soc.* 11, 292–292.
- 5470 Selden, P.A., Huys, R., Stephenson, M.H., Heward, A.P., Taylor, P.N., 2010. Crustaceans from bitumen
5471 clast in Carboniferous glacial diamictite extend fossil record of copepods. *Nat. Commun.* 1, 1–
5472 6.
- 5473 Selden, P.A., Lamsdell, J.C., Qi, L., 2015. An unusual euchelicerate linking horseshoe crabs and
5474 eurypterids, from the Lower Devonian (Lochkovian) of Yunnan, China. *Zool. Scr.* 44, 645–652.
- 5475 Selden, P.A., Shcherbakov, D.E., Dunlop, J.A., Eskov, K.Y., 2014. Arachnids from the Carboniferous of
5476 Russia and Ukraine, and the Permian of Kazakhstan. *Paläontol. Z.* 88, 297–307.
- 5477 Selden, P.A., Shear, W.A., 1996. The first Mesozoic Solifugae (Arachnida), from the Cretaceous of
5478 Brazil, and a redescription of the Palaeozoic solifuge. *Palaeontology* 39, 583–604.
- 5479 Sellards, E.H., 1907. Types of Permian Insects Part II Plectoptera. *Am. J. Sci.* 23, 345–355.
- 5480 Servais, T., Lehnert, O., Li, J., Mullins, G.L., Munnecke, A., Nützel, A., Vecoli, M., 2008. The Ordovician
5481 Biodiversification: revolution in the oceanic trophic chain. *Lethaia* 41, 99–109.
- 5482 Servais, T., Owen, A.W., Harper, D.A.T., Kröger, B., Munnecke, A., 2010. The Great Ordovician
5483 Biodiversification Event (GOBE): The palaeoecological dimension. *Palaeogeogr.*
5484 *Palaeoclimatol. Palaeoecol.* 294, 99–119.
- 5485 Shabica, C.W., Hay, A., 1997. Richardson's guide to the fossil fauna of Mazon Creek. Northeastern
5486 Illinois University, Chicago.
- 5487 Sharma, P.P., Fernández, R., Esposito, L.A., González-Santillan, E., Monod, L., 2015. Phylogenomic
5488 resolution of scorpions reveals multilevel discordance with morphological phylogenetic signal.
5489 *Proc. R. Soc. B Biol. Sci.* 282, 20142953.

- 5490 Sharma, P.P., Kaluziak, S.T., Pérez-Porro, A.R., González, V.L., Hormiga, G., Wheeler, W.C., Giribet,
5491 G., 2014. Phylogenomic Interrogation of Arachnida Reveals Systemic Conflicts in Phylogenetic
5492 Signal. *Mol. Biol. Evol.* 31, 2963–2984.
- 5493 Sharov, A.G., 1961. Otryad Plecoptera (Order Plecoptera). *Paleozojskoe nasekomye Kuznetskovo*
5494 *bassejna* [Paleozoic insects from the Kuznetsk basin]. *Tr. Paleontol. Instituta Akad. Nauk*
5495 *SSSR* 85, 225–234.
- 5496 Shcherbakov, D.E., 1995. A new genus of the Paleozoic order Hypoperlida. *Russ. Entomol. J.* 3, 33–
5497 36.
- 5498 Shcherbakov, D.E., 2000. Permian faunas of Homoptera (Hemiptera) in relation to phytogeography
5499 and the Permo-Triassic crisis. *Paleontol. J.* 34, S251–S267.
- 5500 Shcherbakov, D.E., 2008. On Permian and Triassic insect faunas in relation to biogeography and the
5501 Permian-Triassic crisis. *Paleontol. J.* 42, 15–31.
- 5502 Shear, W.A., Bonamo, P.M., 1988. Devonobiomorpha, a new order of centipeds (Chilopoda) from the
5503 Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centiped orders. *Am.*
5504 *Mus. Novit.* 2927, 1-30.
- 5505 Shear, W.A., Jeram, A.J., Selden, P., 1998. Centiped legs (Arthropoda, Chilopoda, Scutigermorpha)
5506 from the Silurian and Devonian of Britain and the Devonian of North America. *Am. Mus. Novit.*
5507 3231, 1-16.
- 5508 Shelomi, M., Danchin, E.G.J., Heckel, D., Wipfler, B., Bradler, S., Zhou, X., Pauchet, Y., 2016.
5509 Horizontal gene transfer of pectinases from bacteria preceded the diversification of stick and
5510 leaf insects. *Sci. Rep.* 6, 26388.
- 5511 Shen, X., Tian, M., Yan, B., Chu, K., 2015. Phylomitogenomics of Malacostraca (Arthropoda:
5512 Crustacea). *Acta Oceanol. Sin.* 34, 84–92.
- 5513 Shen, Y.-B., 1978. Leaid conchostracans from the Middle Devonian of South China with notes on their
5514 origin, classification and evolution. *Papers for the International Symposium on the Devonian*
5515 *System.* 1-15.

- 5516 Shen, Y.-B., 1983. Restudy of Devonian leaiid conchostracans from Hunan and Guangdong provinces.
5517 Bull. Nanjing Inst. Geol. Palaeontol. Acad. Sin. 6, 185–207.
- 5518 Shen, Y.-B., 1994. A new conchostracan genus (*Loxomegaglyptidae*) from Lower Carboniferous of
5519 Britain. Acta Palaeontol. Sin. 33, 156–165.
- 5520 Shen, Y.-B., Huang, D., 2008. Extant clam shrimp egg morphology: taxonomy and comparison with
5521 other fossil branchiopod eggs. J. Crustac. Biol. 28, 352–360.
- 5522 Shen, Y.-B., Schram, F.R., 2014. Soft-body preservation in the leaiid clam shrimp (Branchiopoda,
5523 Diplostraca) and its palaeoecological implications. Crustaceana 87, 1338–1350.
- 5524 Shen, Y.-B., Taylor, R.S., Schram, F.R., 1998. A new spelaeogriphacean (Crustacea: Peracarida) from
5525 the Upper Jurassic of China. Contrib. Zool. 68, 19–35.
- 5526 Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age
5527 constraint on Burmese amber based on U–Pb dating of zircons. Cretac. Res. 37, 155–163.
- 5528 Shmakov, A.S., 2008. The Jurassic thrips *Liassothrips crassipes* (Martynov, 1927) and its taxonomic
5529 position in the order Thysanoptera (Insecta). Paleontol. J. 42, 47–52.
- 5530 Shmakov, A.S., 2009. The oldest members of the families Aeolothripidae and Thripidae (Insecta:
5531 Thysanoptera) from the Lower Cretaceous of Transbaikalia. Paleontol. J. 43, 428–432.
- 5532 Shultz, J.W., 2007. A phylogenetic analysis of the arachnid orders based on morphological characters.
5533 Zool. J. Linn. Soc. 150, 221–265.
- 5534 Siddall, M.E., Whiting, M.F., 1999. Long-branch abstractions. Cladistics 15, 9–24.
- 5535 Simon, S., Narechania, A., DeSalle, R., Hadrys, H., 2012. Insect Phylogenomics: Exploring the Source
5536 of Incongruence Using New Transcriptomic Data. Genome Biol. Evol. 4, 1295–1309.
- 5537 Simon, S., Strauss, S., von Haeseler, A., Hadrys, H., 2009. A Phylogenomic Approach to Resolve the
5538 Basal Pterygote Divergence. Mol. Biol. Evol. 26, 2719–2730.
- 5539 Sinitsa, S.M., Starukhina, L.P., 1986. New data and problems of stratigraphy and paleontology of
5540 Upper Mesozoic of Trans-Baikal region. New Data Trans-Baikal Geol. 46–51.

- 5541 Sinitshenkova, N.D., 1987. Historical development of stoneflies. Tr Paleontol Inst Akad Nauk SSSR
5542 221, 1–143.
- 5543 Sinitshenkova, N.D., 2005. The oldest known record of an imago of Nemouridae (Insecta: Perlida =
5544 Plecoptera) in the late Mesozoic of eastern Transbaikalia. Paleontol. J. 39, 38–40.
- 5545 Sinitshenkova, N.D., Marchal-Papier, F., Grauvogel-Stamm, L., Gall, J.-C., 2005. The Ephemeroidea
5546 (Insecta) from the Grès à Voltzia (early Middle Triassic) of the Vosges (NE France). Paläontol.
5547 Z. 79, 377–397.
- 5548 Siveter, D.J., 2008. The Silurian Herefordshire Konservat-Lagerstätte: a unique window on the
5549 evolution of life. Proc. Shropsh. Geol. Soc. 13, 58–61.
- 5550 Siveter, D.J., Briggs, D.E.G., Siveter, D.J., Sutton, M.D., Joomun, S.C., 2013. A Silurian myodocope
5551 with preserved soft-parts: cautioning the interpretation of the shell-based ostracod record.
5552 Proc. R. Soc. B Biol. Sci. 280, 20122664.
- 5553 Siveter, D.J., Sutton, M.D., Briggs, D.E., Siveter, D.J., 2004. A Silurian sea spider. Nature 431, 978–
5554 980.
- 5555 Siveter, D.J., Tanaka, G., Farrell, Ú.C., Martin, M.J., Siveter, D.J., Briggs, D.E.G., 2014. Exceptionally
5556 Preserved 450-Million-Year-Old Ordovician Ostracods with Brood Care. Curr. Biol. 24, 801–
5557 806.
- 5558 Smith, M.R., Ortega-Hernández, J., 2014. *Hallucigenia*'s onychophoran-like claws and the case for
5559 Tactopoda. Nature 514, 363–366.
- 5560 Sohn, J.-C., Labandeira, C.C., Davis, D.R., 2015. The fossil record and taphonomy of butterflies and
5561 moths (Insecta, Lepidoptera): implications for evolutionary diversity and divergence-time
5562 estimates. BMC Evol. Biol. 15, 12.
- 5563 Sohn, J.-C., Labandeira, C.C., Davis, D.R., Mitter, C., 2012. An annotated catalog of fossil and
5564 subfossil Lepidoptera (Insecta: Holometabola) of the world. Zootaxa 3286, 1–132.

- 5565 Sologlad, M.E., Fet, V., Kovařík, F., 2005. The systematic position of the scorpion genera
5566 *Heteroscorpion* Birula, 1903 and *Urodacus* Peters, 1861 (Scorpiones: Scorpionoidea).
5567 *Euscorpius* 2005, 1–37.
- 5568 Song, F., Li, H., Jiang, P., Zhou, X., Liu, J., Sun, C., Vogler, A.P., Cai, W., 2016. Capturing the
5569 phylogeny of Holometabola with mitochondrial genome data and Bayesian site-heterogeneous
5570 mixture models. *Genome Biol. Evol.* 8, 1411–1426.
- 5571 Song, H., Amédégno, C., Cigliano, M.M., Desutter-Grandcolas, L., Heads, S.W., Huang, Y., Otte, D.,
5572 Whiting, M.F., 2015. 300 million years of diversification: elucidating the patterns of orthopteran
5573 evolution based on comprehensive taxon and gene sampling. *Cladistics* 31, 621–651.
- 5574 Soriano, C., Gratshev, V.G., Delclòs, X., 2006. New Early Cretaceous weevils (Insecta, Coleoptera,
5575 Curculionoidea) from El Montsec, Spain. *Cretac. Res.* 27, 555–564.
- 5576 Sowerby, J.C., 1836. Descriptive notes respecting the shells figured in Plates XI–XXIII Appendix A:
5577 335–348, in: Fitton, W.H. (Ed.), *Observations on Some of the Strata between the Chalk and the*
5578 *Oxford Oolite in the South-East of England*, Transactions of the Geological Society of London.
5579 pp. 103–389.
- 5580 Spalletti, L.A., Fanning, M., Rapela, C.W., 2009. Dating the Triassic continental rift in the southern
5581 Andes: the Potrerillos Formation, Cuyo basin, Argentina. *Geol. Acta* 6, 267–283.
- 5582 Spears, T., Abele, L.G., 2000. Branchiopod Monophyly and Interordinal Phylogeny Inferred from 18s
5583 Ribosomal DNA. *J. Crustac. Biol.* 20, 1–24.
- 5584 Spears, T., DeBry, R.W., Abele, L.G., Chodyla, K., 2005. Peracarid monophyly and interordinal
5585 phylogeny inferred from nuclear small-subunit ribosomal DNA sequences (Crustacea:
5586 Malacostraca: Peracarida). *Proc. Biol. Soc. Wash.* 118, 117–157.
- 5587 Sroka, P., Staniczek, A.H., Bechly, G., 2015. Revision of the giant pterygote insect *Bojophlebia prokopi*
5588 Kukalová-Peck, 1985 (Hydropalaeoptera: Bojophlebiidae) from the Carboniferous of the Czech
5589 Republic, with the first cladistic analysis of fossil palaeopterous insects. *J. Syst. Palaeontol.* 13,
5590 963–982.

- 5591 Staniczek, A., Bechly, G., Godunko, R., 2011. Coxoplectoptera, a new fossil order of Palaeoptera
5592 (Arthropoda: Insecta), with comments on the phylogeny of the stem group of mayflies
5593 (Ephemeroptera). *Insect Syst. Evol.* 42, 101–138.
- 5594 Starr, H.W., Hegna, T.A., McMenamin, M.A.S., 2016 (in press). Epilogue to the tale of the Triassic
5595 amphipod: *Rosagammarus* McMenamin, Zapata and Hussey, 2013 is a decapod tail (Luning
5596 Formation, Nevada, USA). *J. Crustac. Biol.*
- 5597 Starrett, J., Hedin, M., Ayoub, N., Hayashi, C.Y., 2013. Hemocyanin gene family evolution in spiders
5598 (Araneae), with implications for phylogenetic relationships and divergence times in the
5599 infraorder Mygalomorphae. *Gene* 524, 175–186.
- 5600 Stenderup, J.T., Olesen, J., Glenner, H., 2006. Molecular phylogeny of the Branchiopoda (Crustacea)–
5601 Multiple approaches suggest a “diplostracan” ancestry of the Notostraca. *Mol. Phylogenet.*
5602 *Evol.* 41, 182–194.
- 5603 Stewart, W.D., 1991. Stratigraphy and sedimentology of the Chancellor succession (Middle and Upper
5604 Cambrian) southeastern Canadian Rocky Mountains. (PhD). University of Ottawa, Ottawa,
5605 Canada.
- 5606 Strausfeld, N.J., Andrew, D.R., 2011. A new view of insect–crustacean relationships I. Inferences from
5607 neural cladistics and comparative neuroanatomy. *Arthropod Struct. Dev.* 40, 276–288.
- 5608 Sturm, H., 1998. Erstnachweis fischchenartiger Insekten (*Zygentoma*, Insecta) für das Mesozoikum
5609 (Untere Kreide, Brasilien). *Sencken. Lethaea* 78, 135–140.
- 5610 Sturm, H., Poinar, G.O., 1998. *Cretaceomachilis libanensis*, the Oldest Known Bristle-tail of the Family
5611 Meinertellidae (Machiloidea, Archaeognatha, Insecta) from the Lebanese Amber. *Dtsch.*
5612 *Entomol. Z.* 45, 43–48.
- 5613 Sukatsheva, I.D., Beattie, R., Mostovski, M.B., 2007. *Permomerope natalensis* sp. n. from the
5614 Lopingian of South Africa, and a redescription of the type species of *Permomerope*
5615 (Trichoptera: Protomeropidae). *Afr. Invertebr.* 48, 245–251.

- 5616 Sukatsheva, I.D., Vassilenko, D.V., 2011. Caddisflies from Chernovskie Kopi (Jurassic/Cretaceous of
5617 Transbaikalia). *Zoosymposia* 5, 434–438.
- 5618 Sun, X.-Y., Xia, X., Yang, Q., 2015 (in press). Dating the origin of the major lineages of Branchiopoda.
5619 *Palaeoworld*.
- 5620 Sutton, M.D., Briggs, D.E.G., Siveter, D.J., Siveter, D.J., Orr, P.J., 2002. The arthropod *Offacolus kingi*
5621 (Chelicerata) from the Silurian of Herefordshire, England: computer based morphological
5622 reconstructions and phylogenetic affinities. *Proc. R. Soc. B Biol. Sci.* 269, 1195–1203.
- 5623 Svenson, G.J., Whiting, M.F., 2009. Reconstructing the origins of praying mantises (Dictyoptera,
5624 Mantodea): the roles of Gondwanan vicariance and morphological convergence. *Cladistics* 25,
5625 468–514.
- 5626 Tasch, P., 1987. Fossil Conchostraca of the Southern Hemisphere and continental drift. *Geol. Soc.*
5627 *Am. Mem.* 165, 1–282.
- 5628 Tasch, P., 1962. Vertical extension of mid-continent Leonardian insect occurrences. *Science* 135, 378–
5629 379.
- 5630 Taylor, J.F., Repetski, J.E., Loch, J.D., Leslie, S.A., 2012. Biostratigraphy and chronostratigraphy of
5631 the Cambrian–Ordovician great American carbonate bank, in: Derby, J.R., Fritz, R.D.,
5632 Longacre, S.A., Morgan, W.A., Sternbach, C.A. (Eds.), *The Great American Carbonate Bank:
5633 The Geology and Economic Resources of the Cambrian – Ordovician Sauk Megasequence of
5634 Laurentia*, AAPG Memoir. pp. 15–35.
- 5635 Taylor, R.S., Schram, F.R., Shen, Y.-B., 2001. A new upper Middle Triassic shrimp (Crustacea:
5636 Lophogastrida) from Guizhou, China, with discussion regarding other fossil “mysidaceans”. *J.*
5637 *Paleontol.* 75, 310–318.
- 5638 Taylor, R.S., Shen, Y.-B., Schram, F.R., 1998. New pygocephalomorph crustaceans from the Permian of
5639 China and their phylogenetic relationships. *Palaeontology* 41, 815–834.
- 5640 Terry, M.D., Whiting, M.F., 2005. Mantophasmatodea and phylogeny of the lower neopterous insects.
5641 *Cladistics* 21, 240–257.

- 5642 Tetlie, O.E., Dunlop, J.A., 2008. *Geralinura carbonaria* (Arachnida; Uropygi) from Mazon Creek,
5643 Illinois, USA, and the Origin of Subchelate Pedipalps in Whip Scorpions. J. Paleontol. 82, 299–
5644 312.
- 5645 Thomas, J.A., Trueman, J.W.H., Rambaut, A., Welch, J.J., 2013. Relaxed Phylogenetics and the
5646 Palaeoptera Problem: Resolving Deep Ancestral Splits in the Insect Phylogeny. Syst. Biol. 62,
5647 285–297.
- 5648 Thorell, T., Lindström, G., 1885. On a Silurian scorpion from Gotland. Kungl Sven Vetenskaps 21, 1–
5649 33.
- 5650 Tillyard, R.J., 1918. Mesozoic insects of Queensland. No. 3. Odonata and Protodonata. Proc. Linn.
5651 Soc. New South Wales 43, 417–436.
- 5652 Tillyard, R.J., 1922. Some new Permian insects from Belmont, NSW in the collection of Mr. John
5653 Mitchell. Proc. Linn. Soc. New South Wales. pp. 279–292.
- 5654 Tillyard, R.J., 1926. Kansas Permian insects; Part 7, The order Mecoptera. Am. J. Sci. 133–164.
- 5655 Tillyard, R.J., 1928. Some remarks on the Devonian fossil insects from the Rhynie chert beds, Old
5656 Red Sandstone. Trans. R. Entomol. Soc. Lond. 76, 65–71.
- 5657 Tillyard, R.J., 1932. Kansas Permian insects; Part 15, The order Plecoptera. Am. J. Sci. 97–134.
- 5658 Timm, L., Bracken-Grissom, H.D., 2015. The forest for the trees: evaluating molecular phylogenies
5659 with an emphasis on higher-level Decapoda. J. Crustac. Biol. 35, 577–592.
- 5660 Tong, K.J., Duchêne, S., Ho, S.Y., Lo, N., 2015. Comment on “Phylogenomics resolves the timing and
5661 pattern of insect evolution.” Science 349, 487.
- 5662 Trussova, E.K., 1971. On the first finding of the Mesozoic species of order Anostraca (Crustacea).
5663 Paleontol. Zhurnal 4, 68–73.
- 5664 Trussova, E.K., 1975. On the taxonomic state of Anostraca, Crustacea from the lower Cretaceous of
5665 the Eastern Transbaikal. Paleontol. Sb. 12, 60–66.

- 5666 Tsang, L.M., Schubart, C.D., Ahyong, S.T., Lai, J.C.Y., Au, E.Y.C., Chan, T.-Y., Ng, P.K.L., Chu, K.H.,
5667 2014. Evolutionary History of True Crabs (Crustacea: Decapoda: Brachyura) and the Origin of
5668 Freshwater Crabs. *Mol. Biol. Evol.* 31, 1173–1187.
- 5669 Vakhrameev, V.A., Kotova, I.Z., 1977. Ancient angiosperms and accompanying plants from the Lower
5670 Cretaceous of Transbaikalia. *Palaeontol. J.* 11, 487–495.
- 5671 Valencio, D.A., Mendia, J.E., Vilas, J.F., 1975. Paleomagnetism and K-Ar ages of Triassic igneous
5672 rocks from the Ischigualasto-Ischichuca Basin and Puesto Viejo Formation, Argentina. *Earth*
5673 *Planet. Sci. Lett.* 26, 319–330.
- 5674 van Nieukerken, E.J., Kaila, L., Kitching, I.J., Kristensen, N.P., Lees, D.J., Minet, J., Mitter, J.,
5675 Mutanen, M., Regier, J.C., Simonsen, T.J., Wahlberg, N., Yen, S.-H., Zahiri, R., Adamski, D.,
5676 Baixeras, J., Bartsch, D., Bengtsson, B.Å., Brown, J.W., Bucheli, R.S., Davis, D.R., De Prins,
5677 J., De Prins, W., Epstein, M.E., Gentili-Poole, P., Gielis, C., Hättenschwiler, P., Hausmann, A.,
5678 Holloway, J.P., Kallies, A., Karsholt, O., Kawahara, A., Koster, S.J.C., Kozlov, M.V., Lafontaine,
5679 J.D., Lamas, G., Landry, J.-F., Lee, S., Nuss, M., Park, K.-T., Penz, C., Rota, J., Schmidt, B.C.,
5680 Schintlmeister, A., Sohn, J.C., Solis, M.A., Tarmann, G., Warren, A.D., Weller, S., Yakovlev, Y.,
5681 Zolotuhin, V.V., Zwick, A., 2011. Order Lepidoptera Linnaeus, 1758. *Zootaxa* 3148, 212–221.
- 5682 Vannier, J., Chen, J.-Y., Huang, D.-Y., Charbonnier, S., Wang, X.-Q., 2006. The Early Cambrian origin
5683 of thylacocephalan arthropods. *Acta Palaeontol. Pol.* 51, 201–214.
- 5684 Vannier, J., Schoenemann, B., Gillot, T., Charbonnier, S., Clarkson, E., 2016. Exceptional preservation
5685 of eye structure in arthropod visual predators from the Middle Jurassic. *Nat. Commun.* 7,
5686 10320.
- 5687 Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., Hariri, K. el, Briggs, D.E.G.,
5688 2010. Ordovician faunas of Burgess Shale type. *Nature* 465, 215–218.
- 5689 Van Straelen, V., 1923. Les Mysidacés du Callovien de La Voulte- sur- Rhône (Ardèche). *Bull. Société*
5690 *Géologique Fr.* 23, 431–439.

- 5691 Vía Boada, L., Villalta, J.F., 1966. *Heterolimulus gadeai* nov. gen., nov. sp., representante de una
5692 nueva familia de Limulacea en el Triásico español. Acta Geológica Hispánica 1, 9–11.
- 5693 von Reumont, B.M., Jenner, R.A., Wills, M.A., Dell’Ampio, E., Pass, G., Ebersberger, I., Meyer, B.,
5694 Koenemann, S., Iliffe, T.M., Stamatakis, A., Niehuis, O., Meusemann, K., Misof, B., 2012.
5695 Pancrustacean Phylogeny in the Light of New Phylogenomic Data: Support for Remipedia as
5696 the Possible Sister Group of Hexapoda. Mol. Biol. Evol. 29, 1031–1045.
- 5697 Vonk, R., Schram, F.R., 2007. Three new tanaid species (Crustacea, Peracarida, Tanaidacea) from the
5698 Lower Cretaceous Alava amber in northern Spain. J. Paleontol. 81, 1502–1509.
- 5699 Vršanský, P., Aristov, D., 2014. Termites (Isoptera) from the Jurassic/Cretaceous boundary: Evidence
5700 for the longevity of their earliest genera. Eur. J. Entomol. 111, 137–141.
- 5701 Waddington, J., Rudkin, D.M., Dunlop, J.A., 2015. A new mid-Silurian aquatic scorpion--one step
5702 closer to land? Biol. Lett. 11, 20140815.
- 5703 Wahlberg, N., Wheat, C.W., Peña, C., 2013. Timing and Patterns in the Taxonomic Diversification of
5704 Lepidoptera (Butterflies and Moths). PLoS ONE 8, e80875.
- 5705 Walcott, C.D., 1911. Middle Cambrian Merostomata. Smithson. Misc. Collect. 57, 17–40.
- 5706 Walossek, D., 1993. The upper Cambrian *Rehbachella* and the phylogeny of Branchiopoda and
5707 Crustacea. Lethaia 26, 318–318.
- 5708 Walossek, D., Müller, K.J., 1994. Pentastomid parasites from the Lower Palaeozoic of Sweden. Trans.
5709 R. Soc. Edinb. Earth Sci. 85, 1–37.
- 5710 Walossek, D., Müller, K.J., 1998. Cambrian “Orsten”-type arthropods and the phylogeny of Crustacea,
5711 in: Arthropod Relationships. Springer, pp. 139–153.
- 5712 Waloszek, D., Dunlop, J.A., 2002. A larval sea spider (Arthropoda: Pycnogonida) from the Upper
5713 Cambrian “Orsten” of Sweden, and the phylogenetic position of pycnogonids. Palaeontology
5714 45, 421–446.
- 5715 Wang, B., Zhang, H., 2010. Earliest evidence of fishflies (Megaloptera: Corydalidae): an exquisitely
5716 preserved larva from the Middle Jurassic of China. J. Paleontol. 84, 774–780.

- 5717 Wang, M., Béthoux, O., Bradler, S., Jacques, F.M.B., Cui, Y., Ren, D., 2014. Under Cover at Pre-
5718 Angiosperm Times: A Cloaked Phasmatodean Insect from the Early Cretaceous Jehol Biota.
5719 PLoS ONE 9, e91290.
- 5720 Wang, X., Wang, Y., Zhang, F., Zhang, J., Zhou, Z.-H., Jin, F., Hu, Y.-M., Gu, G., Hai-Chun, Z., 2000.
5721 Vertebrate biostratigraphy of the lower cretaceous Yixian formation in Lingyuan, western
5722 Liaoning and its neighboring southern Nei Mongol (inner Mongolia), China. *Vertebr. Palasiat.*
5723 38, 95–101.
- 5724 Wang, X., Zhou, Z., He, H., Fan, J., Wang, Y., Zhang, J., Wang, Y., Zhang, F., 2005. Stratigraphy and
5725 age of the Daohugou Bed in Ningcheng, Inner Mongolia. *Chin. Sci. Bull.* 50, 2369.
- 5726 Wang, Y., Liu, X., Winterton, S.L., Yang, D., 2012. The First Mitochondrial Genome for the Fishfly
5727 Subfamily Chauliodinae and Implications for the Higher Phylogeny of Megaloptera. *PLoS ONE*
5728 7, e47302.
- 5729 Ware, J.L., Grimaldi, D.A., Engel, M.S., 2010. The effects of fossil placement and calibration on
5730 divergence times and rates: An example from the termites (Insecta: Isoptera). *Arthropod Struct.*
5731 *Dev.* 39, 204–219.
- 5732 Ware, J.L., Litman, J., Klass, K.-D., Spearman, L.A., 2008. Relationships among the major lineages of
5733 Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. *Syst. Entomol.* 33,
5734 429–450.
- 5735 Warnock, R.C.M., Parham, J.F., Joyce, W.G., Lyson, T.R., Donoghue, P.C.J., 2015. Calibration
5736 uncertainty in molecular dating analyses: there is no substitute for the prior evaluation of time
5737 priors. *Proc. R. Soc. B Biol. Sci.* 282, 20141013.
- 5738 Warnock, R.C.M., Yang, Z., Donoghue, P.C.J., 2012. Exploring uncertainty in the calibration of the
5739 molecular clock. *Biol. Lett.* 8, 156–159.
- 5740 Waters, C.N., Davies, S.J., 2006. Carboniferous: extensional basins, advancing deltas and coal
5741 swamps. *Geol. Engl. Wales* 173–223.

- 5742 Waters, C.N., Glover, B.W., Powell, J.H., 1994. Structural synthesis of S Staffordshire, UK:
5743 Implications for the Variscan evolution of the Pennine Basin. J. Geol. Soc. Lond. 151, 697–713.
- 5744 Weber, B., Zhu, M., 2003. Arthropod trace fossils from the Zhujiqing Formation (Meishucunian,
5745 Yunnan) and their palaeobiological implications. Prog. Nat. Sci. 13, 795–800.
- 5746 Wedmann, S., Makarkin, V.N., 2007. A new genus of Mantispidae (Insecta: Neuroptera) from the
5747 Eocene of Germany, with a review of the fossil record and palaeobiogeography of the family.
5748 Zool. J. Linn. Soc. 149, 701–716.
- 5749 Weekers, P.H., Murugan, G., Vanfleteren, J.R., Belk, D., Dumont, H.J., 2002. Phylogenetic analysis of
5750 anostracans (Branchiopoda: Anostraca) inferred from nuclear 18S ribosomal DNA (18S rDNA)
5751 sequences. Mol. Phylogenet. Evol. 25, 535–544.
- 5752 Wellman, C.H., 1993. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven
5753 Group, Scotland. J. Micropalaeontology 12, 47–66.
- 5754 Whalley, P., 1978. New taxa of fossil and recent Micropterigidae with a discussion of their evolution
5755 and a comment on the evolution of Lepidoptera (Insecta). Ann. Transvaal Mus. 31, 71–86.
- 5756 Whalley, P.E., 1985. The systematics and palaeogeography of the Lower Jurassic insects of Dorset,
5757 England. Bull. Br. Mus. Nat. Hist. Geol. 39, 107–189.
- 5758 Whalley, P., 1986. A review of the current fossil evidence of Lepidoptera in the Mesozoic. Biol. J. Linn.
5759 Soc. 28, 253–271.
- 5760 Whalley, P., Jarzembowski, E.A., 1981. A new assessment of *Rhyniella*, the earliest known insect,
5761 from the Devonian of Rhynie, Scotland. Nature 291, 317.
- 5762 Wheat, C.W., Wahlberg, N., 2013. Phylogenomic Insights into the Cambrian Explosion, the
5763 Colonization of Land and the Evolution of Flight in Arthropoda. Syst. Biol. 62, 93–109.
- 5764 Wheeler, W.C., Whiting, M., Wheeler, Q.D., Carpenter, J.M., 2001. The Phylogeny of the Extant
5765 Hexapod Orders. Cladistics 17, 113–169.
- 5766 Whitfield, R.P., 1880. Notice of new forms of fossil crustaceans from the Upper Devonian rocks of
5767 Ohio, with descriptions of new genera and species. Am. J. Sci. 109, 33–42.

- 5768 Whitfield, R.P., 1885. An American Silurian scorpion. *Science* 6, 183–184.
- 5769 Whiting, M.F., 2002. Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and
5770 Siphonaptera. *Zool. Scr.* 31, 93–104.
- 5771 Whiting, M.F., Carpenter, J.C., Wheeler, Q.D., Wheeler, W.C., 1997. The Strepsiptera problem:
5772 Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA
5773 sequences and morphology. *Syst. Biol.* 46, 1–68.
- 5774 Whittington, H.B., 1981. Rare arthropods from the Burgess Shale, Middle Cambrian, British Columbia.
5775 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 329–357.
- 5776 Wiegmann, B.M., Trautwein, M.D., Kim, J.-W., Cassel, B.K., Bertone, M.A., Winterton, S.L., Yeates,
5777 D.K., 2009. Single-copy nuclear genes resolve the phylogeny of the holometabolous insects.
5778 *BMC Biol.* 7, 34.
- 5779 Wiegmann, B.M., Trautwein, M.D., Winkler, I.S., Barr, N.B., Kim, J.-W., Lambkin, C., Bertone, M.A.,
5780 Cassel, B.K., Bayless, K.M., Heimberg, A.M., Wheeler, B.M., Peterson, K.J., Pape, T., Sinclair,
5781 B.J., Skevington, J.H., Blagoderov, V., Caravas, J., Kutty, S.N., Schmidt-Ott, U., Kampmeier,
5782 G.E., Thompson, F.C., Grimaldi, D.A., Beckenbach, A.T., Courtney, G.W., Friedrich, M., Meier,
5783 R., Yeates, D.K., 2011. Episodic radiations in the fly tree of life. *Proc. Natl. Acad. Sci.* 108,
5784 5690–5695.
- 5785 Wiens, J.J., Lapoint, R.T., Whiteman, N.K., 2015. Herbivory increases diversification across insect
5786 clades. *Nat. Commun.* 6, 8370.
- 5787 Wilkinson, R.D., Steiper, M.E., Soligo, C., Martin, R.D., Yang, Z., Tavaré, S., 2011. Dating primate
5788 divergences through an integrated analysis of palaeontological and molecular data. *Syst. Biol.*
5789 60, 16–31.
- 5790 Williams, M., Siveter, D.J., Salas, M.J., Vannier, J., Popov, L.E., Ghobadi Pour, M., 2008. The earliest
5791 ostracods: the geological evidence. *Lethaia* 88, 11–21.
- 5792 Wills, M.A., 2001. How good is the fossil record of arthropods? An assessment using the stratigraphic
5793 congruence of cladograms. *Geol. J.* 36, 187–210.

- 5794 Wills, M.A., Briggs, D.E., Fortey, R.A., Wilkinson, M., Sneath, P.H., 1998. An arthropod phylogeny
5795 based on fossil and recent taxa, in: Edgecombe, G.D. (Ed.), *Arthropod Fossils and Phylogeny*.
5796 Columbia University Press, New York, pp. 33–105.
- 5797 Wills, M.A., Jenner, R.A., Dhubhghaill, C.N., 2009. Eumalacostracan evolution: conflict between three
5798 sources of data. *Arthropod Syst. Phylogeny* 67, 71–90.
- 5799 Wilson, G.D.F., 2009. The phylogenetic position of the Isopoda in the Peracarida (Crustacea:
5800 Malacostraca). *Arthropod Syst. Phylogeny* 67, 159–198.
- 5801 Wilson, G.D.F., 2012. Fossils in the phylogeny of isopod crustaceans (Arthropoda). Presented at the
5802 2012 GSA Annual Meeting, Charlotte, NC.
- 5803 Wilson, H.M., 2001. First Mesozoic scutigeromorph centipede, from the Lower Cretaceous of Brazil.
5804 *Palaeontology* 44, 489–495.
- 5805 Wilson, H.M., 2006. Juliformian Millipedes from the Lower Devonian of Euramerica: Implications for
5806 the Timing of Millipede Cladogenesis in the Paleozoic. *J. Paleontol.* 80, 638–649.
- 5807 Wilson, H.M., Anderson, L.I., 2004. Morphology and Taxonomy of Paleozoic Millipedes (Diplopoda:
5808 Chilognatha: Archipolypoda) from Scotland. *J. Paleontol.* 78, 169–184.
- 5809 Wilson, H.M., Martill, D.M., 2001. A new japygid dipluran from the Lower Cretaceous of Brazil.
5810 *Palaeontology* 44, 1025–1031.
- 5811 Wilson, J.S., von Dohlen, C.D., Forister, M.L., Pitts, J.P., 2013. Family-Level Divergences in the
5812 Stinging Wasps (Hymenoptera: Aculeata), with Correlations to Angiosperm Diversification.
5813 *Evol. Biol.* 40, 101–107.
- 5814 Wingstrand, K.G., 1972. Comparative spermatology of a pentastomid, *Raillietiella hemidactyli*, and a
5815 branchiuran crustacean, *Argulus foliaceus*, with a discussion of pentastomid relationships. Det
5816 K. Dan. Vidensk. Selsk. Biol. Skr. 19, 1–72.
- 5817 Winterton, S.L., Hardy, N.B., Wiegmann, B.M., 2010. On wings of lace: phylogeny and Bayesian
5818 divergence time estimates of Neuropterida (Insecta) based on morphological and molecular
5819 data. *Syst. Entomol.* 35, 349–378.

- 5820 Wipfler, B., Bai, M., Schoville, S., Dallai, R., Uchifune, T., Machida, R., Cui, Y., Beutel, R.G., 2014. Ice
5821 Crawlers (Grylloblattodea)—the history of the investigation of a highly unusual group of insects.
5822 J. Insect Biodivers. 2, 1–25.
- 5823 Wipfler, B., Machida, R., Müller, B., Beutel, R.G., 2011. On the head morphology of Grylloblattodea
5824 (Insecta) and the systematic position of the order, with a new nomenclature for the head
5825 muscles of Dicondylia. Syst. Entomol. 36, 241–266.
- 5826 Wirkner, C.S., Richter, S., 2010. Evolutionary morphology of the circulatory system in Peracarida
5827 (Malacostraca; Crustacea). Cladistics 26, 143–167.
- 5828 Wissler, L., Gadau, J., Simola, D.F., Helmkampf, M., Bornberg-Bauer, E., 2013. Mechanisms and
5829 Dynamics of Orphan Gene Emergence in Insect Genomes. Genome Biol. Evol. 5, 439–455.
- 5830 Withers, T.H., 1914. Some Cretaceous and Tertiary cirripedes referred to *Pollicipes*. Annals and
5831 Magazine of Natural History, Series 8, 14, 167–206.
- 5832 Withers, T.H., 1935. Catalogue of fossil Cirripedia in the Department of Geology. Vol II. Cretaceous.
5833 Trustees of the British Museum (Natural History), London.
- 5834 Wolfe, J.M., Hegna, T.A., 2014. Testing the phylogenetic position of Cambrian pancrustacean larval
5835 fossils by coding ontogenetic stages. Cladistics 30, 366–390.
- 5836 Womack, T., Slater, B.J., Stevens, L.G., Anderson, L.I., Hilton, J., 2012. First cladoceran fossils from
5837 the Carboniferous: Palaeoenvironmental and evolutionary implications. Palaeogeogr.
5838 Palaeoclimatol. Palaeoecol. 344–345, 39–48.
- 5839 Wood, H.M., Matzke, N.J., Gillespie, R.G., Griswold, C.E., 2013. Treating Fossils as Terminal Taxa in
5840 Divergence Time Estimation Reveals Ancient Vicariance Patterns in the Palpimanoid Spiders.
5841 Syst. Biol. 62, 264–284.
- 5842 Wu, H., Huang, D., 2012. A New Species of *Liadotaulius* (Insecta: Trichoptera) from the Middle
5843 Jurassic of Daohugou, Inner Mongolia. Acta Geol. Sin. 86, 320–324.
- 5844 Xie, X., Wang, Y., Shen, H., 2004. Facies Analysis and Sedimentary Environment Reconstruction of
5845 the Late Carboniferous in Zhongwei, Ningxia. Acta Sedimentol. Sin. 22, 19–28.

- 5846 Xiong, Y., Gao, Y., Yin, W., Luan, Y., 2008. Molecular phylogeny of Collembola inferred from ribosomal
5847 RNA genes. *Mol. Phylogenet. Evol.* 49, 728–735.
- 5848 Xu, X., Liu, F., Cheng, R.-C., Chen, J., Xu, X., Zhang, Z., Ono, H., Pham, D.S., Norma-Rashid, Y.,
5849 Arnedo, M.A., Kuntner, M., Li, D., 2015. Extant primitively segmented spiders have recently
5850 diversified from an ancient lineage. *Proc. R. Soc. B Biol. Sci.* 282, 20142486.
- 5851 Yang, F., 1987. Early Late Carboniferous ammonoids from Zhongwei, Ningxia Autonomous Region,
5852 China. *Geoscience* 1, 157–172.
- 5853 Yang, J.-S., Lu, B., Chen, D.-F., Yu, Y.-Q., Yang, F., Nagasawa, H., Tsuchida, S., Fujiwara, Y., Yang,
5854 W.-J., 2013. When Did Decapods Invade Hydrothermal Vents? Clues from the Western Pacific
5855 and Indian Oceans. *Mol. Biol. Evol.* 30, 305–309.
- 5856 Yang, S., Tian, S., Zheng, Z., 1988. Namurian conodonts from Xiaoyuchuan, Ningxia. *Prof. Pap.*
5857 *Stratigr. Palaeontol.* 22, 23–30.
- 5858 Yang, Z., Rannala, B., 2006. Bayesian estimation of species divergence times under a molecular clock
5859 using multiple fossil calibrations with soft bounds. *Mol. Biol. Evol.* 23, 212–226.
- 5860 Yoshizawa, K., 2011. Monophyletic Polyneoptera recovered by wing base structure. *Syst. Entomol.* 36,
5861 377–394.
- 5862 Yoshizawa, K., Johnson, K.P., 2003. Phylogenetic position of Phthiraptera (Insecta: Paraneoptera) and
5863 elevated rate of evolution in mitochondrial 12S and 16S rDNA. *Mol. Phylogenet. Evol.* 29, 102–
5864 114.
- 5865 Yoshizawa, K., Saigusa, T., 2001. Phylogenetic analysis of paraneopteran orders (Insecta: Neoptera)
5866 based on forewing base structure, with comments on monophyly of Auchenorrhyncha
5867 (Hemiptera). *Syst. Entomol.* 26, 1–13.
- 5868 Yuan, J., Zhang, X., Liu, C., Sun, X., Sivaramasamy, E., Li, F., Xiang, J., 2016. Comparative genomics
5869 analysis of decapod shrimps in the Pancrustacea clade. *Biochem. Syst. Ecol.* 64, 111–121.
- 5870 Yuan, X., Chen, Z., Xiao, S., Zhou, C., Hua, H., 2011. An early Ediacaran assemblage of macroscopic
5871 and morphologically differentiated eukaryotes. *Nature* 470, 390–393.

- 5872 Yuan, X., Xiao, S., Yin, L., Knoll, A.H., Zhou, C., Mu, X., 2002. Doushantuo fossils: life on the eve of
5873 animal radiation. China University of Science and Technology Press, Hefei, China.
- 5874 Zambito, J.J., Benison, K.C., Foster, T., Soreghan, G.S., Kane, M., Soreghan, M., 2012.
5875 Lithostratigraphy of the Permian Red Beds and Evaporites in the Rebecca K. Bounds Core,
5876 Greeley County, Kansas. Kans. Geol. Surv. Open-File Rep. 2012, 45.
- 5877 Zhang, C., Stadler, T., Klopstein, S., Heath, T.A., Ronquist, F., 2016. Total-Evidence Dating under the
5878 Fossilized Birth–Death Process. Syst. Biol. 65, 228–249.
- 5879 Zhang, J.-F., 2015. Archisargoid flies (Diptera, Brachycera, Archisargidae and Kovalevisargidae) from
5880 the Jurassic Daohugou biota of China, and the related biostratigraphical correlation and
5881 geological age. J. Syst. Palaeontol. 13, 857–881.
- 5882 Zhang, J.-F., Kluge, N.J., 2007. Jurassic larvae of mayflies (Ephemeroptera) from the Daohugou
5883 formation in Inner Mongolia, China. Orient. Insects 41, 351–366.
- 5884 Zhang, X., Han, J., Shu, D., 2002. New occurrence of the Burgess Shale arthropod *Sidneyia* in the
5885 Early Cambrian Chengjiang Lagerstätte (South China), and revision of the arthropod *Urokodia*.
5886 Alcheringa 26, 1–8.
- 5887 Zhang, X., Maas, A., Haug, J.T., Siveter, D.J., Waloszek, D., 2010. A Eucrustacean Metanauplius from
5888 the Lower Cambrian. Curr. Biol. 20, 1075–1079.
- 5889 Zhang, X., Siveter, D.J., Waloszek, D., Maas, A., 2007. An epipodite-bearing crown-group crustacean
5890 from the Lower Cambrian. Nature 449, 595–598.
- 5891 Zhang, Z., Schneider, J.W., Hong, Y., 2013. The most ancient roach (Blattodea): a new genus and
5892 species from the earliest Late Carboniferous (Namurian) of China, with a discussion of the
5893 phylomorphogeny of early blattids. J. Syst. Palaeontol. 11, 27–40.
- 5894 Zhao, C., Liu, X., Yang, D., 2014. Wing Base Structural Data Support the Sister Relationship of
5895 Megaloptera and Neuroptera (Insecta: Neuropterida). PLoS ONE 9, e114695.

- 5896 Zherikhin, V.V., Mostovski, M.B., Vršanský, P., Blagoderov, V., Lukashevich, E.D., 1998. The unique
5897 Lower Cretaceous locality Baissa and other contemporaneous fossil insect sites in North and
5898 West Transbaikalia, in: Proceedings of the First International Palaeoentomological Conference.
5899 Moscow.
- 5900 Zhou, D., Zhang, D., Ding, G., Shi, L., Hou, Q., Ye, Y., Xu, Y., Zhou, H., Xiong, C., Li, S., Yu, S., Hong,
5901 S., Yu, X., Zou, P., Chen, C., Chang, X., Wang, W., Lv, Y., Sun, Y., Ma, L., Shen, B., Zhu, C.,
5902 2014. Genome sequence of *Anopheles sinensis* provides insight into genetics basis of
5903 mosquito competence for malaria parasites. BMC Genomics 15, 42.
- 5904 Zhou, Z., 2006. Evolutionary radiation of the Jehol Biota: chronological and ecological perspectives.
5905 Geol. J. 41, 377–393.
- 5906 Zhu, Q., Hastriter, M.W., Whiting, M.F., Dittmar, K., 2015. Fleas (Siphonaptera) are Cretaceous, and
5907 evolved with Theria. Mol. Phylogenet. Evol. 90, 129–139.
- 5908 Zrzavý, J., Hypsa, V., Vlaskova, M., 1998. Arthropod phylogeny: taxonomic congruence, total evidence
5909 and conditional combination approaches to morphological and molecular data sets, in: Fortey,
5910 R.A., Thomas, R.H. (Eds.), Arthropod Relationships, The Systematics Association Special
5911 Volume Series. Chapman & Hall, London.
- 5912 Zrzavý, J., Štys, P., 1997. The basic body plan of arthropods: insights from evolutionary morphology
5913 and developmental biology. J. Evol. Biol. 10, 353–367.
- 5914 Zwick, A., Regier, J.C., Zwickl, D.J., 2012. Resolving Discrepancy between Nucleotides and Amino
5915 Acids in Deep-Level Arthropod Phylogenomics: Differentiating Serine Codons in 21-Amino-
5916 Acid Models. PLoS ONE 7, e47450.
- 5917 Zwick, P., 2000. Phylogenetic System and Zoogeography of the Plecoptera. Annu. Rev. Entomol. 45,
5918 700–746.
- 5919

5920 **FIGURE CAPTIONS**

5921

5922 **Fig. 1.** Calibration diagram for Ecdysozoa (nodes 2-5, 22-23, 34, 41). Altocrust. = Altocrustacea.

5923 Numbers in this and all other calibration diagrams are ages in Ma.

5924

5925 **Fig. 2.** Major fossil calibrations for (A) nodes 2-3: *Rusophycus* trace fossils, GSC 85983, scale bar

5926 20mm, image credit M. Coyne; (B-C) nodes 4, 22, 34, 41: *Yicaris dianensis*, YKLP 10840, scale bars

5927 100µm, images credit X. Zhang; (B) whole specimen; (C) detail of epipodites; (D) node 5:

5928 *Wisangocaris barbarahardya*, SAM P43679a, scale bar 5mm; (E) nodes 23-25, 27: *Cowiedesmus*

5929 *eroticopodus*, AMS F.64845, scale bar 2mm, image credit Y. Zhen; (F) nodes 64-65: *Rhyniella*

5930 *praecursor*, BMNH In.38228, scale bar 200µm, image credit NHMUK.

5931

5932 **Fig. 3.** Calibration diagram for non-arachnid Chelicerata (nodes 6-8).

5933

5934 **Fig. 4.** Calibration diagram for non-tetrapulmonate Arachnida (nodes 9-16). Pseudos. =

5935 Pseudoscorpiones.

5936

5937 **Fig. 5.** Chelicerate fossil calibrations for (A) node 6: *Haliestes dasos*, OUM C.29571, scale bar 500µm,

5938 image credit D. Siveter, M. Sutton, D. Briggs & D. Siveter; (B) node 7: *Chasmataspis*-like resting

5939 traces, MBA 1084, scale bar 20mm, image credit J. Dunlop; (C) node 13: *Protofeaella peetersae*,

5940 NHMII3115, scale bar 500µm, image credit H. Henderickx; (D) node 10: *Eophalangium sheari*, PBM

5941 3503, scale bar 1mm, image credit J. Dunlop; (E) node 14: *Electrokoenenia yaksha*, NIGP 163263,

5942 scale bar 500µm, image credit M. Engel; (F) node 15: *Cratosolpuga wunderlichi*, SMNK 1268PAL,

5943 scale bar 5mm, image credit P. Selden; (G) node 9: *Eramoscorpius brucensis*, holotype ROM 5324,

5944 scale bar 10mm, image credit D. Rudkin & J. Waddington; (H) node 9: *Palaeophonon loudonensis*,

5945 NMS 1897.122.196, scale bar 20mm, image credit: J. Lamsdell; (I-J) node 12: *Cornupalpatum*

5946 *burmanicum*, scale bars 100 µm, image credit G. Poinar; (I) Holotype A-10-160; (J) Paratype A-10-261;
5947 (K) node 11: *Protacarus crani*, BMNH In.24665, scale bar 100µm, image credit NHMUK.

5948

5949 **Fig. 6.** Calibration diagram for Tetrapulmonata (nodes 17-21).

5950

5951 **Fig. 7.** Tetrapulmonata fossil calibrations for (A) nodes 17-19: *Parageralinura naufraga*, LWL Ar.K.1,
5952 scale bar 5mm, image credit C. Brauckmann; (B) node 20: *Graeophonus anglicus*, BMNH In 31233,
5953 scale bar 5mm, image credit J. Dunlop; (C, D) node 21: *Palaeothele montceauensis*, images credit P.
5954 Selden; (C) Holotype MNHN 51961, scale bar 2mm; (D) Reconstructed specimen BMNH In.62050,
5955 scale bar 0.2mm; (E) node 21: *Arthrolycosa* sp., PIN 5431/9, scale bar 1mm, image credit P. Selden.

5956

5957 **Fig. 8.** Calibration diagram for Myriapoda (nodes 24-33). Chilogn. = Chilognatha, Scutigerom. =
5958 Scutigeromorpha, Geophilom. = Geophilomorpha.

5959

5960 **Fig. 9.** Myriapod fossil calibrations for (A-B) node 26: *Electroxenus jezzinensis*, MNHN JS 231/1, scale
5961 bar 0.5mm, image credit D. Azar; (C-E) node 28: *Crussolum* sp., images credit L. Anderson; (C)
5962 Forcipular segment, slide AUGD 12308, scale bar 0.5mm; (D) Prefemur of a trunk leg, slide AUGD
5963 12307, scale bar 0.2mm; (E) Tibia of a trunk leg, slide AUGD 12307, scale bar 0.2mm; (F) node 29:
5964 *Fulmenocursor tenax*, SMNS 64275, scale bar 5mm, image credit G. Bechly; (G-H) node 30:
5965 *Devonobius delta*, scale bars 0.1mm, images credit W. Shear; (G) Head and anterior part of trunk,
5966 AMNH slide 411-15-AR18; (H) Forcipular segment, AMNH slide 4329-AR4; (I) nodes 31-32:
5967 *Mazoscolopendra richardsoni*, FMNH PE29002, scale bar 5mm, image credit J. Wittry; (J-K) node 33:
5968 *Kachinophilus pereirai*, AMNH Bu-Ba41a; (J) Head and anterior part of trunk, scale bar 0.3 mm; (K)
5969 Posterior body segments, scale bar 0.1mm.

5970

5971 **Fig. 10.** Calibration diagram for Oligostraca (nodes 35-40).

5972

5973 **Fig. 11.** Oligostraca fossil calibrations for (A) nodes 35-36: *Boeckelericambria pelturae*, UB W116,
5974 scale bar 50µm, image credit D. Waloszek; (B) nodes 37, 39-40: *Luprisca incuba*, YPM IP 307300,
5975 scale bar 500µm, image credit D. Siveter, G. Tanaka, U. Farrell, M. Martin, D. Siveter & D. Briggs; (C-
5976 E) node 38: *Cytherellina submagna*, ZPAL O.60/001, images credit E. Olempska; (C) steinkern left
5977 lateral view, scale bar 200 µm; (D) soft anatomy of posterior region, scale bar 100µm; (E) walking legs
5978 and presumed furca, scale bar 50µm.

5979

5980 **Fig. 12.** Calibration diagram for Copepoda and Thecostraca (nodes 42-47).

5981

5982 **Fig. 13.** Calibration diagram for Malacostraca (nodes 48-56). Verunip. = Verunipeltata, Tanaid =
5983 Tanaidacea.

5984

5985 **Fig. 14.** Multicrustacea fossil calibrations for (A) node 42: *Arenosicaris inflata*, PRI 10130, scale bar
5986 10mm, image credit J. Collette; (B) node 43: *Kabatarina pattersoni*, NHMUK 63466, scale bar 100µm,
5987 image credit G. Boxshall; (C-D) node 44: *Rhamphoverritor reduncus*, OUM C.29587, scale bars
5988 500µm, image credit D. Briggs, M. Sutton, D. Siveter & D. Siveter; (C) lateral views with (left) and
5989 without (right) head shield; (D) transverse section before serial grinding; (E) nodes 45-46: *Illilepas*
5990 *damrowi*, FMNH P32055, scale bar 5mm, image credit J. Wittry; (F-G) node 48: *Cinerocaris magnifica*,
5991 images credit D. Briggs, M. Sutton, S. Siveter & D. Siveter; (F) OUM C.29566, reconstruction in lateral
5992 view with (top) and without (bottom) head shield, scale bar 2mm; (G) holotype C.29565, sub-
5993 transverse section, scale bar 1mm; (H-I) nodes 49, 55-56: *Palaeopalaemon newberryi*, KSU 3484,
5994 scale bars 5mm, image credit W. Jones; (H) left view; (I) right view; (J) nodes 52-53: *Hesslerella*
5995 *shermani*, FMNH PE 16527, latex cast whitened with ammonium chloride, scale bar image credit T.
5996 Hegna; (K) node 50: *Anaspidites antiquus*, AMS F64765, scale bar 5mm, image credit S. Ah Yong; (L-
5997 M) node 54: *Alavatanaais carabe*, scale bars 500 µm, images credit A. Sánchez-García; (L) holotype

5998 MCNA 9537; (M) MCNA 13888 lateral view.

5999

6000 **Fig. 15.** Calibration diagram for Allotriocarida (nodes 57-63).

6001

6002 **Fig. 16.** Allotriocarida fossil calibrations for (A) node 57: *Rehbachella kinnekullensis*, UB 611, scale
6003 bar 200µm, image credit D. Waloszek; (B) node 58: *Lepidocaris rhyniensis*, NHMUK In. 24493, scale
6004 bar 200µm, image credit NHMUK; (C) node 60: *Chenops yixianensis*, CNU-CAL-HP-2009001, scale
6005 bar 10mm, image credit T. Hegna; (D) node 61: *Leaia chinensis*, NIGP 51786, scale bar 1mm, image
6006 credit Y. Shen; (E) node 62: *Dundgobiestheria mandalgobiensis*, ED-A-14-1, scale bar 1 mm, image
6007 credit G. Li; (F) node 63: *Smirnovidaphnia smirnovi*, PIN 1873/100, scale bar 200 µm, image credit A.
6008 Kotov.

6009

6010 **Fig. 17.** Calibration diagram for non-neopteran Hexapoda (nodes 64-73). Microc. = Microcoryphia,
6011 Zygent. = Zygentoma, Euplect. = Euplectoptera.

6012

6013 **Fig. 18.** Hexapoda fossil calibrations for (A) node 70: *Delitzschala bitterfeldensis*, BGR X 9216, scale
6014 bar 2mm, image credit C. Brauckmann; (B) node 68: *Cretaceomachilis libanensis*, Milki No. 194/35,
6015 scale bar 500µm, image credit G. Poinar; (C) node 69: *Burmalepisma cretacicum*, B-TH-1, scale bar
6016 500µm, image credit G. Poinar; (D) node 67: *Rhyniognatha hirsti*, BMNH IN. 38234, scale bar 200µm,
6017 image credit NHMUK; (E) node 72: *Triassonurus doliiformis*, Louis Grauvogel collection No. 9304,
6018 scale bar 10mm, image credit L. Grauvogel-Stamm.

6019

6020 **Fig. 19.** Calibration diagram for Polyneoptera (nodes 75-83). Dermap. = Dermaptera, Notop. =
6021 Notoptera, Phasm. = Phasmatodea.

6022

6023 **Fig. 20.** Polyneoptera fossil calibrations for (A) node 75: *Qilianiblatella namurensis*, CNU-NX1-303,

6024 scale bar 5mm, image credit D. Ren; (B) node 77: *Palaeotaeniopteryx elegans*, PIN 1197/333, scale
6025 bar 1mm, image credit N. Sinitshenkova; (C) node 78: *Raphogla rubra*, Ld LAP 415 B, scale bar 5
6026 mm, image credit S. Fouché; (D) node 80: *Cretophasmomima melanogramma*, CNU-PHA-
6027 NN2012002, scale bar 10mm, image credit D. Ren; (E) node 76: *Rhadinolabis phoenicica*, Azar
6028 collection 1013, scale bar 500µm, image credit M. Engel;; (F) node 81: *Echinosomiscus primoticus*,
6029 NIGP 163536, scale bar 2mm, image credit M. Engel; (G) node 79: *Juramantophasma sinica*, NIGP
6030 142171, scale bar 10mm, image credit D. Huang.

6031

6032 **Fig. 21.** Calibration diagram for Condylgnatha and Psocodea (nodes 74, 84-88).

6033

6034 **Fig. 22.** Condylgnatha fossil calibrations for (A) nodes 85, 87: *Aviorrhyncha magnifica*, holotype
6035 MNHN Avion No. 2, scale bar 1mm, image credit A. Nel; (B) node 86: *Fusithrips crassipes*, PIN
6036 3064/8547, scale bar 200µm, image credit A. Rasnitsyn.

6037

6038 **Fig. 23.** Calibration diagram for Hymenoptera, Neuropterida, and Coleopterida (nodes 89-96).

6039 Hymenopt. = Hymenoptera, Mec. = Mecopterida, Megalopt. = Megaloptera.

6040

6041 **Fig. 24.** Calibration diagram for Mecopterida (nodes 97-103). Mecopt. = Mecoptera.

6042

6043 **Fig. 25.** Holometabola fossil calibrations for (A) node 90: *Triassoxyela foveolata*, PIN 2070/1, scale bar
6044 1mm, image credit A. Rasnitsyn; (B) node 92: *Elmothone martynovae*, MCZ 5585, scale bar 2mm,
6045 image credit Museum of Comparative Zoology, Harvard University (©President and Fellows of Harvard
6046 College); (C) node 93: *Eochauliodes striolatus*, CNU-MEG-NN2011004 P/C, scale bar 5mm, image
6047 credit D. Ren; (D) node 96: *Triadogyrus sternalis*, PIN 3320/13, scale bar 2mm, image credit A.
6048 Rasnitsyn; (E) node 97: *Permopanorpa inaequalis*, YPM IP 005058, scale bar 1mm, image credit J.
6049 Utrup; (F) node 98: *Archaeolepis mane*, BMNH In. 59397, scale bar 2mm, image credit NHMUK; (G)

- 6050 node 99: *Liadotaulius maior*, LGA 1995, scale bar 2mm, image credit J. Ansorge; (H) node 100:
- 6051 *Parasabatinca aftimacrai*, holotype, scale bar 2mm, image credit D. Azar; (I) node 101:
- 6052 *Pseudonannochorista willmanni*, PIN 966/21, scale bar 1mm, image credit A. Bashkuev; (J) node 103:
- 6053 *Grauvogelia arzvilleriana*, Louis Grauvogel collection No. 5514, scale bar 1mm, image credit L.
- 6054 Grauvogel-Stamm.

FOSSIL CALIBRATIONS FOR THE ARTHROPOD TREE OF LIFE

AUTHORS

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ABSTRACT

Fossil age data and molecular sequences are increasingly combined to establish a timescale for the Tree of Life. Arthropods, as the most species-rich and morphologically disparate animal phylum, have received substantial attention, particularly with regard to questions such as the timing of habitat shifts (e.g. terrestrialisation), genome evolution (e.g. gene family duplication and functional evolution), origins of novel characters and behaviours (e.g. wings and flight, venom, silk), biogeography, rate of diversification (e.g. Cambrian explosion, insect coevolution with angiosperms, evolution of crab body plans), and the evolution of arthropod microbiomes. We present herein a series of rigorously vetted calibration fossils for arthropod evolutionary history, taking into account recently published guidelines for best practice in fossil calibration. These are restricted to Palaeozoic and Mesozoic fossils, no deeper than ordinal taxonomic level, nonetheless resulting in 80 fossil calibrations for 102 clades. This work is especially timely owing to the rapid growth of molecular sequence data and the fact that many included fossils have been described within the last five years. This contribution provides a resource for systematists and other biologists interested in deep-time questions in arthropod evolution.

28

29 **KEYWORDS**

30

31 Arthropods; Fossils; Phylogeny; Divergence times

32

33 **ABBREVIATIONS**

34

35 AMNH, American Museum of Natural History; AMS, Australian Museum, Sydney; AUGD, University of
36 Aberdeen; BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin; BMNH, The Natural
37 History Museum, London; CNU, Key Laboratory of Insect Evolutionary & Environmental Change,
38 Capital Normal University, Beijing; DE, Ulster Museum, Belfast; ED, Ibaraki University, Mito, Japan;
39 FMNH, Field Museum of Natural History; GMCB, Geological Museum of China, Beijing; GSC,
40 Geological Survey of Canada; IRNSB, Institut Royal des Sciences Naturelles de Belgique, Brussels;
41 KSU, Kent State University; Ld, Musée Fleury, Lodève, France; LWL, Landschaftsverband Westfalen-
42 Lippe-Museum für Naturkunde, Münster; MACN, Museo Argentino de Ciencias Naturales, Buenos
43 Aires; MBA, Museum für Naturkunde, Berlin; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-
44 Gasteiz, Álava, Spain; MCZ, Museum of Comparative Zoology, Harvard University; MGSB, Museo
45 Geológico del Seminario de Barcelona; MN, Museu Nacional, Rio de Janeiro; MNHN, Muséum
46 national d'Histoire naturelle, Paris; NHMUK, The Natural History Museum, London; NIGP, Nanjing
47 Institute of Geology and Palaeontology; NMS, National Museum of Scotland; OUM, Oxford University
48 Museum of Natural History; PBM, Palaöbotanik Münster; PIN, Paleontological Institute, Moscow; PRI,
49 Paleontological Research Institution, Ithaca; ROM, Royal Ontario Museum; SAM, South Australian
50 Museum, Adelaide; SM, Sedgwick Museum, University of Cambridge; SMNK, Staatliches Museum für
51 Naturkunde, Karlsruhe; SMNS, Staatliches Museum für Naturkunde, Stuttgart; TsGM, F.N. Chernyshev
52 Central Geologic Prospecting Research Museum, St. Petersburg; UB, University of Bonn; USNM, US
53 National Museum of Natural History, Smithsonian Institution; UWGM, University of Wisconsin Geology
54 Museum; YKLP, Yunnan Key Laboratory for Palaeobiology, Yunnan University; YPM, Yale Peabody

Figure 1

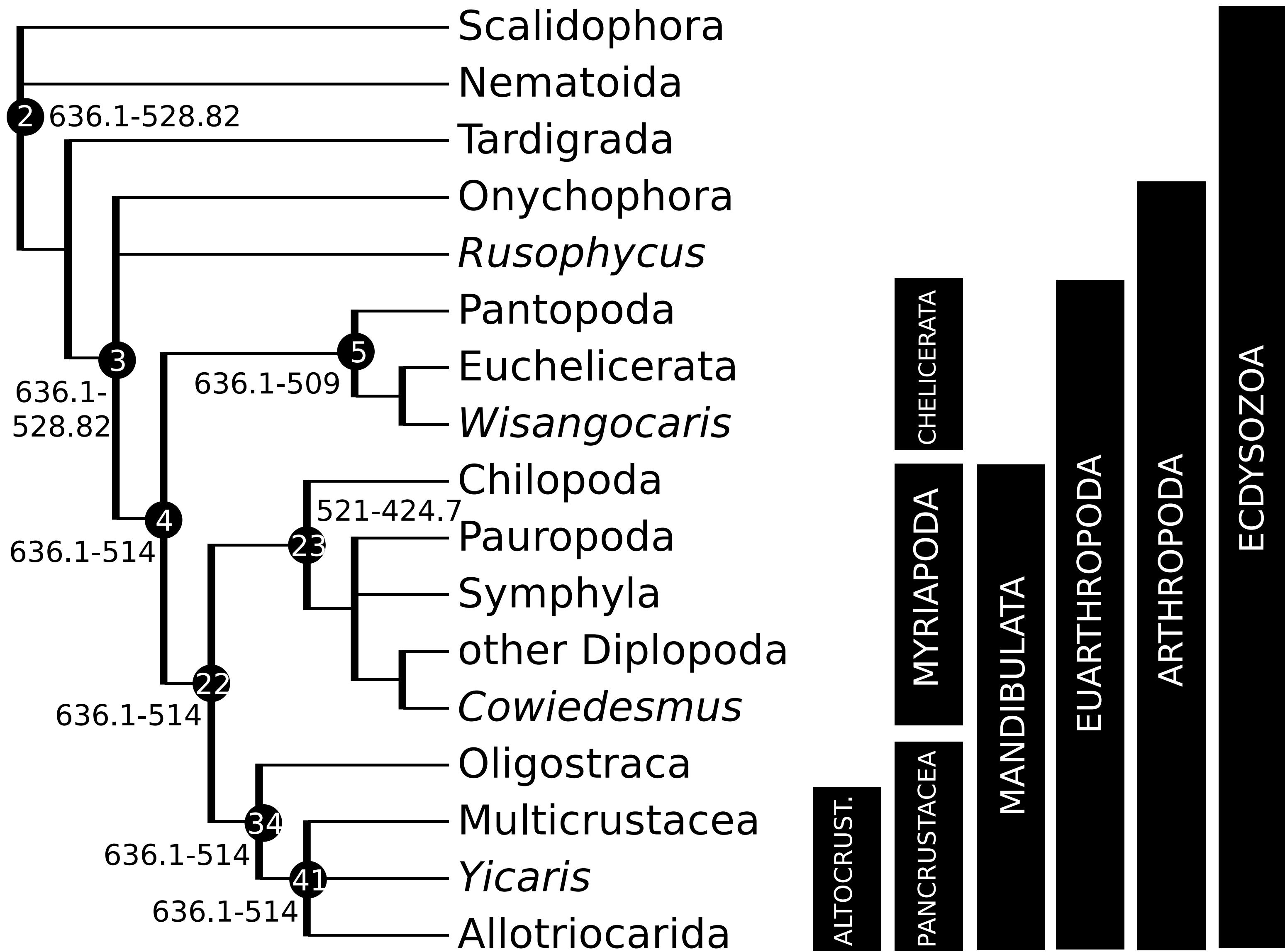
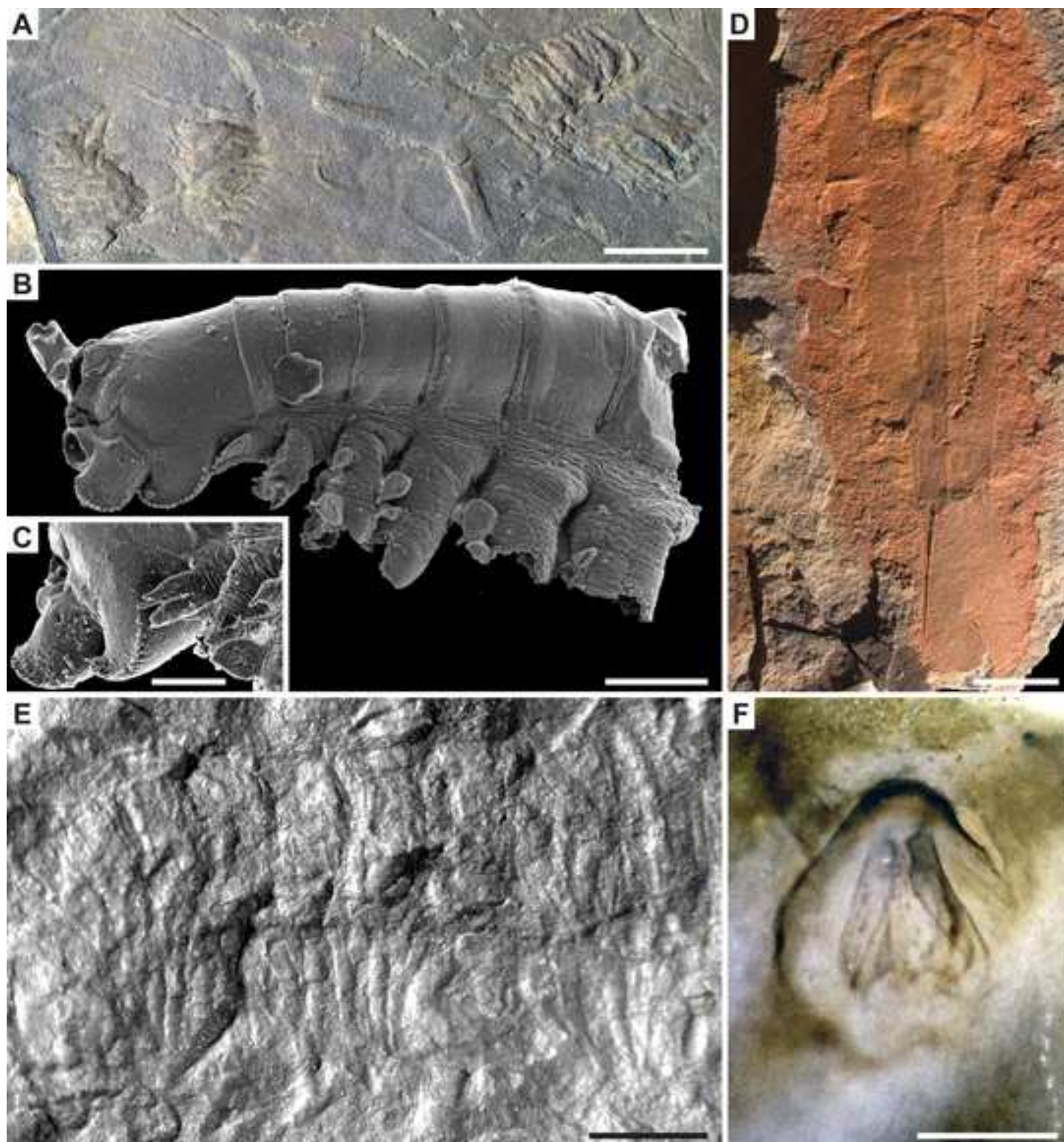


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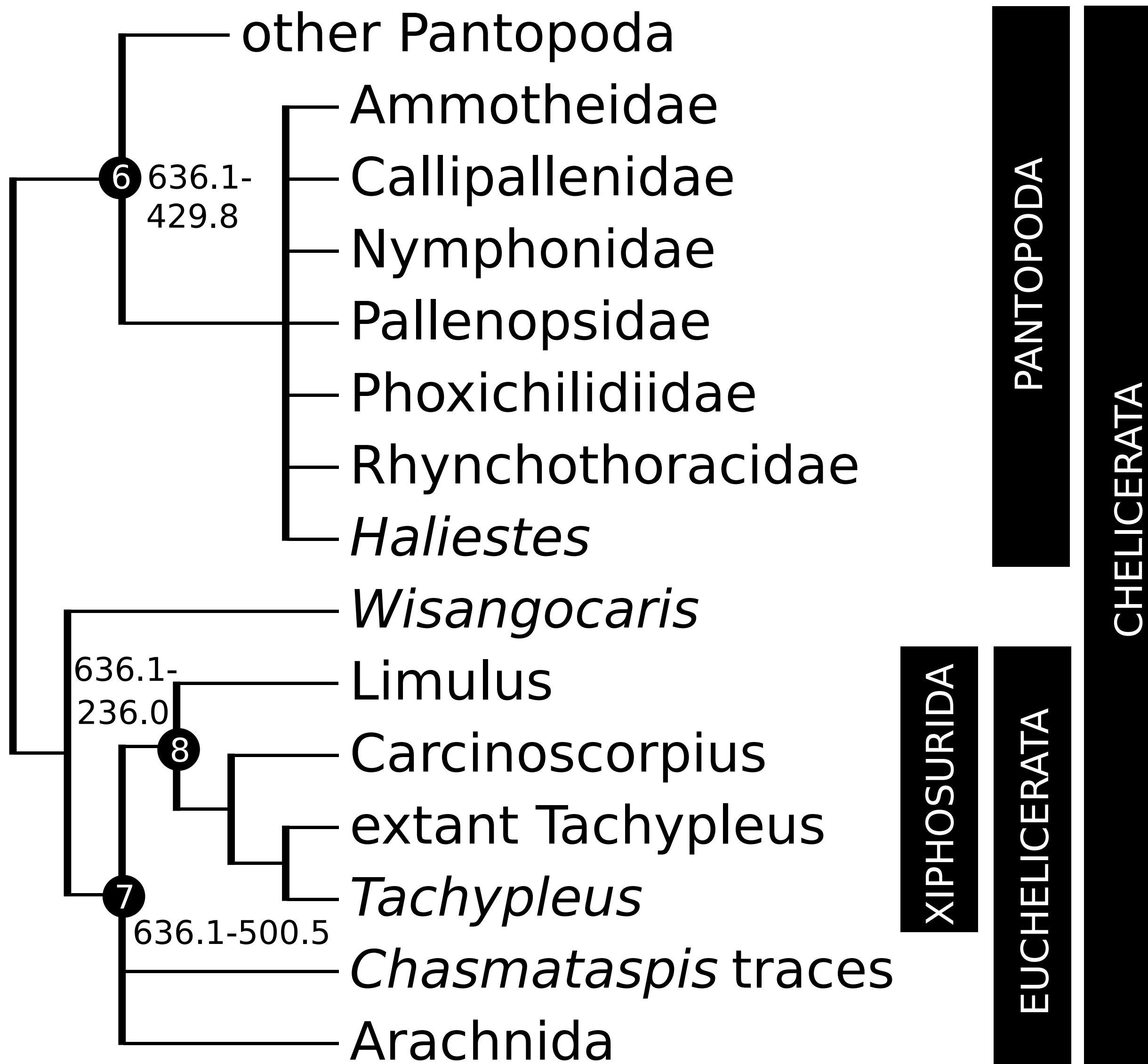


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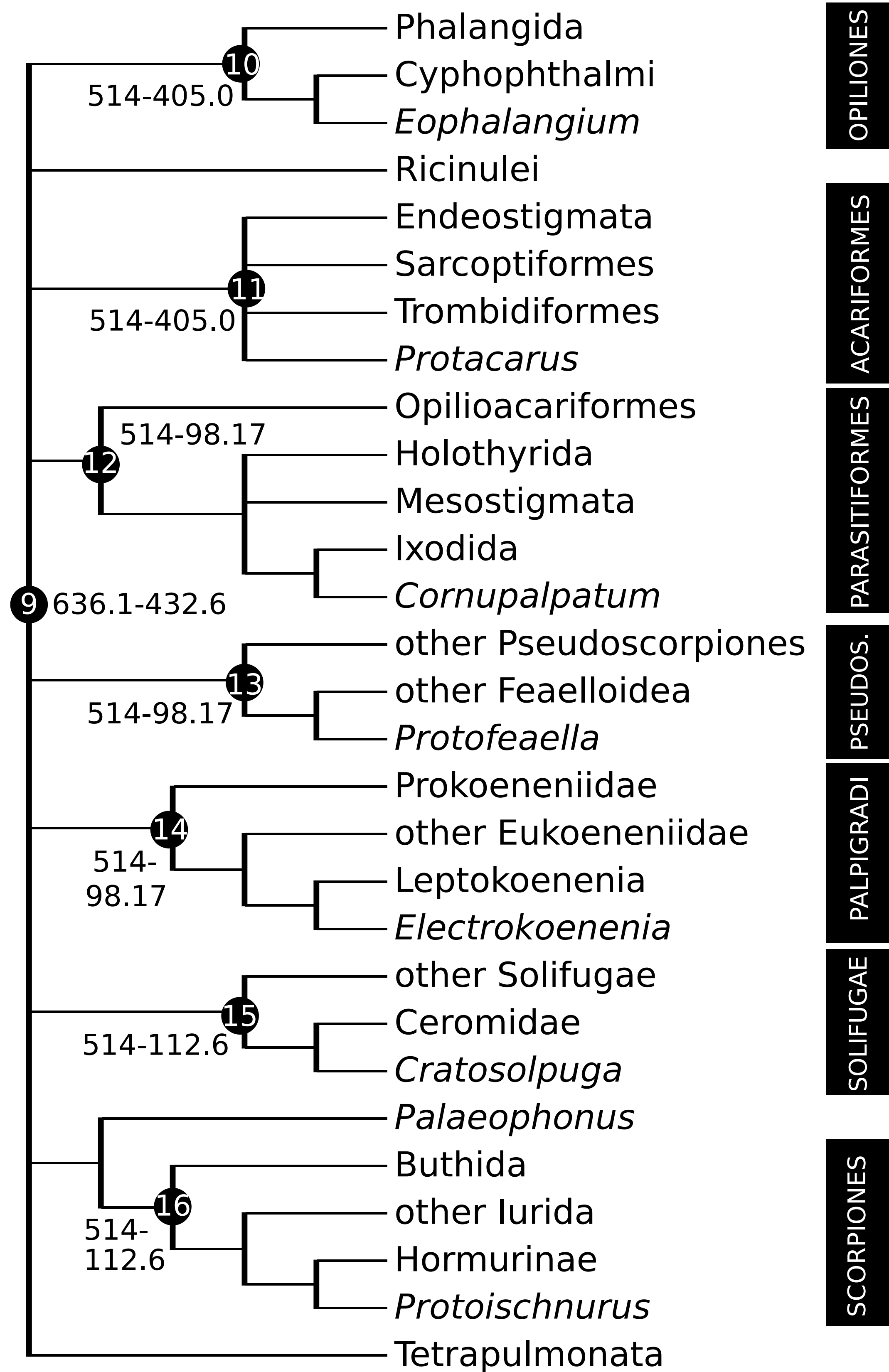


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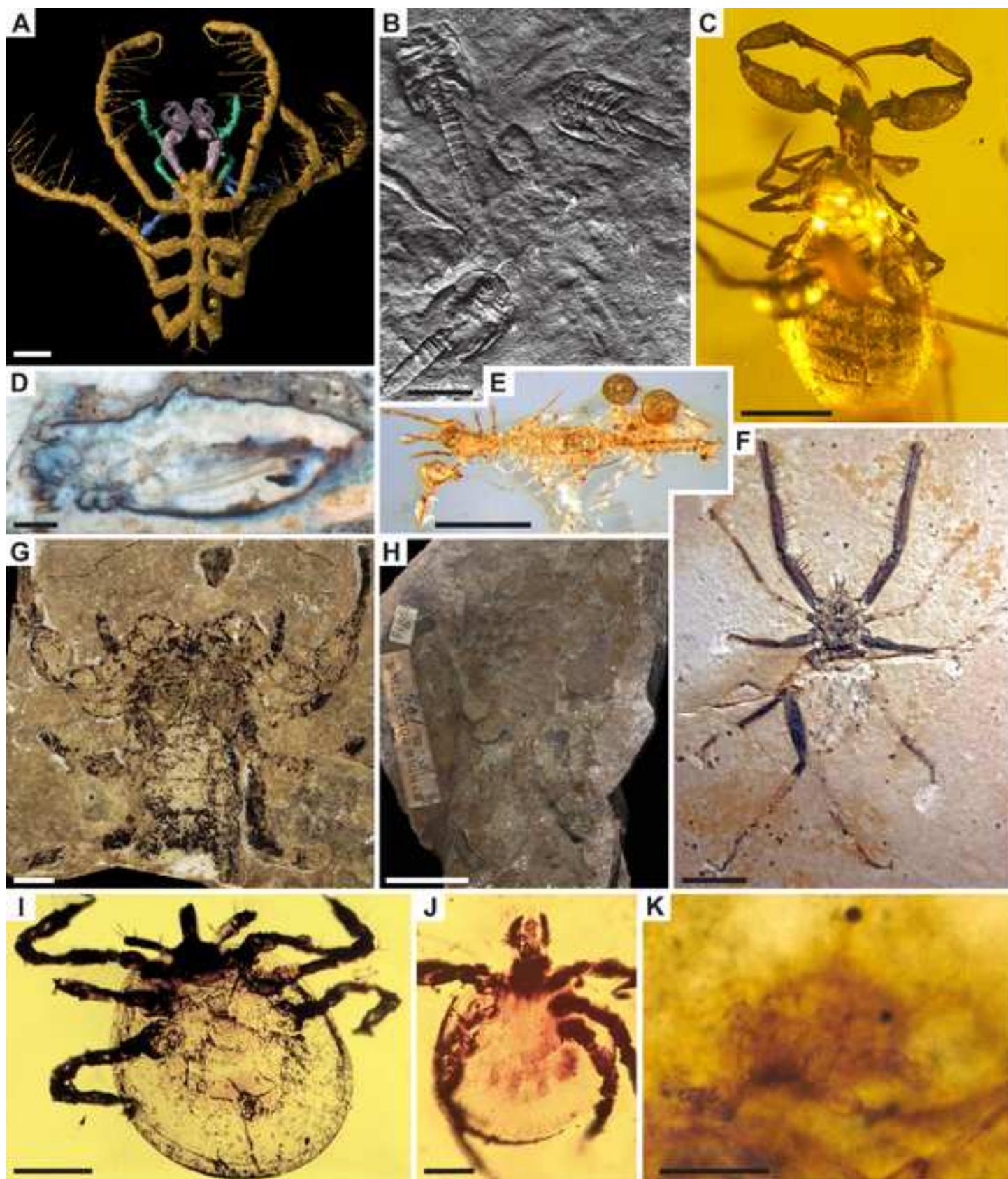


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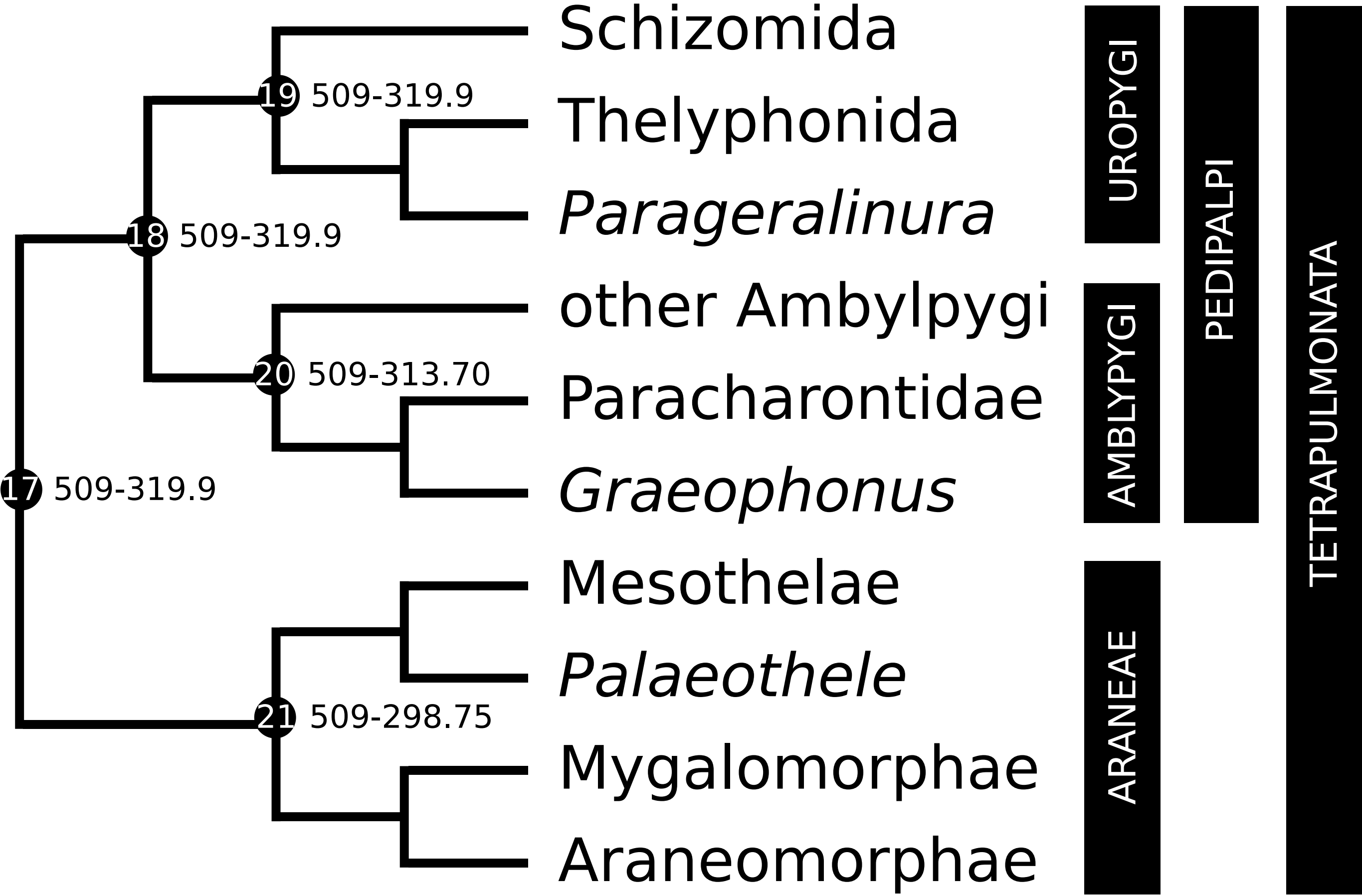


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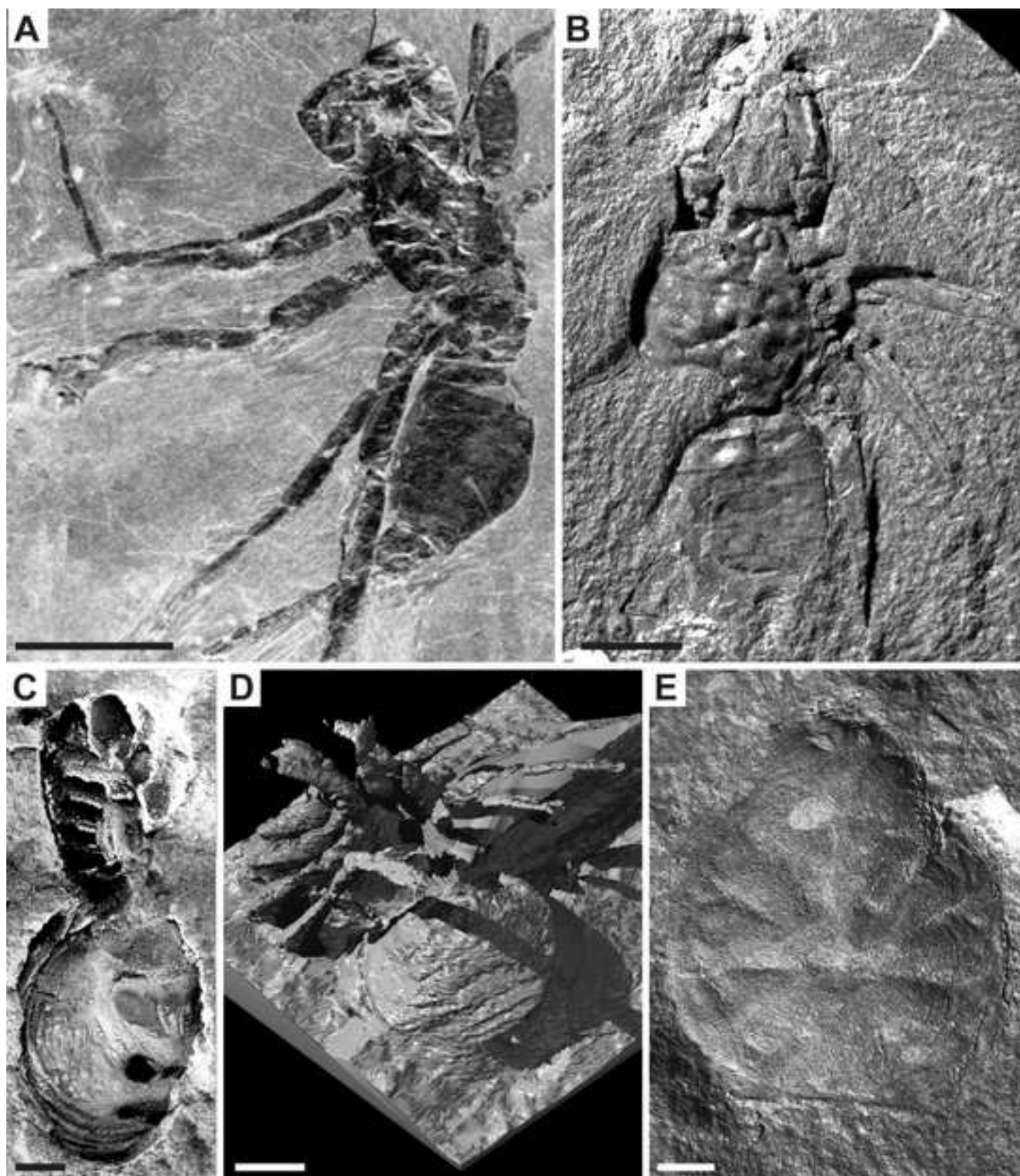


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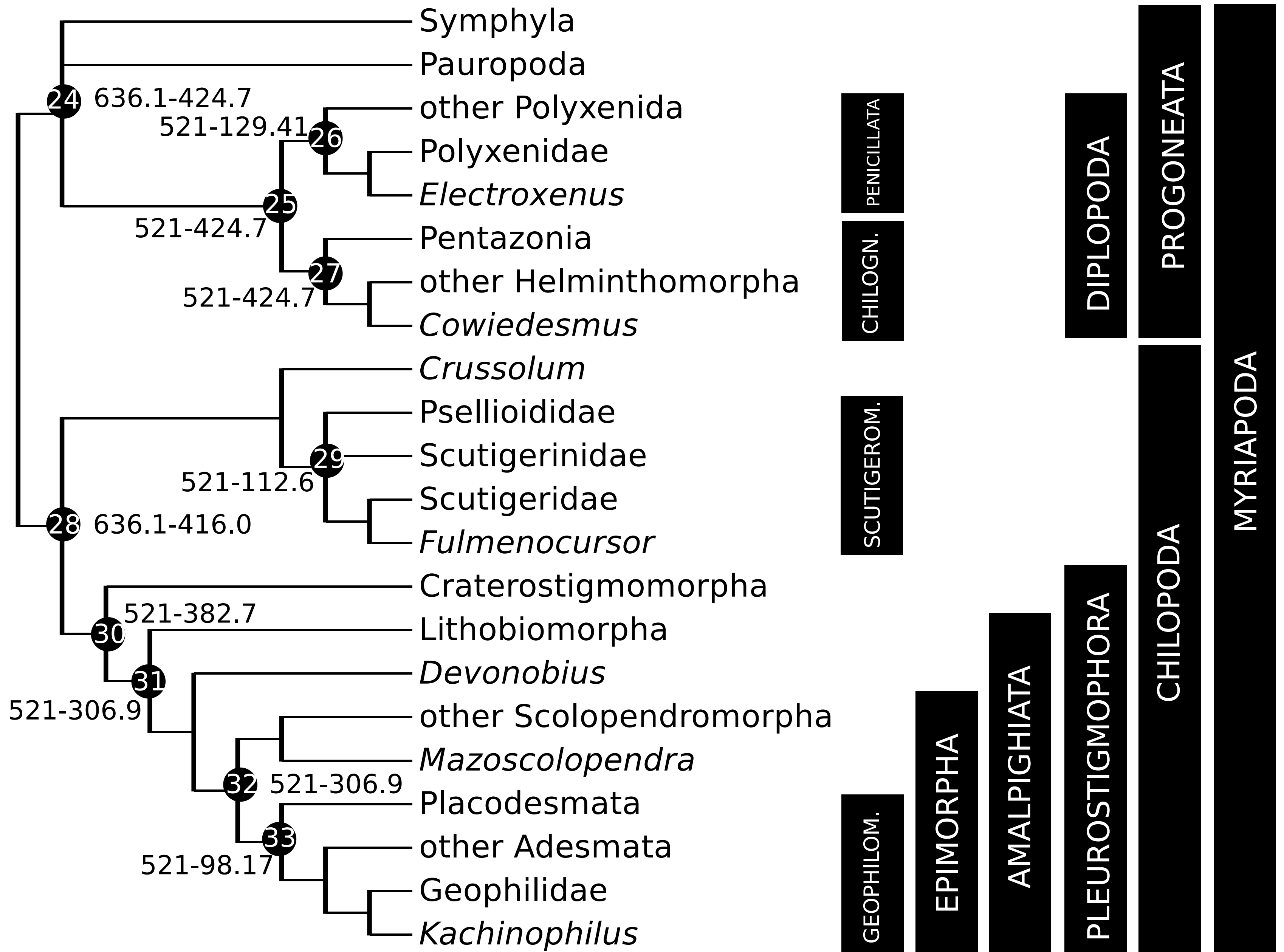


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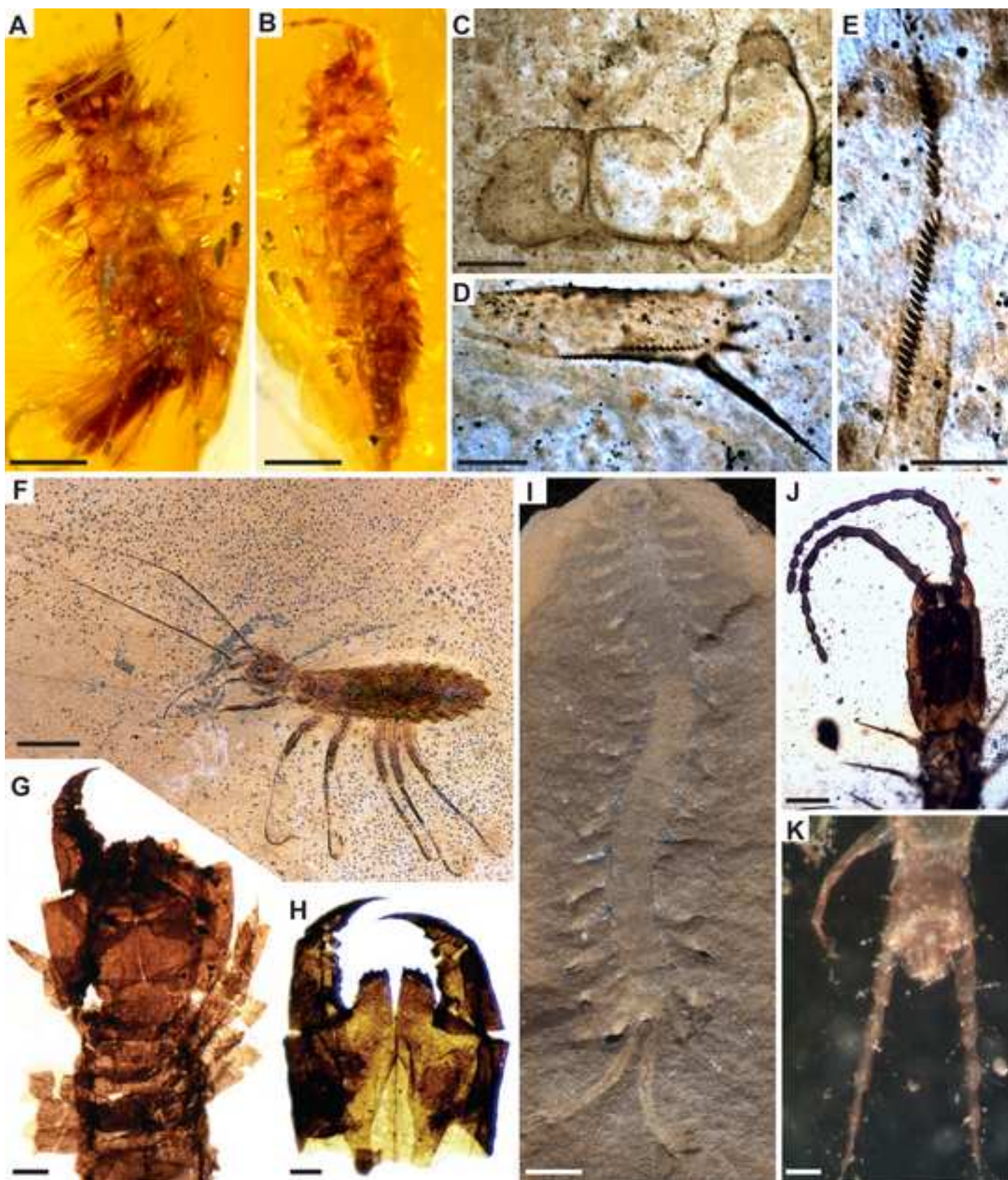


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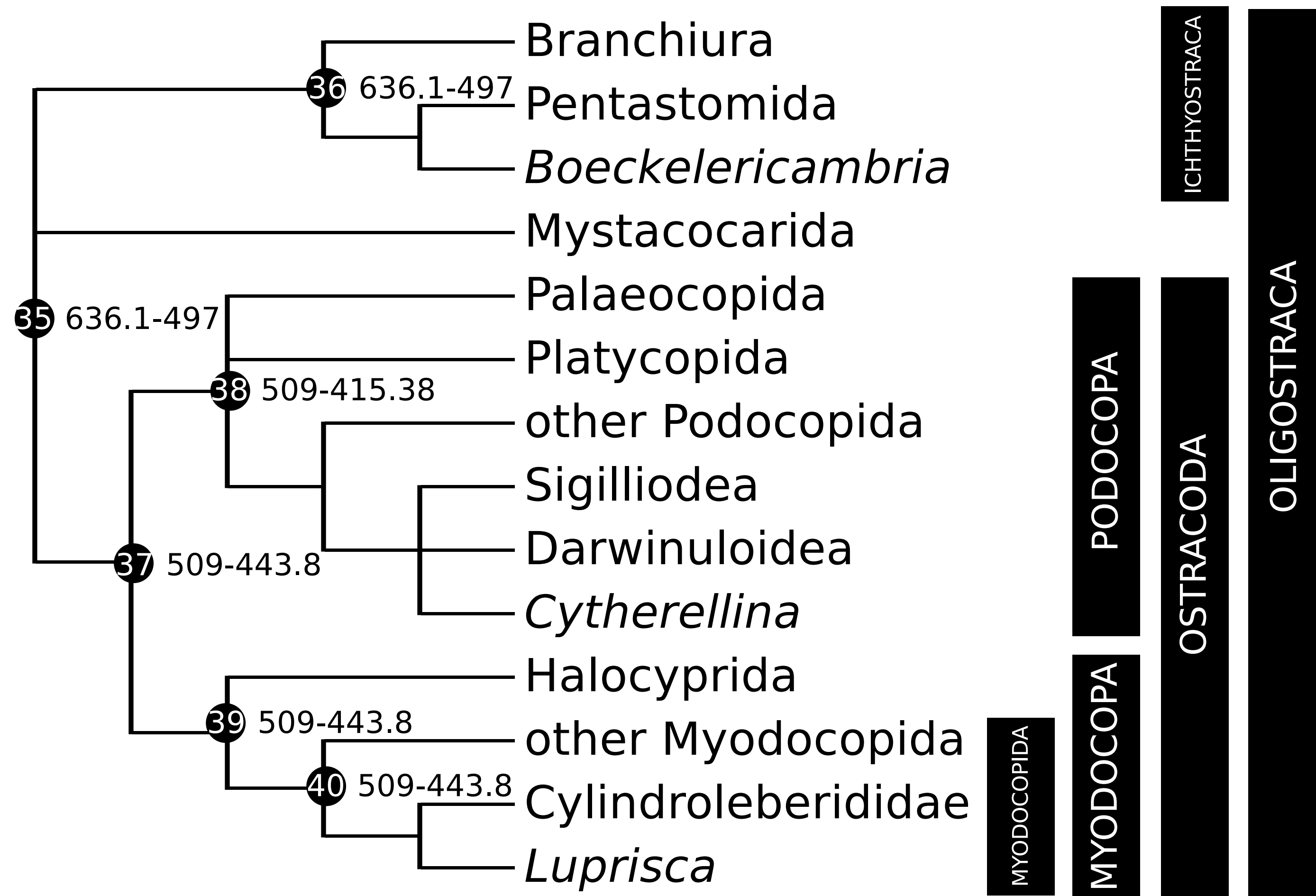
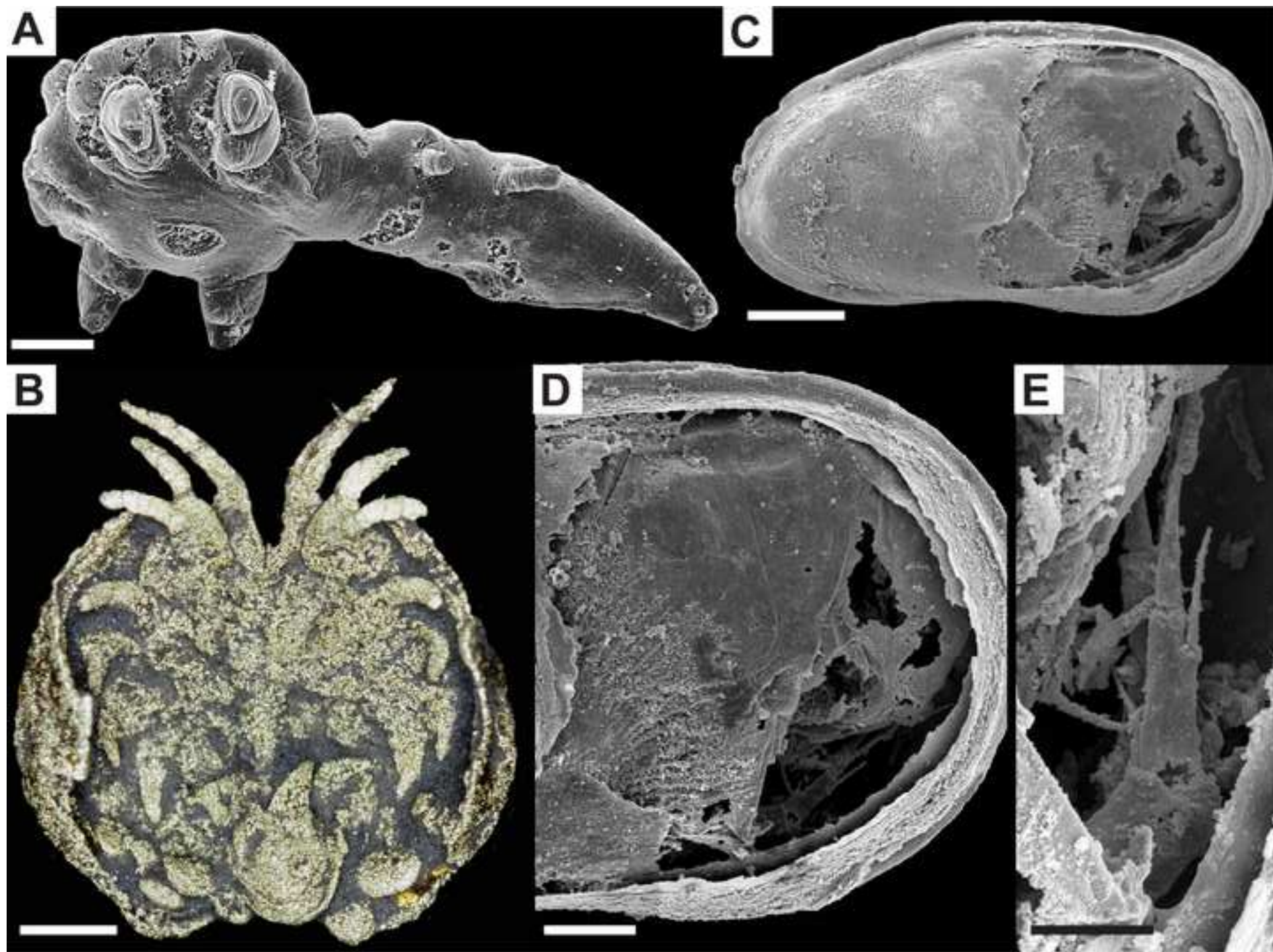


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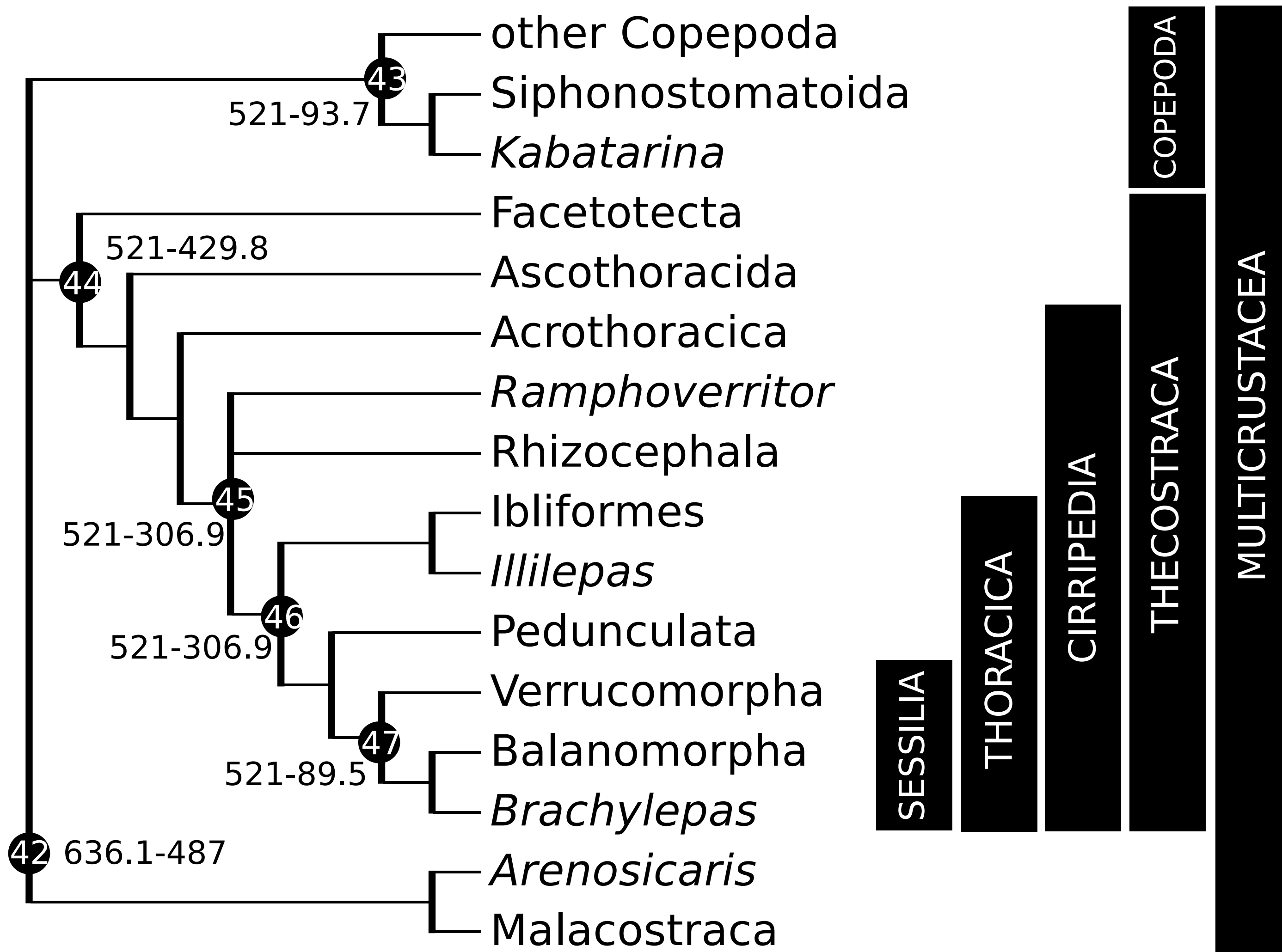


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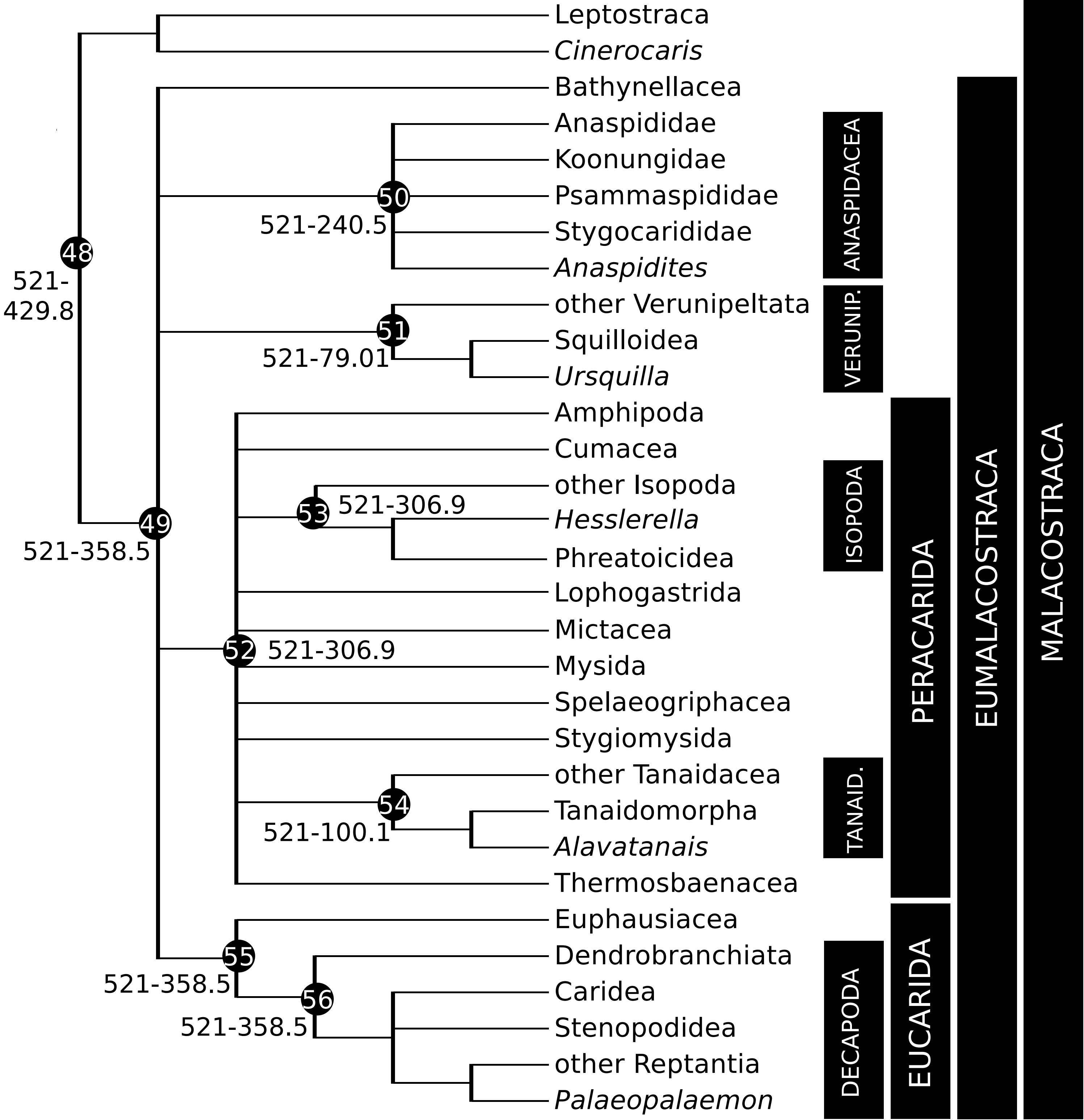
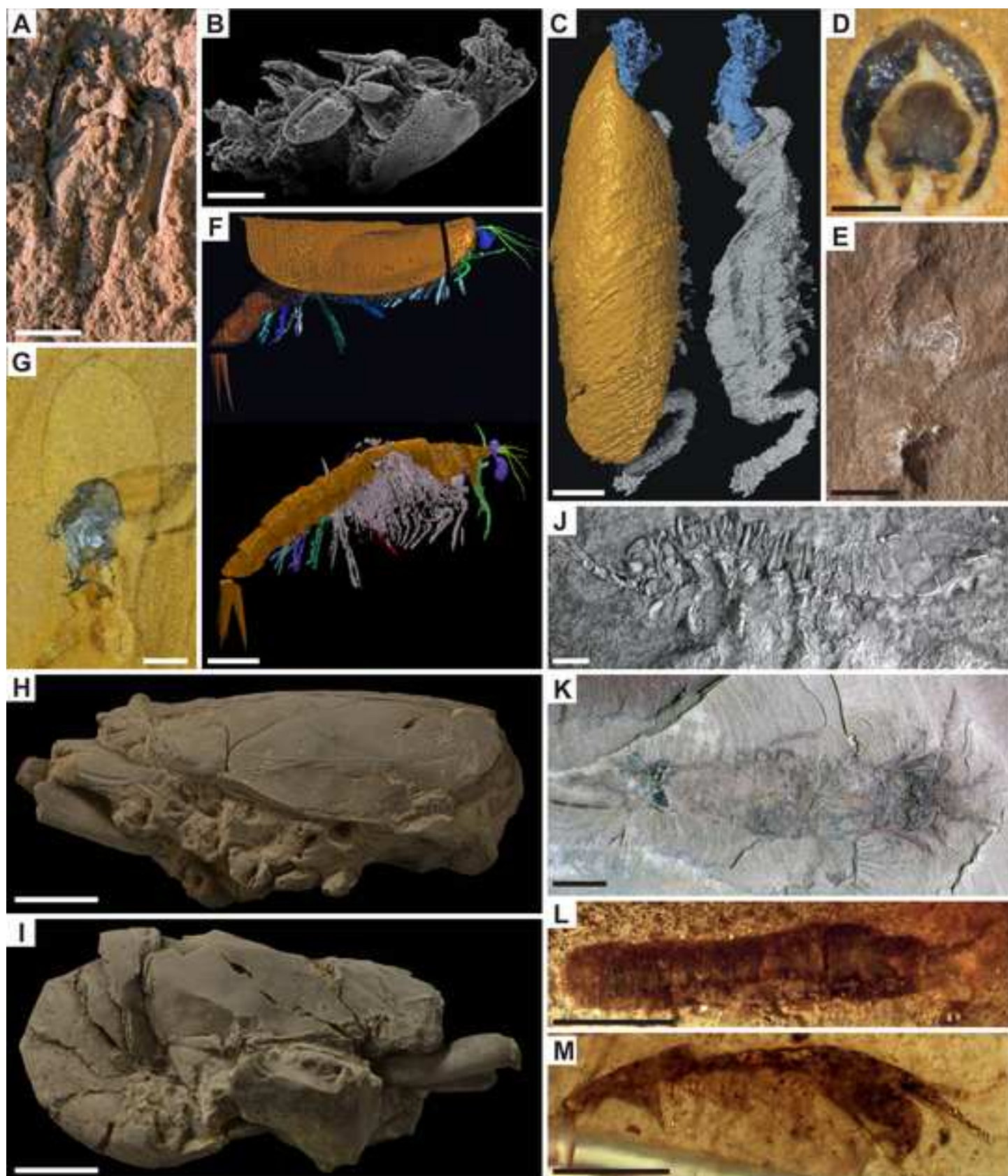


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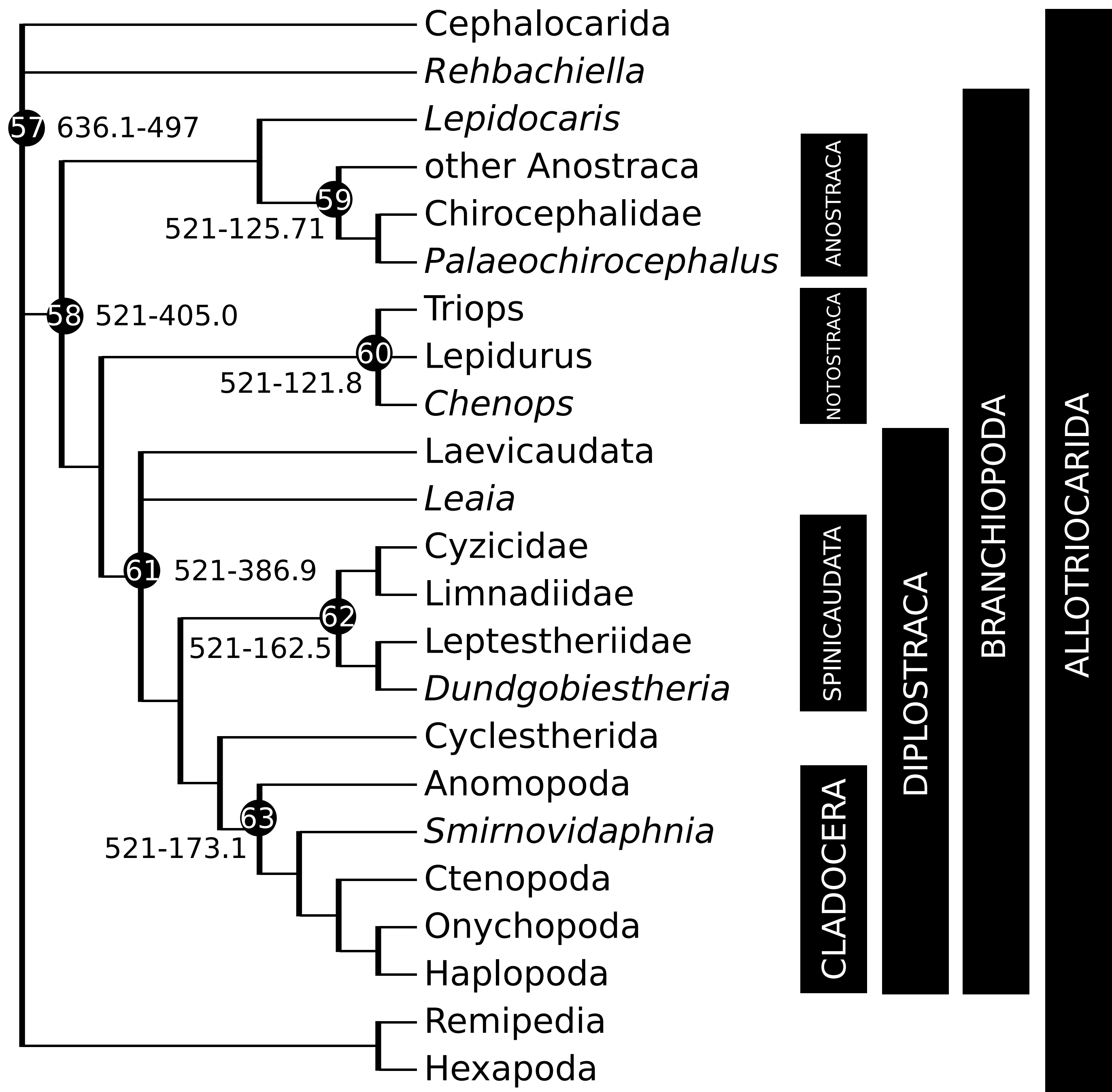


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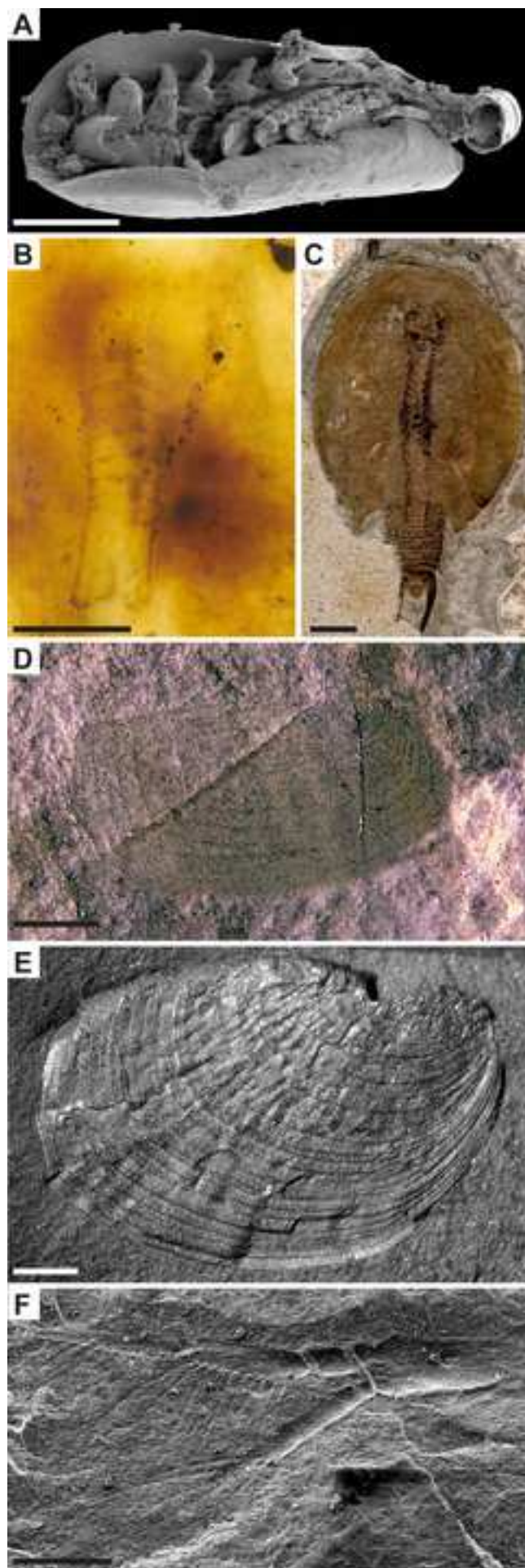


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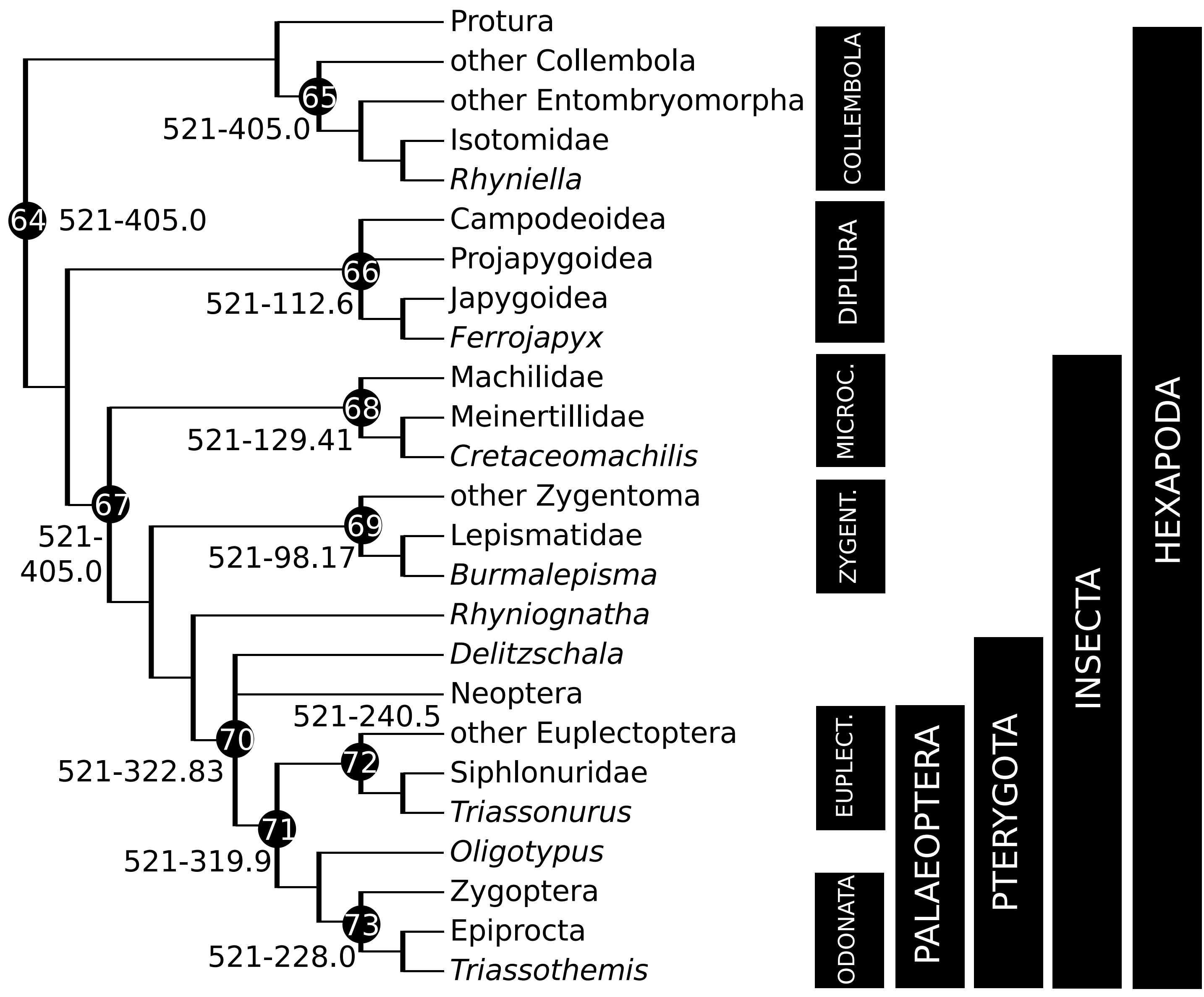
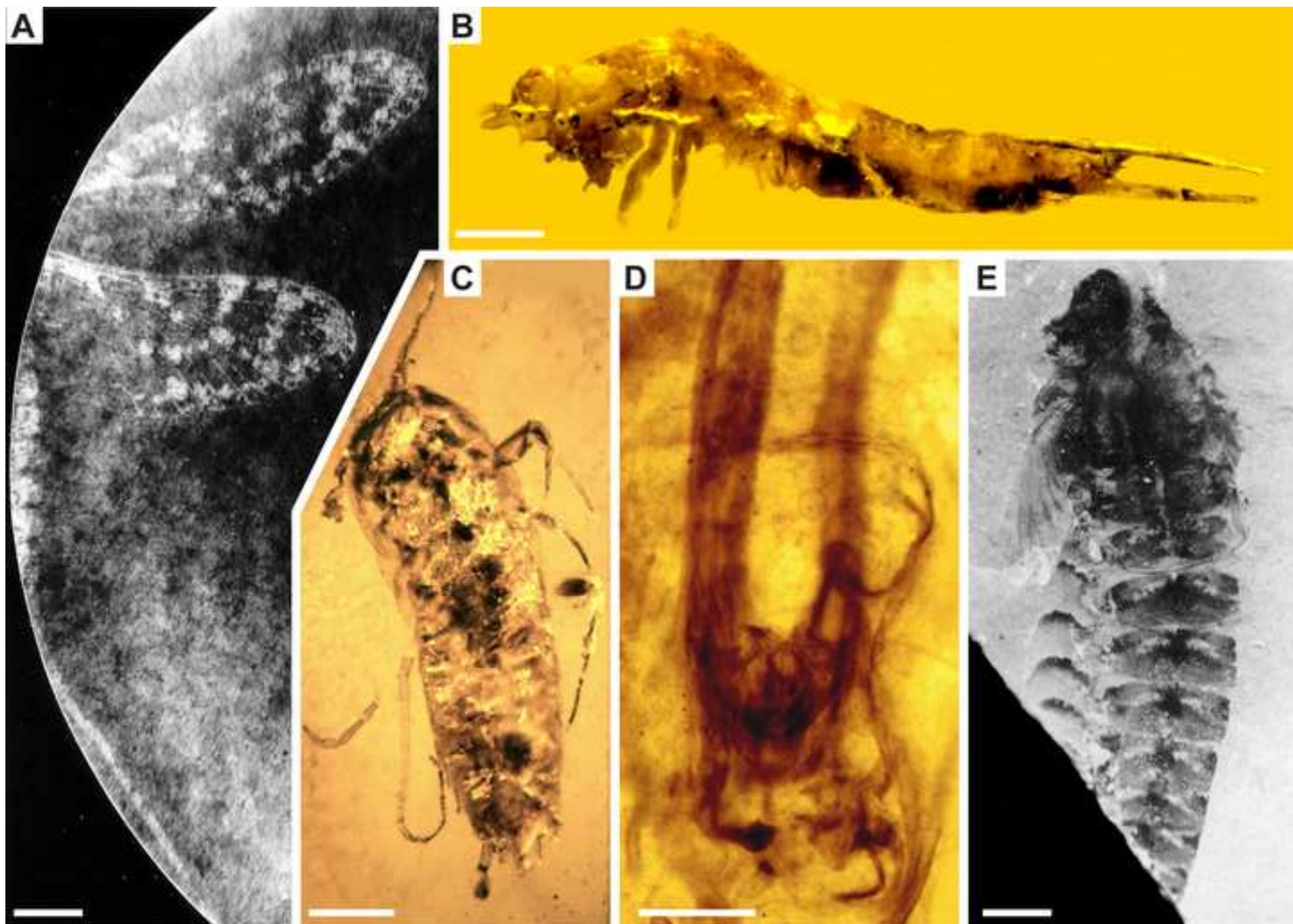


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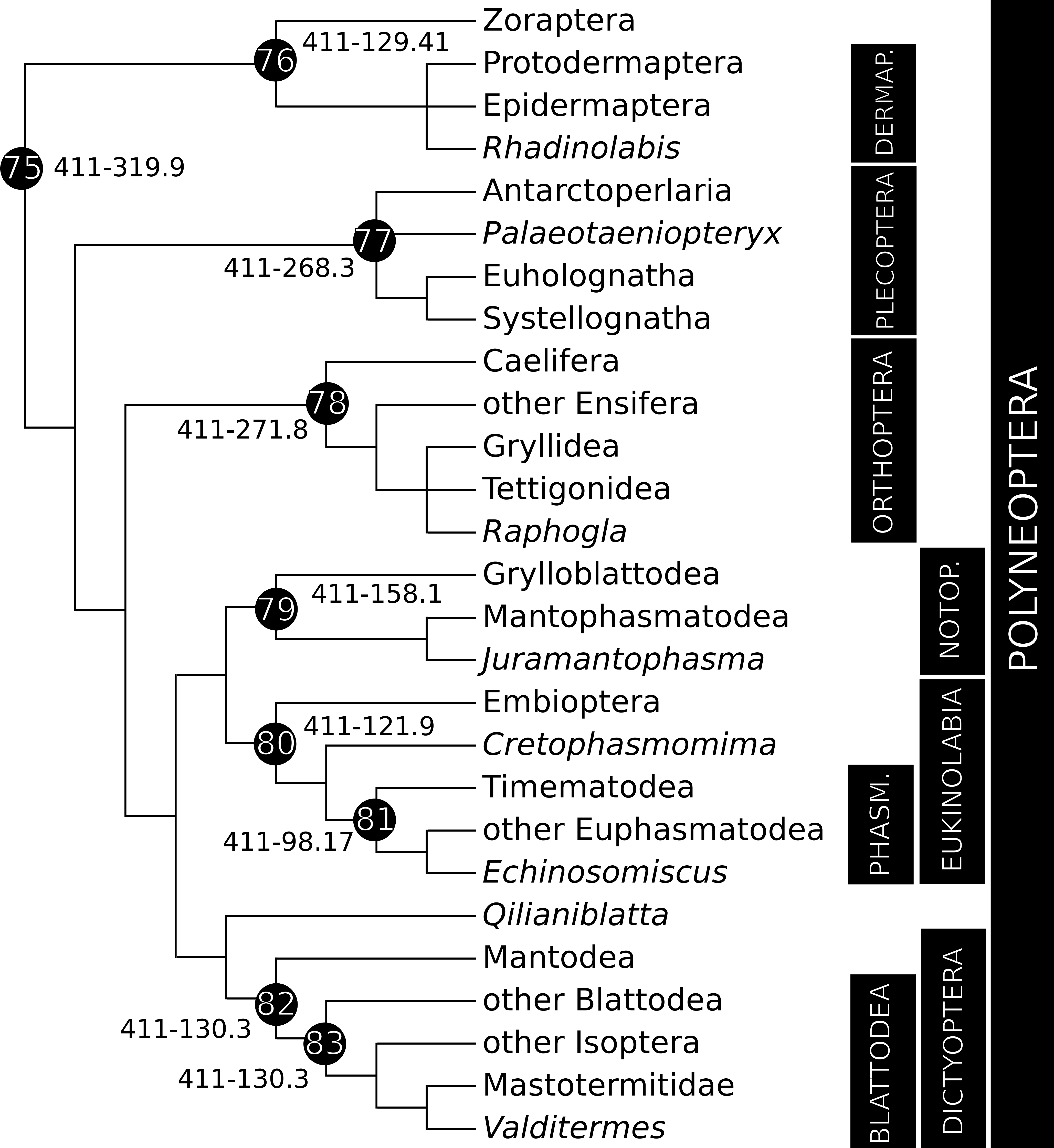


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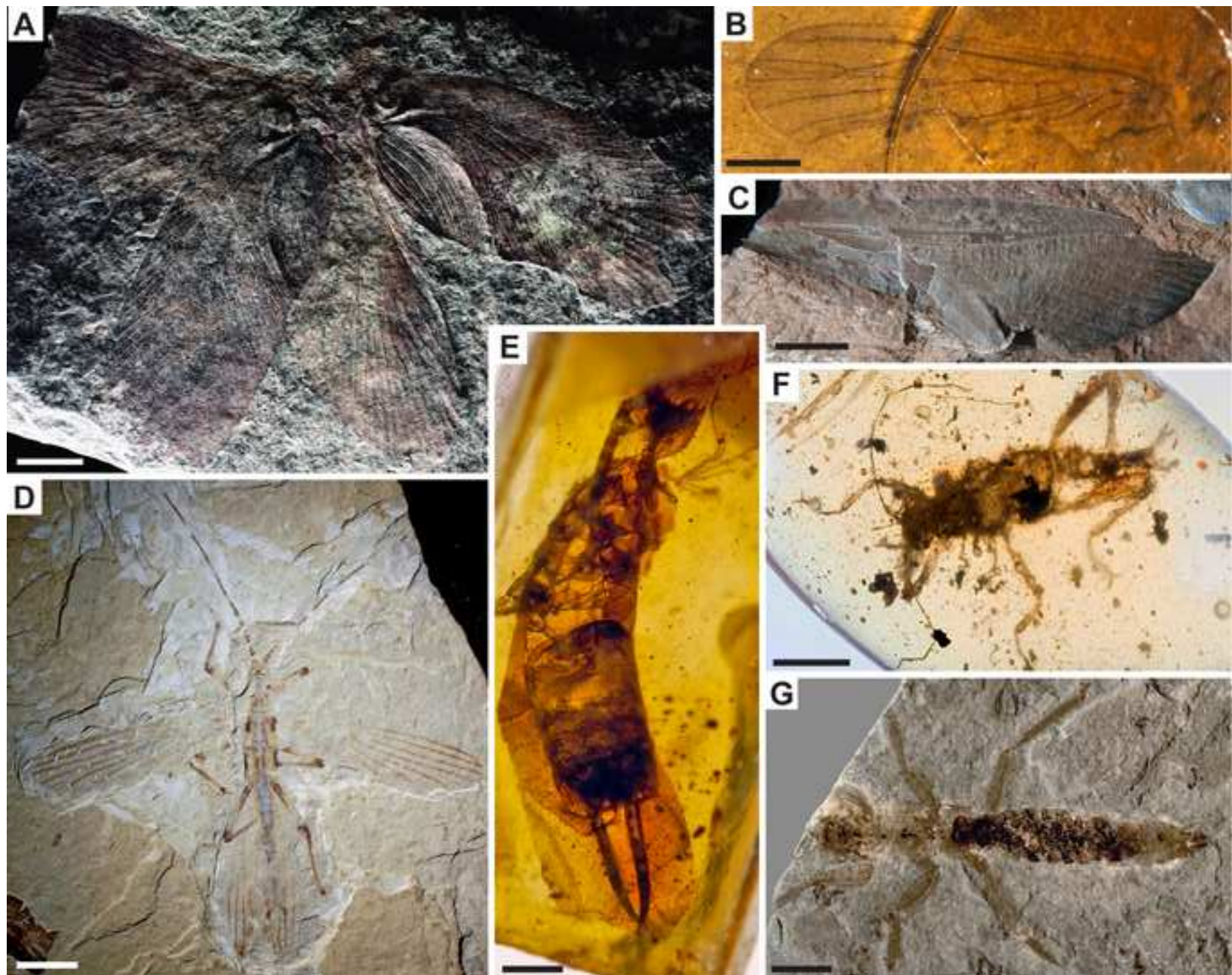


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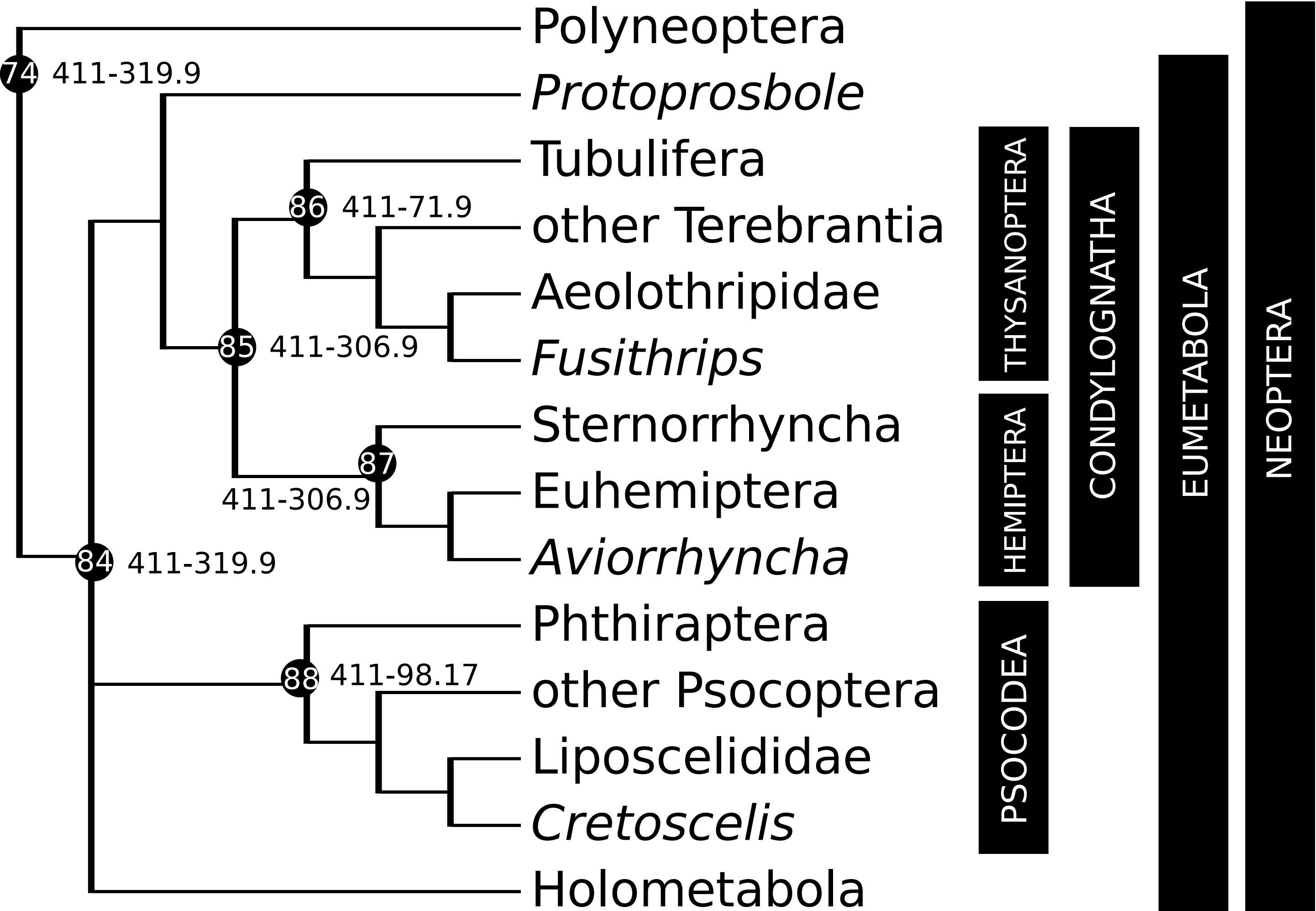


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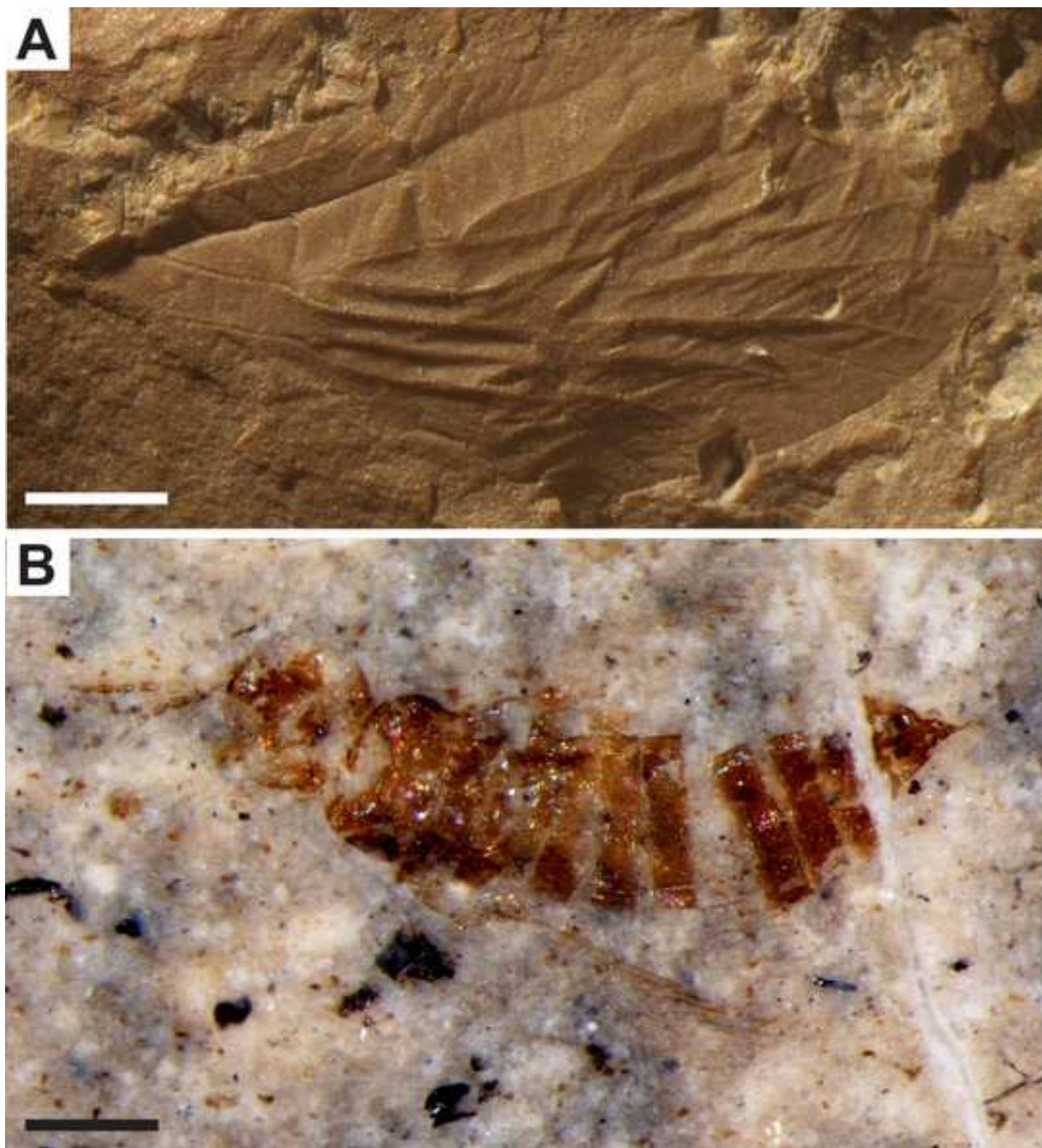


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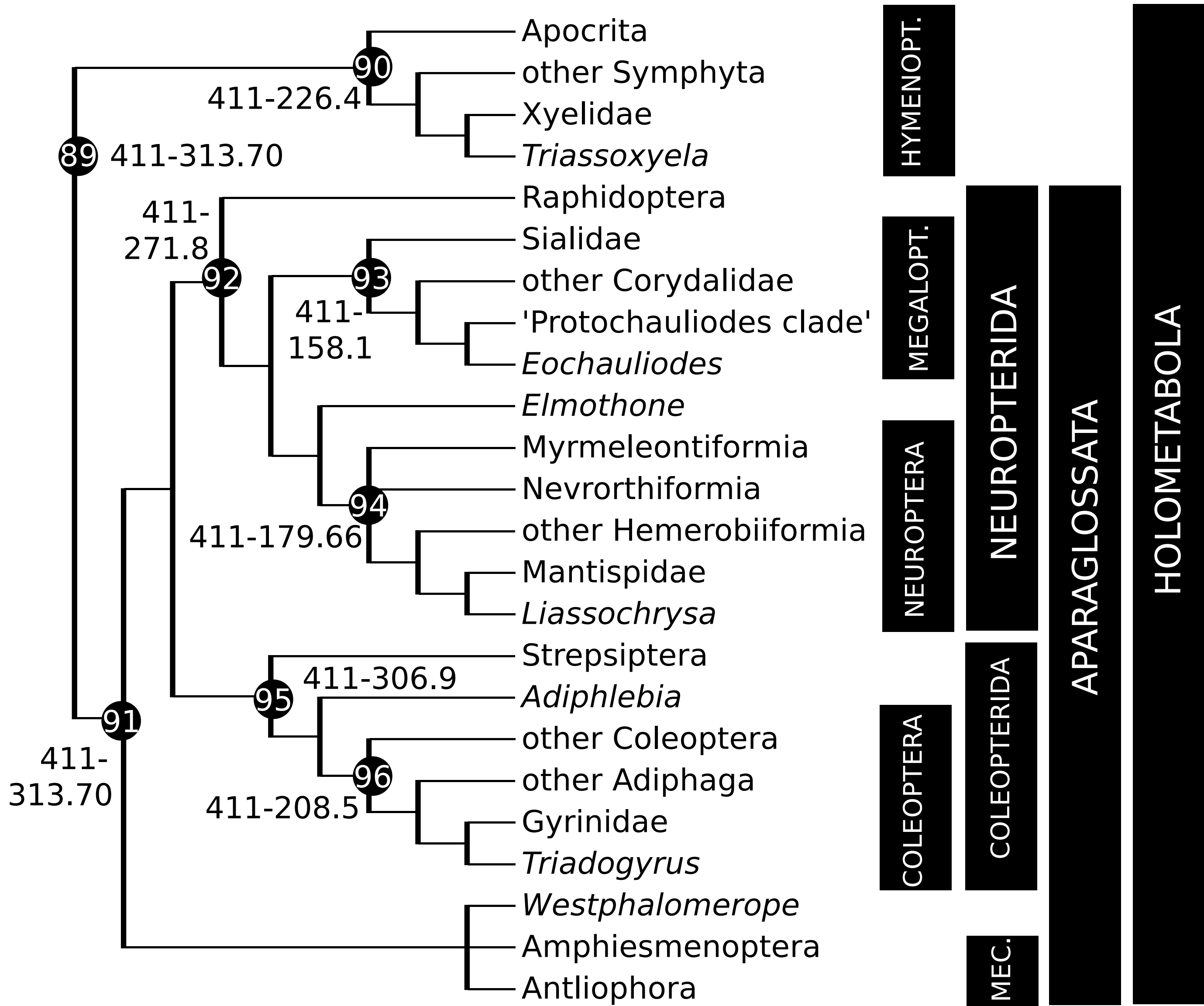


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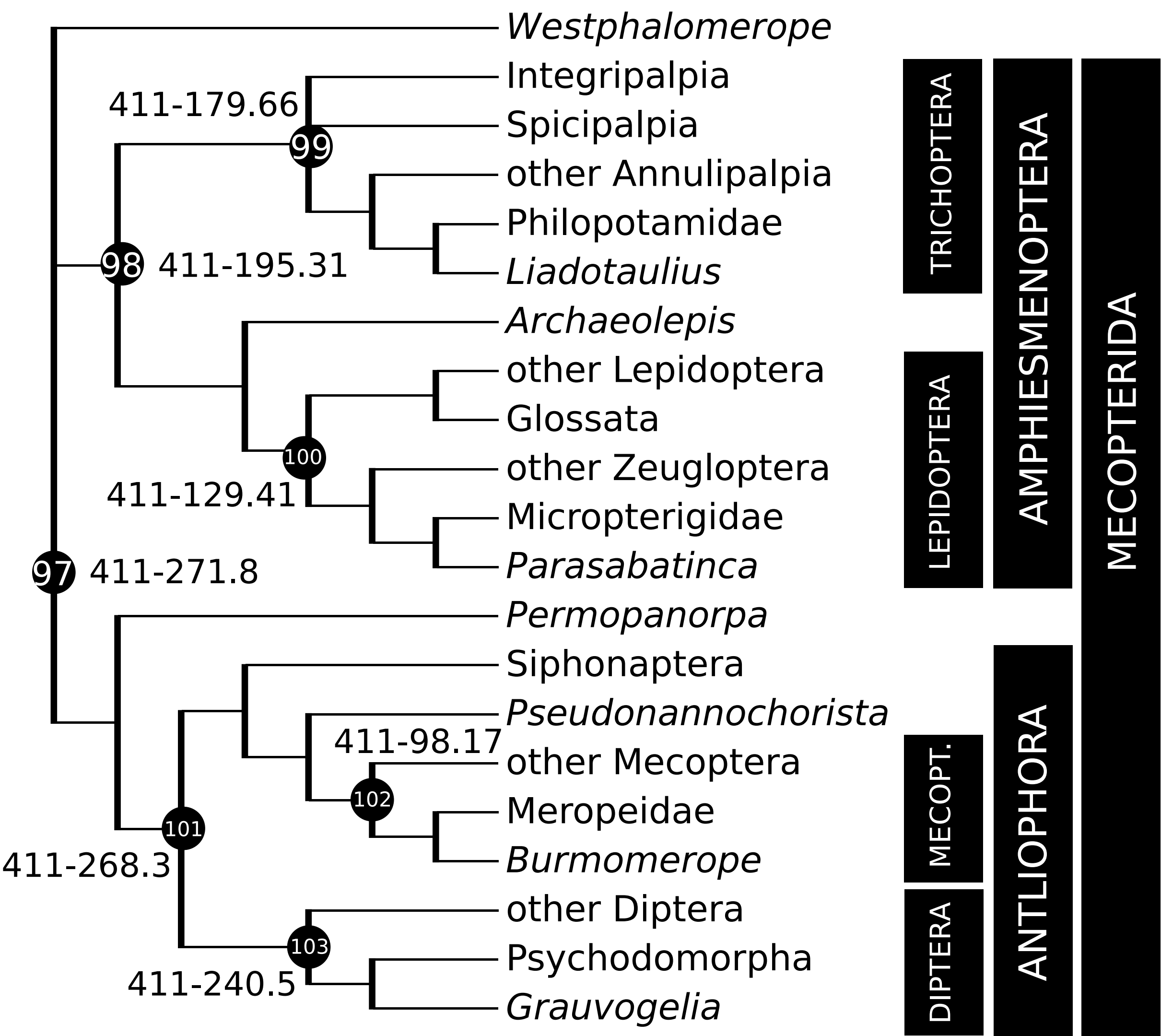


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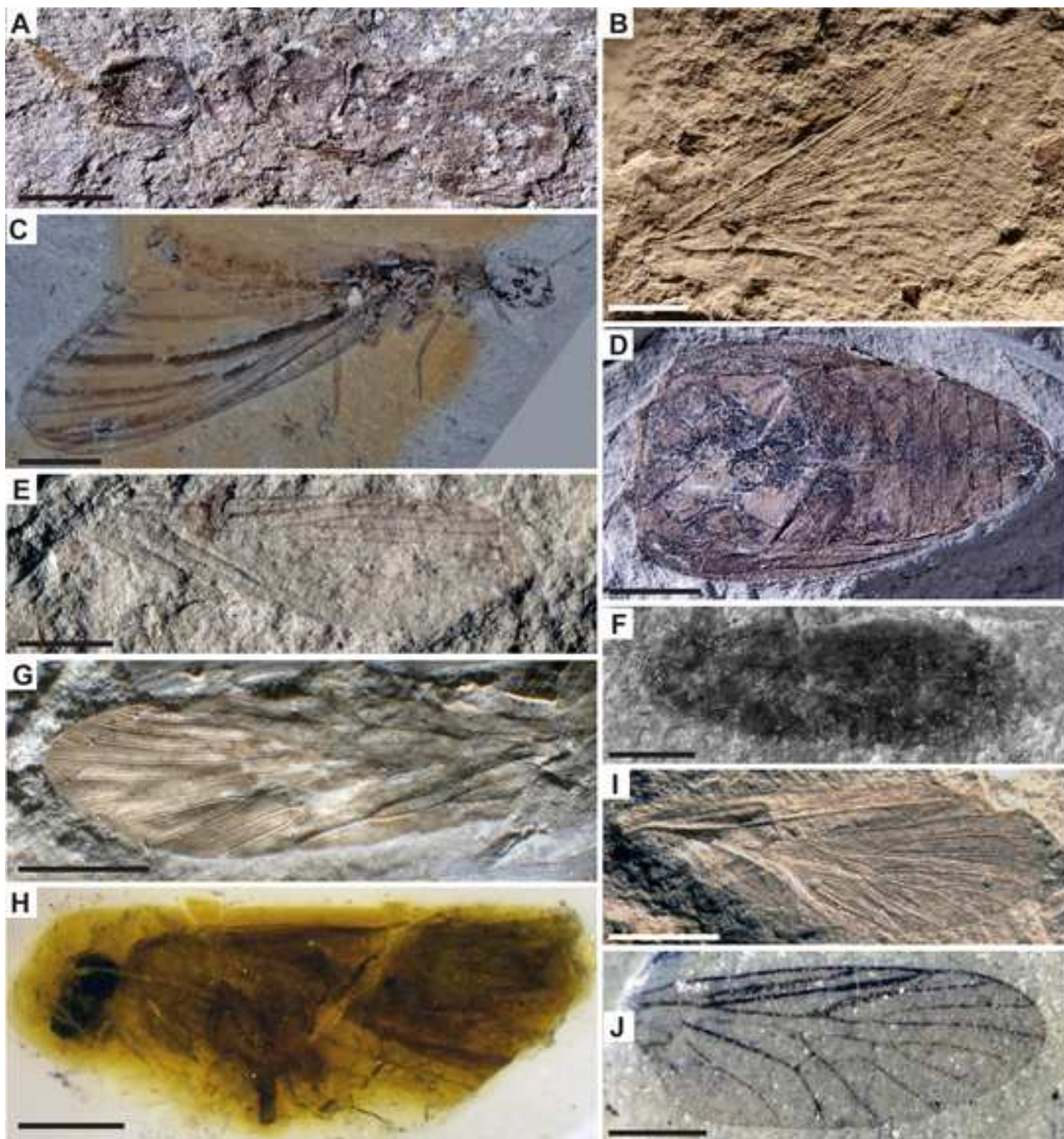


Table A.1

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