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Fossils from the Montceau-les-Mines Lagerstätte (305 Ma) shed light on the anatomy, ecology and phylogeny of Carboniferous millipedes

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Arthropods constitute a highly diverse group of animals dominated by insects, arachnids, crustaceans, and myriapods, the latter consisting of two important classes: Chilopoda and Diplopoda. Diplopods are remarkable by their diversity and disparity and have a long and rich fossil record going back to the Silurian. X-ray Microtomography (μ CT) reveals here the detailed morphology of two diplopods from the Carboniferous (Kasimovian; ca 305 Ma) Lagerstätte of Montceau-les-Mines, namely *Amynilyspes fatimae* (Pentazonia) and *Blanziulus parriati* (Juliformia), allowing 3D-reconstructions to be made. Important features of amynilyspedids exemplified by *Amynilyspes*, are observed for the first time such as the telopods, 21 pairs of walking legs, 13 tergites and the anal shield. Details of the ocular field, antennae and mandibles provide key information on the sense organs of these ancient myriapods as well as their capacities to process food. The presence of possible spiracles in *B. parriati* indicates a probable adaptation to living in terrestrial environments. Intraspecific

28 differences seen in the appendages of *Amynilyspes fatimae* suggest that late
29 Carboniferous pill millipedes had sexual dimorphic features closely similar to those of
30 extant millipedes. *A. fatimae* and *B. parriati* are interpreted as two detritivore millipedes
31 living in a vegetated and humid environment (e.g. forest, swamp, litter) that are likely
32 to have played the role of recycling plant detritus as do numerous present-day
33 myriapods.

34

35 **Keywords :** Myriapoda; Diplopoda; Montceau-les-Mines Lagerstätte; Carboniferous;
36 Pentazonia; Juliformia

37

38

39

40 **Introduction**

41 Arthropods are key elements of modern aquatic and terrestrial ecosystems with more
42 than one million species described so far. As inhabitants of a huge variety of aquatic,
43 terrestrial and aerial environments they play a pivotal role in food chains and trophic
44 webs. Their rich Cambrian fossil record exemplified by Burgess-Shale-type (BST)
45 Lagerstätten reveals the very ancient origin and diversification of the group from
46 possible cycloneuralian worm-like ancestors and its early split into chelicerates and
47 mandibulates (crustaceans, insects and myriapods) during the Cambrian (Vannier *et al.*
48 2018; Aria 2022). Together with insects, arachnids and some crustaceans (e.g.
49 isopods), myriapods are among the most successful colonizers of terrestrial
50 environments, with more than 16, 000 described extant species distributed in 160
51 families (Wilson & Hannibal 2005; Stoev *et al.* 2010; Brusca 2016). Myriapods are
52 characterized by an elongated body with multiple leg-bearing segments (Stoev *et al.*

53 2010), and are divided into four classes: Chilopoda (centipedes), Symphyla (garden
54 centipedes), Pauropoda and Diplopoda (millipedes). While most centipedes are fast
55 running predators (e.g. *Scolopendra*), with only one pair of legs per segment (Brusca
56 2016), most of the 12, 000 described diplopods (millipedes) are detritivores, being
57 characterized by diplosegments bearing two pairs of legs each (Stoev *et al.* 2010).
58 Diplopoda typically burrow into soil and litter, thus being important recyclers of
59 vegetable matter (Lavelle & Spain 2002).

60

61 Myriapods can be traced back to at least the Silurian, (Ludlow Series, ca 425 Ma)
62 with archipolypods millipedes and kamperids being the earliest known myriapods and
63 arthropod colonizers of terrestrial environment (Almond 1985). Millipedes strongly
64 diversified into various groups during the Devonian such as the Eoarthropleurida
65 (Størmer 1976) and the Microdecemplicida (Wilson & Shear 1999; Kraus &
66 Brauckmann 2003). It was also during the Devonian that derived clades like the
67 Helminthomorpha with derived gonopods (Wilson & Anderson 2004) appeared.
68 Millipedes step into the Lower Carboniferous with other archipolypods (Wilson &
69 Anderson 2004) and diversify through the Upper Carboniferous being typically
70 associated with coal swamp environments (Shear & Edgecombe 2010). These upper
71 Carboniferous myriapods include archipolypods (Burke 1973, 1979) and other extinct
72 forms that have been placed into groups with various taxonomic ranking such as
73 Pleurojulida (Wilson & Hannibal 2005), Pentazonia (Hannibal & Feldmann 1981;
74 Hannibal 1984; Racheboeuf *et al.* 2004), Helminthomorpha (Hoffman 1963; Hannibal
75 *et al.* 2004) and Arthropleurida. The latter are distinguished from the aforementioned
76 taxa by their very large size approaching over 2 m in length and 40 cm in width

77 (Briggs 1979; Briggs *et al.* 1984; Kraus & Brauckmann 2003; Martino & Greb 2009;
78 Davies *et al.* 2021).

79

80 The Upper Carboniferous, Kasimovian (ca 305 Ma) Montceau-les-Mines Lagerstätte
81 (Saône-et-Loire, France) is a rich source of information on the colonization of
82 terrestrial environments by plants and animals and is a unique window on the
83 evolution of groups such as myriapods and chelicerates. The myriapods from
84 Montceau are typically found embedded in sideritic nodules and preserved in three
85 dimensions (Perrier & Charbonnier 2014; McCoy *et al.* 2015). They are represented
86 by two diplopod species: *Amynilyspes fatimae* (Racheboeuf, Hannibal & Vannier,
87 2004) and *Blanziulus parriati* (Langiaux & Sotty, 1976). Techniques used by previous
88 authors (Racheboeuf *et al.* 2004) such as invasive mechanical preparation and latex
89 casts damaged fine anatomical structures (e.g. appendages, head parts). In order to
90 re-study this exceptional material in optimal conditions we gave preference to non-
91 destructive techniques such as X-Ray microtomography (μ CT) that allows high-
92 resolution anatomical exploration to be performed (Garwood *et al.* 2011, 2016 for
93 similar methods applied to other arthropods from Montceau). New morpho functional
94 interpretations of these Carboniferous millipedes are also proposed based on
95 detailed comparisons with extant diplopods, that altogether shed light on still poorly
96 known aspects of extinct millipedes' autecology, habitats and adaptations to living on
97 land. Phylogenetic analyses were performed based on a new and enriched set of
98 characters obtained from μ CT reconstructions; they clarify the position of the
99 Montceau millipedes in the evolutionary tree of myriapods.

100

101

102 **Geological and environmental context**

103 The Montceau-les-Mines Lagerstätte (Late Pennsylvanian, Kasimovian, $307.0 \pm$
104 0.1 Ma – 303.7 ± 0.1 Ma; Cohen *et al.* 2013) lies within the Blanzay-Montceau-les-
105 Mines coal basin at the southern boundary of the Stephano-Permian graben of
106 Blanzay-Le Creusot-Bert (Perrier & Charbonnier 2014; Fig. 1). The Late
107 Pennsylvanian Series exposed at Montceau-les-Mines consists of silty claystones
108 with intercalations of sandstones and iron carbonates (Perrier & Charbonnier 2014)
109 and includes, from the base to the top: the Great Seams Formation (Assise de
110 Montceau), the Upper Seams Formation (Assise des Carrières) and the later
111 Pennsylvanian-Permian transition (Assise du Ponsard) (Perrier & Charbonnier 2014).
112 Horizons with concentrations of fossiliferous sideritic nodules are bounded with thin
113 iron carbonate layers (Perrier & Charbonnier 2014). Research on the Montceau
114 Lagerstätte led by professional scientists and amateurs started during the 1970's and
115 concentrated on three main sites (Saint-Louis, Saint-François and Sainte-Hélène;
116 Charbonnier 2014) until the exploitation of coal measures came to an end in the
117 1990's and all open mines were flooded making new exploration impossible.
118 Over the years, fossiliferous layers yielded abundant nodules (about 120 000, Sotty
119 1980) containing remains of plants and animals, often exquisitely preserved in three
120 dimensions and now deposited in the collections of the Natural History Museum in
121 Autun (Saône-et-Loire, France). Plant remains clearly indicate that the
122 paleoenvironment associated with the Montceau Lagerstätte was humid and densely
123 occupied by arborescent and herbaceous plants in the vicinity of riverbanks, lakes
124 and swamps whereas mesoxerophytes presumably lived in drier areas (Doubinger
125 1983, 1994; Langiaux 1994; Charbonnier *et al.* 2008). Arthropods seem to have
126 dominated the fauna in diversity and abundance with crustaceans such as syncarids

127 (Perrier *et al.* 2006), ostracods and branchiopods (conchostracans see Vannier *et al.*
128 2003) and terrestrial elements such as arachnids (Garwood *et al.* 2016), insects
129 (Langiaux 1975; Béthoux & Nel 2010; Garwood 2011; Garwood *et al.* 2012),
130 myriapods (Langiaux & Sotty 1976; Racheboeuf *et al.* 2004) and merostomes
131 (Racheboeuf *et al.* 2002). Other members of the fauna include abundant bivalves
132 (Babin 1985, 1994), annelids (Pacaud & WDI 1981; Pleijel *et al.* 2004), hagfishes
133 (Poplin *et al.* 2001), chondrichthyans (Langiaux & Sotty 1977; Heyler & Poplin 1994),
134 sarcopterygians (Olive *et al.* 2012), acanthodians, actinopterygians (Langiaux & Sotty
135 1977; Heyler & Poplin 1994) and tetrapods (Dutuit & Heyler 1994; Germain 2008).

136 [Insert Fig 1 here]

137

138 **Material and Methods**

139

140 **Fossil material**

141 Pioneer workers used to split nodules collected in the field and prepare fossils
142 mechanically in the lab. External moulds were typically prepared by removing mineral
143 in-fillings from cavities before making silicon or latex casts (e.g. Racheboeuf *et al.*
144 2002, 2004). This method generally failed to provide a faithful replica of the whole
145 animal, (e.g. embedded appendages and internal organs missing). X-ray
146 microtomography is used here to overcome these drawbacks to obtain high-definition
147 anatomical details in a non-destructive way and eventually 3D-models allowing virtual
148 dissection to be made.

149

150 We studied five specimens. μ CT data were obtained for three specimens of
151 *Amynilyspes fatimae* (Racheboeuf *et al.* 2004) from the Saint-Louis site:

152 MNHN.F.SOT 2134 (holotype), MNHN.F.SOT 14983 (paratype) and MNHN.F.SOT
153 2129 (paratype) (Fig. 2A, B, C). The remaining specimens MNHN.F.SOT. 73422c
154 and MNHN.F.SOT. 2124 (described as *Arthropleura* sp. but re-identified as *A.*
155 *fatimae* with the scan results) were not included in the present study due to their poor
156 preservation and the lack of information they give in comparison to the previously
157 cited specimens. We also studied 65 specimens (mainly from the Saint-Louis site) of
158 *Blanziulus parriati* (Langiaux & Sotty 1977). Four of them were CT-scanned:
159 MNHN.F.SOT 2114A; MNHN.F.SOT 5148; MNHN.F.SOT 2113 and MNHN.F.SOT
160 81522 (Fig 2E, F, G, H). All studied specimens are deposited in the collections of the
161 Muséum d'Histoire Naturelle d'Autun (repository numbers MNHN.F.SOT).

162 [Insert Fig 2 here]

163 **Imaging methods**

164 All specimens were photographed with a Canon EOS 5D SR camera mounted with a
165 Canon 100 mm macro lens. μ CT data were obtained with a GE Sensing & Inspection
166 Technologies Phoenix X-ray Phoenix v|tome|x CT-scan at the MATEIS laboratory of
167 INSA, Lyon, operating at 140 kV for all specimens. The intensity of the source current
168 was 80 μ A for all specimens of *A. fatimae* and *B. parriati* (MNHN.F.SOT. 2113;
169 MNHN.F.SOT 2114a and MNHN.F.SOT. 5148) and 100 μ A for *B. parriati*
170 (MNHN.F.SOT. 81522). Voxel size was 25 μ m for all specimens of *A. fatimae* and *B.*
171 *parriati* (MHNHN.F.SOT.5148), 30 μ m for *B. parriati* (MHNH.F.SOT 2113) and 10 μ m
172 for *B. parriati* (MHNH.F.SOT 2114a and MHNHN.F.SOT 81522). The type specimens
173 of *A. fatimae* (MNHN.F.SOT 2134, MNHN.F.SOT 14983 and MNHN.F.SOT 2129)
174 were also scanned with a μ CT SKyscan 1272 of the Morphology Laboratory at the
175 Research Museum Alexander Koenig, Bonn, Germany, operated at 100 kV with a
176 source current of 61 μ A and a voxel size of 6 μ m. Scans were segmented with the

177 Avizo® software. 3D models of each specimen described in this paper are present in
178 the MorphoMuseumM journal under this 3D dataset: Lheritier M., Vannier J.,
179 Escarguel G., Perrier V., 2022. 3D models related to the publication: Fossils from the
180 Montceau-les-Mines Lagerstätte (305 Ma) shed light on the anatomy, ecology and
181 phylogeny of Carboniferous millipedes. Photos and images were edited using
182 Inkscape (v. 0.92.4) and Gimp (v. 2.10.18).

183

184 **Extant myriapods**

185 *Glomeris marginata* (Villers, 1789) and *Glomeris guttata* (Risso, 1826) were used for
186 anatomical comparisons with the fossils from Montceau. They were collected by Jean
187 Vannier in Provence near Saint-Pantaléon (Luberon Massif, Vaucluse, France;
188 43°53, 17' 94" N; 5°13, 3' 08" E) from litter and soils planted with oak trees and kept
189 with their original substrate in a humid terrarium. Selected specimens were fixed with
190 5% glutaraldehyde, transferred to alcoholic series before being dried through the
191 critical point method, then mounted on stubs for being imaged with a Quanta 250
192 Scanning Electron Microscope (SEM) at the Centre Technologique des
193 Microstructures (CTμ) of the Université Claude Bernard Lyon 1.

194

195 **Phylogenetic analyses**

196 We investigated the phylogeny of fossil and extant diplopod myriapods through a
197 two-level approach first focusing on Montceau's fossil taxa *Amynilyspes fatimae* and
198 *Blanziulus parriati*, then extending the analyses to other fossil taxa. In both cases,
199 analyses were done first at a larger-scale, Diplopoda class level, then focussing on
200 relationships within the Pentazonia subclass. All four resulting morphological

201 datasets were analysed through Maximum Parsimony (MP) and Bayesian Inference
202 (BI) methods.

203

204 **Analyses focusing on *Amynilyspes fatimae* and *Blanziulus parriati*.** The
205 phylogenetic relationships of *Amynilyspes fatimae* and *Blanziulus parriati* were first
206 investigated through a two-step approach including a larger-scale analysis at the
207 Diplopoda class level and a smaller-scale analysis at the Pentazonia subclass level.
208 At the larger-scale level, 15 extant orders of Diplopoda were included along with
209 *Amynilyspes fatimae* and *Blanziulus parriati*. The class Pauropoda was coded as the
210 outgroup. The data matrix, comprising 45 morphological characters, was based on
211 the matrix from Blanke & Wesener (2014), including 18 head characters, 22 body
212 characters and 5 sexual characters. The MP analysis (unordered multistate Wagner
213 Parsimony using the branch-and-bound algorithm and ACCTRAN character-state
214 optimization) was made using PAUP_ v. 4.0a169 software (Swofford 1993).
215 Alongside consistency index (CI), retention index (RI) and rescaled consistency index
216 (RC); nonparametric bootstrap supports (1000 replicates) of the internal nodes were
217 calculated. The BI analyses were made with MrBayes v. 3.2.7 software (Ronquist *et*
218 *al.* 2012). The analyses were made using four chains (one cold and three heated)
219 and two independent runs, a temperature parameter for heated chains of 0.02, two
220 million cycles of the MCMC algorithm including a 25% burn-in phase and a Markov
221 chain sampling rate of 1,000 cycles, following three different models of evolutionary
222 rates distributions: a constant mutation rate, a non-constant rate following a Gamma
223 law distribution and a non-constant rate following a Log-Normal law distribution.
224 Other data (e.g. minESS and PSRF diagnostic metrics) are included in Appendix 2.

225 In addition to this Diplopoda class-level analysis, we more specifically focused on the
226 Pentazonia subclass by considering a dataset made of *A. fatimae* plus eight extant
227 species : *Eupeyerimhoffia archimedis* (Strasser, 1965) and *Glomeris marginata* for
228 the order Glomerida; *Procyliosoma leae* (Silvestri, 1917) and *Sphaerotherium*
229 *giganteum* (Porat, 1872) for the order Sphaerotheriida; *Glomeridesmus* sp. and
230 *Termitodesmus ceylonicus* (Silvestri, 1911) for the order Glomeridesmida and
231 *Madabolus maximus* (Wesener & Enghoff, 2008) and *Pseudocentrobolus aureus*
232 (Wesener, 2009) for the order Spirobolida. *Madabolus maximus* was coded as the
233 outgroup. The data matrix includes 47 morphological characters selected from
234 Blanke & Wesener (2014), Wesener (2016a) and Oeyen & Wesener (2018) for their
235 ability to discriminate these four Pentazonia orders. Among them, 21 are head
236 characters, 18 are body characters, and 8 are sexual characters. The settings for the
237 MP and BI analyses are the same as cited previously.

238

239 **Analyses including different diplopod fossils.** A second set of analyses, including
240 other Mesozoic and Cenozoic extinct diplopods, was made at both Diplopoda class
241 and Pentazonia subclass levels in order to investigate their potential effect on the
242 phylogenetic position of *A. fatimae* and *B. parriati*. Five extinct species, all from the
243 Burmese ambers (98.79 M.a, Shi *et al.* 2012), were added to the Diplopoda
244 phylogeny: the Platydesmida *Andrognathus burmiticus* (Moritz & Wesener 2019), the
245 Siphonophorida *Siphonophora hui* (Jiang *et al.* 2019), the Spirostreptida
246 *Electrocambala ornata* (Moritz & Wesener 2021), the Callipodida *Burmanopetalum*
247 *inexpectatum* (Stoev *et al.* 2019) and the Polyxenida *Phryssonotus burmiticus*
248 (Cockerell 1917; Su *et al.* 2019).

249 For the Pentazonia-level phylogeny, two extinct species were added: the Glomerida
250 *Hyleoglomeris groehni* (Wesener 2019) from the Baltic Amber (28-40 M.a, Weitschat
251 & Wichard 2010) and an unnamed specimen assigned to Spirobolida: BuB1145 from
252 the Cretaceous Burmese amber (Wesener & Moritz 2018). BuB1145 was coded as
253 the outgroup here.

254 In all cases, the parameters for the MP and the BI analyses were the same as their
255 equivalent in the first set of analyses.

256

257 **Systematic palaeontology**

258 Subphylum **Myriapoda** Latreille, 1802

259 Class **Diplopoda** Blainville in Gervais (1844)

260 Order **Amynilyspedida** Hoffman & Moore, 1969

261 **Diagnosis** (emended from Racheboeuf *et al.* 2004).—Moderate to large-sized
262 diplopods with 13 terga and an anal shield. Dorsal surface of terga may be flattened.

263 **Remarks**.— The studied Amynilyspedida have 13 terga against 12 in sphaerotheriids
264 (e.g. Wesener 2014) and 10/11 in glomerids (e.g. Enghoff *et al.* 2015).

265

266 Family **Amynilyspedidae** Hoffman & Moore, 1969

267 **Diagnosis** (emended from Racheboeuf *et al.* 2004).—Up to 30 mm long
268 amynilyspedids with 14 terga and prominent, simple spines. Large ovoid ocular fields
269 with ommatidia. No ozopores

270 **Remarks**.— Amynilyspedidae is monogeneric (*Amynilyspes*).

271

272 Genus **Amynilyspes** Scudder, 1882

273 **Diagnosis**.—As for the family.

274 **Remarks**—Four species have been assigned to the genus: *Amynilyspes wortheni*
275 (Scudder 1882) from the Mazon Creek Lagerstätte (Upper Carboniferous, Illinois,
276 USA); *A. typicus* (Fritsch 1899) from the Gaskohle in Nýrany (Upper Carboniferous,
277 Bohemia, Czech Republic); *A. crescens* (Fritsch 1899) from the same locality as *A.*
278 *typicus*, and *A. fatimae* from Montceau-les-Mines. *A. wortheni* has been revised by
279 Racheboeuf *et al.* (2004) and might be conspecific to *A. typicus*. *A. crescens* was
280 only known from one specimen which is currently missing (Förster 1973). Copeland
281 (1957) described the species: *A. springhillensis* that was later revised (Rolfe 1969)
282 and assigned to *Arthropleura*.

283

284 *Amynilyspes fatimae* Racheboeuf, Hannibal & Vannier, 2004

285

286

287 *Amynilyspes typicus*. Fritsch 1899

288 *Amynilyspes typicus* Langiaux & Sotty 1977, p. 55, fig. 9.4a.

289 *Amynilyspes cf. typicus*. Poplin 1994, p. 294.

290 *Amynilyspes fatimae* new species., Racheboeuf *et al.* 2004, figs. 2-6.

291 *Amynilyspes fatimae*. Charbonnier 2010, fig. IV.2

292

293 **Holotype:** MNHN.F.SOT 2134 from Montceau-les-Mines, Saint-Louis site
294 (Racheboeuf *et al.* 2004).

295

296 **Diagnosis** (emended from Racheboeuf *et al.* 2004).—*Amynilyspes* with terga 3–13
297 dorsally flattened in their anterior half and weakly to markedly rounded in their
298 posterior half, without transverse sulcus between the two areas; two rows of

299 dorsolateral spines; shield without spines. Twenty pairs of legs each connected to a
300 stigmatic plate. Head with a pair of seven-segmented antennae and a pair of well-
301 developed ocular fields. Male with at least one pair of telopods at the posterior body
302 end.

303

304 **Description.**— Head present in all specimens (Fig 3B, C and F) although poorly
305 preserved in MNHN.F.SOT 14983. Maximum length (Fig 4A) and width (Fig 4C)
306 2.1 mm and 2.4 mm, respectively. One antenna well preserved in MNHN.F.SOT
307 2134 (Fig 3B), complete pair preserved in MNHN.F.SOT 2129 (Fig. 3F), with seven
308 segments varying in length from 0.9 to 2.6 mm. MNHN.F.SOT 2134 and
309 MNHN.F.SOT 2129 display key elements of mouth apparatus such as the mandibular
310 base (maximum length and width 1.7 mm and 0.5 mm, respectively), the gnathal lobe
311 (maximum length and width 1.5 mm and 1.1 mm) and the gnathochilarium bearing
312 well-defined gnathochilarial stipes (maximum length and width 0.3 mm and 1.3 mm;
313 best preserved in MNHN.F.SOT 2129) (Fig. 3B, F). Bulges interpreted as lateral eyes
314 best seen in MNHN.F.SOT 2134 (only left eye) and MNHN.F.SOT 2129 (Fig. 3B, F),
315 maximum eye width (fig. 4E) of 0.5 mm. Ommatidia not observed. Ridge present
316 between antenna and mandible base in MNHN.F.SOT.2134 (Fig. 3B).

317

318 Body consisting of 13 terga and an anal shield (Fig 3A, C, E) with a maximum body
319 length (from terga 3 to the anal shield) (Fig 4A) of 22.6 mm. Tergum length from 1.3 to
320 1.5 mm, width from 3.4 to 5.6 mm and maximum margin thickness (Fig 4A) of 0.3 mm.
321 First tergum (collum) much smaller, length from 0.4 to 2 mm and width from 0.8 to
322 2.8 mm. Second tergum (thoracic shield) much larger, 3.2 and 6.8 mm in maximum
323 length and width respectively, maximum margin thickness (Fig 4C) of 0.2 mm. Anal

324 shield from 1.1 to 2.1 mm long, 2.1 to 3.2 mm wide and margin thickness of 0.32 mm.
325 Sternite 5 to 12 visible in MNHN.F.SOT 2134 (Fig. 3A) altogether 10.8 mm long, each
326 sternite being approximately 1.3 mm long and 1.4 mm wide. Dorsal spines present on
327 terga 3-12 of all specimens (MNHN.F.SOT. 2134; MNHN.F.SOT 14983; MNHN.F.SOT
328 2129, Fig 3A, C, E) with a maximum axial length (Fig 4A) of 2.2 mm. Incomplete
329 digestive tract visible in MNHN.F.SOT. 2134 and MNHN.F.SOT. 2129 (Fig 3A, E),
330 running below the terga and above the stigmatic plates.

331

332 Twenty pairs of walking legs with two pairs per segments. Maximum leg length is
333 3.8 mm. Each leg consists of seven segments. Terminal podomere bearing claw
334 usually poorly preserved. The penultimate legs of a presumed male (MNHN.F.SOT
335 14983) (Fig 3C) are modified into a pair of anterior telopods (length of 0.8 mm) and
336 appear as a pincer-shaped, three-jointed apparatus formed by telopodites (Fig 3D)
337 that may represent the functional analogue of the clasping apparatus seen in extant
338 pill millipedes.

339

340 Discussion.— Our study confirms major morphological differences between *A.*
341 *fatimae* and other *Amynilyspes* species as already noted in Racheboeuf *et al.* 2004.
342 The cuticle of *A. wortheni*, *A. typicus* and *A. crescens* is ornamented whereas that of
343 *A. fatimae* is smooth. Moreover, *A. wortheni* has one more tergite than *A. fatimae*.
344 The cephalic shield of *A. wortheni* has spines whereas its penultimate segment lacks
345 ornament. The opposite situation is observed in *A. fatimae*. The detailed morphology
346 of the head and appendages of other *Amynilyspes* remains poorly known, making
347 interspecific comparisons difficult.

348

[Insert Fig 3 here]

349 Superorder **Juliformia** Attems, 1926

350 **Diagnosis** (emended from Enghoff in Minelli 2015).—Essentially cylindrical
351 millipedes with an elongate body, length 4-344 mm, diameter 0.4-20 mm. Head
352 usually with eyes, each consisting of one to at least 68 ommatidia, normally arranged
353 in a triangular to ovoid patch, sometimes in a single line. Tömösváry organ absent.
354 Antennae with six antennomeres plus apical disc, disc with four, exceptionally up to
355 at least 20 sensory cones. Mandibles: gnathal lobe massive, with a simple or lobed
356 premandibular tooth, a lobed dentate lamella, four or more pectinate lamellae and a
357 prominently developed molar plate. Gnathochilarium variably composed, order and
358 family-specific. Trunk with 18-101 body rings, excluding telson. Collum large,
359 covering posterior part of head. Terga, pleurites, stigmatic plates and sternites fused
360 into complete body rings, except that sterna may be free on the first few rings.
361 Defence glands present, consisting of a single compartment, opening through lateral
362 ozopores and mostly secreting benzoquinones. Legs with six podomeres (coxa,
363 prefemur, femur, postfemur, tibia, tarsus). Coxal pores absent, except on leg-pair 2 in
364 some Julida. Male leg-pairs 8 and 9 modified into gonopods. Male gonopores
365 opening through paired penes behind leg-pair 2, or (Spirobolida) distal part of
366 gonoduct eversible. Female gonopores opening through sclerotized vulvae behind
367 leg-pair 2, each vulva consisting of a simple operculum and a more complicated
368 bursa.

369 [Insert Fig 4 here]

370 Order **Incertae sedis**

371

372 Superfamily **Xyloiulidea** Cook & Collins, 1895

373 **Diagnosis** (emended from Wilson 2006).— Juliforms with tergites, pleurites, and
374 sternites fused into complete rings. Trunk rings ornamented with longitudinal
375 striations. 40-50 trunk rings in adults. Ozopores present. Length of legs equal to half
376 the height of the trunk rings or less.

377 **Remarks**—Langiaux & Sotty 1976 placed *B. parriati* into this superfamily based on
378 the longitudinal striations (diagnostic of the Xyloiulidea superfamily) observed in the
379 holotype. No such striations were observed on the scanned specimens but the
380 presence of transversal ridges in all specimens including the holotype seems to be
381 diagnostic of *B. parriati* and seems to indicate that we have specimens of the same
382 species. Other characters described as diagnostic of this superfamily such as the
383 number of trunk rings, the fusion of terga, pleura and sternites (only the terga and
384 pleura are fused in the studied specimens) and the full lengths of legs were not
385 observed. As the superfamily Xyloiulidea is an extinct clade composed of only
386 Palaeozoic species, the characters used for describing this taxon are based on
387 specimens with inferior preservation thus the pertinence of these characters to
388 describe this clade are highly debatable. That is why we consider that we can still
389 place *B. parriati* (holotype and scanned specimens) as a Xyloiulidea even with this
390 lack of diagnostic characters.

391

392 Family **Xyloiulidae** Cook & Collins 1895

393 **Diagnosis**.—Xyloiulidea with entire prozonites and metazonites striated. No
394 differences between the striations on the prozonite and those of the metazonite.
395 Diameter of the metazonite slightly greater than that of the prozonite.

396 **Remarks**—No such striations were observed on the scanned specimens. However,
397 they are present on the holotype. As noted above, we can confirm that the scanned

398 specimens represent the same species as the holotype of *B. parriati*. Thus we see no
399 problem with placing the scanned specimens as *B. parriati* into the Xyloiulidae family.

400

401 Genus **Blanziulus** Langiaux & Sotty 1976

402 **Type species.**—*Blanziulus parriati*. Monotypic genus. Holotype: MNHN.F.SOT 76-H-
403 1-A from Montceau-les-Mines, Sainte-Hélène site (Fig 2D).

404 **Diagnosis** (modified after Langiaux & Sotty 1976).— Xyloiulidae with at least 53
405 segments. Pleuroterga with thin transversal ridges.

406

407 *Blanziulus parriati* Langiaux & Sotty 1976

408

409 *Blanziulus parriati* n. sp.; Langiaux & Sotty 1976, p. 43, fig. 1, pl. 4.

410 *Blanziulus parriati*; Chabard & Poplin 1999, p. 183-184 ; fig p. 183.

411 Unnamed myriapod; Perrier & Charbonnier 2014, p. 11, pl. 4, Fig N

412

413 **Diagnosis.**— As for the genus.

414 **Description.**— Left part of the head present in MNHN.F.SOT. 2114a (Fig. 5B) and
415 MNHN.F.SOT. 5148 (Fig. 5D). Maximum length (Fig. 4B) and width (Fig. 4D) (for left
416 part) of 3.4 mm and 1.2 mm respectively. Left antenna preserved in MNHN.F.SOT.
417 2114a, 2.6 mm long and consists of six segments. Mandibular apparatus present in
418 MNHN.F.SOT. 2114a (Fig. 5B) with cardo (0.4 mm long and 0.3 mm wide) and stipes
419 (0.8 mm long and 0.4 mm wide). Ovoid ocular fields preserved in MNHN.F.SOT.
420 2114a (only left eye) and MNHN.F.SOT. 5148 (Fig. 5B, D). Maximum field width of
421 0.7 mm (Fig. 4F). Ommatidia not observed.

422

423 None of the studied specimens is complete (total number of pleuroterga unknown).
424 Maximum number of pleuroterga observed is 53 (without collum and telson) on
425 MNHN.F.SOT. 81522 (Fig. 5G), length of 50 mm. Pleurotergum length (Fig 4B) from
426 1.2 to 1.4 mm and width (Fig 4D) from 1 to 3.4 mm. First pleurotergum (collum) large,
427 covering posterior part of the head (0.9 to 2 mm and 0.8 to 4.6 mm in length and
428 width, respectively). Eight sternites in MNHN.F.SOT. 2113 (Fig 5E) altogether 6 mm
429 long. Each sternite = 1 mm long and 2.9 mm wide. Longitudinal ridges present in the
430 posterior part of each pleuroterga. Ridge length (Fig 4E) going from 0.2 to 0.5 mm.
431 Digestive tract present in MNHN.F.SOT. 81522 (Fig. 5H) with a total length of
432 23.8 mm.

433

434 Exact number of leg pairs unknown due to the incompleteness of specimens. 73
435 pairs in MNH.F.SOT. 81522 (Fig. 5G). Collum and second pleurotergum with one pair
436 of legs. Pleuroterga 4-53 with two pairs of legs. Possible pair of legs for segment
437 three not present on MNHN.F.SOT. 2114a (Fig. 5A) and MNHN.F.SOT. 5148
438 (Fig 5C) so it is impossible to determine if there is only one pair on this segment
439 similarly to the collum and second pleurotergum (like in extant juliforms) or two pairs
440 like the following pleuroterga. Maximum leg length of 4.6 mm. Each leg consists of
441 seven segments. First pair of legs in assumed male (MNHN.F.SOT. 5148) modified
442 in the shape of enlarged claspers (length of 0.9 mm) with a reduced claw (Fig. 5D).

443

444 **Discussion.**—The presence of a pair of claspers of this shape in male individuals
445 was only observed on extant millipedes from the Julida order until now. However,
446 molecular phylogeny (Miyazawa *et al.* 2015) asserts a Triassic origin to the Julida
447 order. As no other Palaeozoic fossil millipedes with this same kind of sexual

448 dimorphism was ever found, we cannot infer that the presence of these claspers are
449 a diagnostic character of the *Blanziulus* genus, the Xyloiulidae family or even the
450 Xyloiulidea superfamily.

451 [Insert Fig 5 here]

452 **Phylogenetic results**

453 ***Amynilyspes fatimae***

454 As for the first Pentazonia-level phylogenetic analysis (including eight extant species
455 plus *A. fatimae*), the maximum parsimony (MP) branch-and-bound research returns
456 one MP tree with a total length of 62 steps involving 46 parsimony-informative
457 characters, a consistency index of 0.903, a retention index of 0.912 and a rescaled
458 consistency index of 0.824. *A. fatimae* branches as a sister taxon of the
459 Sphaerotheriida (Fig. 6B). The resulting clade is defined by characters 31B, 41 and
460 42 (see Appendix 1 for the characters used and their different states). They share
461 twenty or so leg pairs (character 31B) and a male penultimate leg pair modified into
462 an anterior telopod (character 41) with a long femur (character 42). Bootstrap
463 supports indicate that the tree is globally robust, the two weakest nodes being related
464 to the relationship between *A. fatimae* and the Sphaerotheriida and the relation
465 between them and the Glomerida. The Bayesian Inferences (BI) shows the same
466 result regardless of the selected evolutionary rate distribution, pointing toward a
467 phylogenetic signal robust to the evolutionary rate variation model imposed to the
468 inference algorithm (Annex 3). In the BI, we observe the same synapomorphies as in
469 the MP tree (characters 31B, 41 and 42).

470 [Insert Fig 6 here]

471 As for the second Pentazonia-level analysis (including two additional extinct taxa:
472 *Hyleoglomeris groehni* and BuB1145), the MP branch-and-bound research returns

473 one MP tree with a total length of 72 steps with all characters being parsimony-
474 informative, a CI of 0.778, a RI of 0.816 and a RC of 0.635. Bootstrap supports
475 remain high but a partial non-resolution of *H. groehni* and *A. fatimae* positions is
476 obtained (Fig. 7B), as the likely consequence of the high amount of unobserved
477 character states in the two added fossil taxa. We observe the same synapomorphies
478 for the clade Sphaerotheriida + *A. fatimae* as in the first Pentazonia-level
479 phylogenetic MP analysis. As for the Bayesian inferences, the three evolutionary rate
480 models group *A. fatimae* with Sphaerotheriida with the same synapomorphies than in
481 the first Pentazonia-level BI analyses. However, in these trees, the clade Glomerida
482 is more closely related to the clade Glomeridesmida than to the clade
483 Sphaerotheriida, a grouping that is also observed in molecular phylogenies
484 (Benavides *et al.* 2023). This Glomerida-Glomeridesmida clade is defined by an
485 antennae placed centrally (character 5A), a large, horse-shoe-shaped Tömösváry
486 organ (character 8), and a gnathochilarium with a very large gula (character 9).
487 In the two Pentazonia-level phylogenetic analyses, we observe an autapomorphy for
488 *Amynilyspes fatimae* which possesses 13 terga unlike in Glomerida and
489 Sphaerotheriida (character 19).

490

491 In the two Diplopoda-level analyses, *A. fatimae* appears, as for the Pentazonia-level
492 analyses, included in the Subclass Pentazonia as a sister-taxon of the Order
493 Sphaerotheriida with relatively high bootstrap supports (Fig 6A and Fig 7A). However,
494 there are no clear synapomorphic characters for this grouping, the only shared
495 character being a reversion to eyes with numerous ocelli (character 5, see Appendix
496 1). Finally, we observe the same phylogenetic scenario for *A. fatimae* in the four

497 different phylogenies, providing strong evidence for the position of *A. fatimae* as
498 sister-taxon of the order Sphaerotheriida.

499

500 ***Blanziulus parriati***

501 As for the first Diplopoda-level analysis (15 extant orders plus *A. fatimae* and *B.*
502 *parriati*), the MP analysis returns a MP tree with a total length of 77 steps and 43
503 parsimony-informative characters, a CI of 0.727, a RI of 0.870 and a RC of 0.632.
504 Bootstrap supports are high. Based on available data, *B. parriati* is placed in an
505 unresolved position inside the Superorder Juliformia (Fig 6A). The same result as for
506 MP is obtained through BI for all three evolutionary rate distributions, with high
507 Bayesian scores except for the branching of *B. parriati* (Appendix 2).

508 [Insert Fig 7 here]

509 For the second Diplopoda-level analysis (including six additional Cretaceous species:
510 *Andrognathus burmiticus*, *Siphonophora hui*, *Electrocambala ornata*,
511 *Burmanopetalum inexpectatum*, and *Phryssonotus burmiticus*), we obtain one MP
512 tree with a total tree length of 84 steps, 43 parsimony-informative characters, a CI of
513 0.670, a RI of 0.873 and a RC of 0.592. The scores remain high in the MP analysis
514 (Fig. 7A). A partial non-resolution of the position of *Siphonophora hui*, inside the
515 Colobognatha and *Electrocambala ornata* inside the Juliformia are obtained. The BI
516 analyses show the same results as the MP analysis whatever the evolutionary rate
517 distribution (Appendix 2). The lower scores and the partial non-resolution are due to
518 the high amount of unobserved character states in the additional fossil taxa.

519

520 **Discussion**

521

522 **Feeding**

523 The feeding apparatus of extant pill millipedes is composed of a pair of mandibles
524 and a pair of first maxilla called the gnathochilarium. The mandibles themselves have
525 two distinct elements: a mandibular base and a gnathal lobe (Fig 8A). In modern pill
526 millipedes, the function of this gnathal lobe is to grasp food with a movement
527 opposed to that of the gnathochilarium. In other words, if the gnathochilarium lowers,
528 the gnathal lobes would automatically open to help bring food into the mouth (Koch
529 2015a). The mandibular apparatus in *A. fatimae* is morphologically similar to that of
530 extant pill millipedes with a mandible base, a gnathal lobe and a gnathochilarium
531 (only the gnathochilarial stipes are observed on *A. fatimae*) (Fig 8D). Like in extant
532 pill millipedes, the mandible base of *A. fatimae* is relatively voluminous (width larger
533 than head width) (Fig 8A, D). These mandibular features are typically seen in extant
534 chewing-biting millipedes that feed on hard remains like dead trunks or twigs (Koch
535 2015a).

536

537 The mandibular apparatus of extant Juliformia is different from that of pill millipedes. It
538 has a mandibular base (composed of a cardo and a stipes), a gnathal lobe and a
539 gnathochilarium (Fig 8H). It is also less voluminous than that of pill millipedes like in
540 other extant Helminthomorpha (Koch 2015a). In *B. parriati*, the mandibular apparatus
541 is morphologically similar to that of extant Juliformia with a mandible base made a
542 cardo + a stipes (Fig 8K). Its less voluminous shape suggests a preference for softer
543 remains such as dead leaves. Neither the gnathal lobe nor the gnathochilarium were
544 found in *B. parriati*. However, since the feeding apparatus of *B. parriati* and extant
545 Juliformia both share important similarities, the lack of these two elements is attributed
546 to preservation.

547

548 The digestive system of extant millipedes is divided into a foregut, midgut, and hindgut
549 (Fig 9A). The foregut runs from the mouth to the esophageal valve and accommodates
550 the salivary glands. The midgut where the major part of the digestion occurs runs from
551 the esophageal valve to the pylorus. Final stages of digestion occur through the hindgut
552 and feces are excreted via the rectum. None of the specimens from Montceau display
553 a complete digestive tract. In *A. fatimae* it appears as an evenly tubular midgut that
554 extends into a hindgut with a differentiated rectum (Fig 9B, C). The digestive tract of
555 *B. parriati* is similarly incomplete and mainly represented by a tubular midgut and
556 possible remains of a pylorus (anterior most part of the hindgut) and a rectum
557 (MNHN.F.SOT. 81522; Fig 9D). No identifiable gut content is preserved that could be
558 used to infer the diet of *A. fatimae* and *B. parriati*. However, the mandibular morphology
559 of both species strongly indicates capacities to process relatively hard detritus such as
560 fragments of wood bark for *A. fatimae* and possibly softer food such as fern remains
561 for *B. parriati*. These feeding modes and diets are common among extant millipedes.

562

[Insert Fig 8 here]

563 **Sensory organs**

564 The most visible sensory organs of extant millipedes are the antennae that bear
565 apical cones (autapomorphy of diplopods) and more or less developed eyes.

566 Antennae are inserted either frontally or more laterally following the groups.

567 Antennae play a leading role as a major tactile and chemical sensory organ.

568 Millipedes tap the substrate with their antennae for environmental identification

569 (Müller & Sombke 2015) and the antennae are considered to have a major role in
570 sensing the environment in blind millipedes (Hopkin & Read 1992).

571

572 Most extant millipedes have eyes bearing more or less numerous ommatidia
573 distributed over the ocular field. There are two types of eyes in extant diplopods: 1)
574 large ocular fields with numerous ommatidia (50-90) (Fig 8J, N); 2) 1-2 rows of eyes
575 with less than 10 ommatidia each (e.g. Glomerida, Fig 8B). The exact visual
576 capacities and sensory importance of these eyes is still in debate (Müller & Sombke
577 2015). Since millipedes react to light (Cloudsley-Thompson 1951) and some species
578 show a different behaviour if they are illuminated at night (McKillup 1988), these eyes
579 are clearly sensitive to light variations.

580 [Insert Fig 9 here]

581 The antennae of *A. fatimae* are seven segmented and inserted laterally like those of
582 extant Sphaerotheriida (Fig 8B, D, E). Those of *B. parriati* have close counterparts in
583 modern Juliformia (Fig 8J, L). It is uncertain whether the absence of an apical cone
584 (most distal antennomere) in both Carboniferous species is due to preservation or is
585 an original biological origin. However, the tip of the antennae often appears to be
586 broken (Fig 8E, L) which would confirm an artefactual origin.

587
588 The ocular field of *A. fatimae* is similar to that of extant Sphaerotheriida (Fig 8G, N).
589 That of *B. parriati* is larger, more ovoid and recalls the ocular configuration seen in
590 extant Juliformia (Fig 8J, M). Inferring the visual properties of *A. fatimae* and *B. parriati*
591 requires the recognition of ommatidia that are unfortunately lacking in the studied fossil
592 specimens.

593
594 Many extant millipedes have additional paired sensory features known as the
595 Tömösváry organs located posteriorly to the antennal basis (Fig 8A, B). Homology of
596 these organs among arthropods as well as their exact function are still unresolved.

597 Various hypotheses have been proposed concerning the function of these organs
598 such sensing vibrations or sound (Verhoeff 1928; Pflugfelder 1933; Schömann 1956;
599 Meske 1961), or detecting CO₂ (Yamana *et al.* 1986, 1998; Yamana & Toh 1987). No
600 trace of this organ has been found in the fossil specimens from Montceau.

601

602 **Locomotion**

603 The leg of extant diplopods consists of seven podomeres, from proximal to distal:
604 coxa, prefemur, femur, postfemur, tibia, tarsus and claw (Fig 8C). There are two pairs
605 of legs per segment. The only exceptions are Helminthomorpha in which the collum
606 and several adjacent segments (depending on the group) bear a single pair of legs.
607 These segments bearing a single pair of legs are usually referred as the thorax of
608 millipedes (Koch 2015a). Two types of locomotion are observed in extant millipedes:
609 1) one in which body stretching plays a major role (e.g. pill millipedes, Koch 2015b),
610 2) a second one with less body deformation, seen in ring-forming and more
611 elongated millipedes such as Juliformia and Nematophora (Fattahi & Spinello 2014).
612 Many recent diplopods have a very elongated and flexible body and a large number
613 of legs that allow them to move into interstices and find their way through loosely
614 compressed plant-based litter.

615

616 The legs of *A. fatimae* and *B. parriati* are virtually identical to those of extant
617 millipedes in their basic architecture and distribution. They have seven podomeres
618 (Fig 8F, I) and each tergum (for *A. fatimae*) and non-thoracic pleurotergum (for *B.*
619 *parriati*) is provided with two pairs of them (Fig 3A, C, D and Fig 5A). The thorax of *B.*
620 *parriati* consists of the collum and the second pleurotergum (Fig 5A). As the pair(s) of
621 legs are not preserved on the third pleurotergum, it is uncertain whether this

622 pleurotergum is a thoracic or non-thoracic segment. Comparisons with the legs of
623 extant myriapods suggest that the locomotion mode of *A. fatimae* was comparable
624 with that of extant pill millipedes and that of *B. parriati* was close to that of ring-
625 forming millipedes (millipede with fused pleura and terga, e.g. Julida). We suggest
626 that *A. fatimae* and *B. parriati* could move through their environment (litter or
627 hard/semihard substratum) in a manner comparable with that of modern diplopods.

628

629 **Gas exchange**

630 Diplopods are terrestrial arthropods that breath through a tracheal system open to the
631 exterior via spiracles (cuticular openings through which dioxygen and carbon dioxide
632 exchange occur; Fig. 10A, B). This tracheal system is composed of either branched
633 (Pentazonia and Penicillata) or unbranched (Helminthomorpha) pouches used as air-
634 collecting sacks, dust containers (Verhoeff 1928) and possibly tracheoles. *A. fatimae*
635 from Montceau preserves no trace of such respiratory system. In contrast, small
636 cuticular openings occur along the sternites of *B. parriati* (Fig 10C, D) that may be
637 interpreted as spiracles. However, the spiracles of extant diplopods are much smaller
638 than the openings observed in *B. parriati* (80 μm long and 10 μm wide for extant
639 spiracles versus 700 μm and 300 μm in *B. parriati*). This discrepancy may be
640 explained by taphonomic alterations such as the loss of thin cuticular material around
641 spiracles after death that possibly enlarged openings. If this interpretation is correct,
642 then *B. parriati* may have possessed spiracles and a tracheal system typical of
643 terrestrial arthropods and corresponding to that of other Helminthomorpha (spiracles,
644 tracheal pouches, unbranched tracheal stems and tracheoles).

645

[Insert Fig 10 here]

646 **Reproduction**

647 Extant millipedes have a well-marked sexual dimorphism. Males have reduced or
648 modified pairs of appendages (i.e., telopods in Pentazonia or gonopods in
649 Helminthomorpha) and are generally smaller. In some species with fixed number of
650 rings, males may have more leg pairs than their female counterparts (Minelli & Michalik
651 2015). These specialised appendages are usually involved in sperm transfer and/or for
652 grasping the partner during copulation. In some other groups (e.g. Chordeumatida),
653 females can also bear reduced or modified pairs of sexual appendages. In extant
654 Pentazonia (Glomerida and Sphaerotheriida) the differentiated penultimate and most
655 distal appendages (called telopods) are used by males to seize the female antennae
656 and transfer sperm to the vulva (Haacker 1969).

657

658 One specimen of *A. fatimae* has telopods and can be reasonably interpreted as a male
659 (Fig 11A, C). Larger conspecific specimens lack this dimorphic feature and may
660 represent females or alternatively sexually immature individuals. In extant Glomerida
661 and Sphaerotheriida, males have generally more legs than females (Minelli & Michalik
662 2015). Possible missing legs make the presence of this dimorphic feature uncertain in
663 the fossil specimens. The specialised appendages seen in males of *A. fatimae* are
664 likely to have been involved in copulatory behaviour as observed in extant taxa such
665 as *Sphaerotherium* (Haacker 1968) in which sexual partners make contact head to tail
666 with their ventral side.

667

[Insert Fig 11 here]

668 Another dimorphic feature is seen in one specimen of *B. parriati* that has specialised
669 first legs armed with enlarged claspers (see Fig 11B, D). This feature has counterparts
670 in male individuals of extant mongoliulid and parajulid millipedes (Julida). The other

671 specimen with the front part preserved has no such feature and is approximately twice
672 as small as the presumed male. However, as females are generally larger than males
673 in extant species, uncertainty remains concerning its sexual identity. It may rather
674 represent a sexually immature juvenile. We assume that *B. parriati* had a mating
675 behaviour comparable with that of extant Mongoliulidae and Parajulidae - i.e. that
676 males positioned themselves on female by grasping the mouth parts of females with
677 their claspers (Minelli & Michalik 2015).

678

679 **Defence**

680 Extant diplopods have evolved morphological defence systems such as volvation (fig.
681 12C) and spines. Diplopods have also evolved chemical deterrence through
682 repugnatorial glands whose openings are scattered over the exoskeleton (i.e.
683 ozopores). The morphology of *A. fatimae* is consistent with the capacity to enrol as
684 indicated by well-developed potentially overlapping margins (Fig 12A, D) and the
685 presence of an antennal groove along the head sides (Fig 12B, F). These grooves
686 may correspond to the openings seen in extant millipedes (e.g. Glomerida and
687 Sphaerotheriida), through which antennae exit when the animal is enrolled (Wesener
688 2010; Hadrián & Šipoš 2016). *A. fatimae* had spines (Fig 12F) that may have
689 provided the animal with additional physical protection against predators if we
690 assume that it could roll up on itself. In extant pill millipedes and isopods (Smigel &
691 Gibbs 2008), volvation is often interpreted as limiting water loss (Hadrián & Šipoš
692 2016). Similarly, one may speculate that *A. fatimae* also used volvation to resist
693 desiccation which remains a major challenge for arthropods living on land. Like
694 Racheboeuf *et al.* (2004), we did not find any traces of ozopores (repugnatorial
695 glands openings) on *A. fatimae*. It is noteworthy that ozopores are present in some

696 Pentazonia (notably in Glomerida) (Koch 2015a). It is uncertain whether *A. fatimae*
697 had comparable defence organs. The absence of ozopores may be original or the
698 result of taphonomic alteration.

699 [Insert Fig 12 here]

700 No spines or traces indicating other physical and chemical defence (ozopores) occur
701 in *B. parriati* either. Ozopores are common in extant Helminthomorpha and also
702 occur in Lower Carboniferous (Shear 1993) and possibly Lower Devonian (Wilson
703 2006) representatives of the group. Ozopores are always extremely small (size about
704 50 μm). If originally present in *B. parriati* they might have disappeared through
705 taphonomic processes.

706

707 Even though extant millipedes are able to defend themselves by various chemical of
708 physical ways, they are preyed upon by animals as vertebrates (Hopkin & Read
709 1992), beetles (Eisner *et al.* 1998; Brunke *et al.* 2009), ants (Suzzoni *et al.* 2000),
710 arachnids (Carrel & Britt 2009) and slugs (Herbert 2000). Potential predators in the
711 Montceau biota are numerous and may have included early terrestrial vertebrates
712 such as *Phlegethontia*, aistopods (early “snake-like” vertebrates) (Germain 2008) as
713 well as spiders (Garwood *et al.* 2016) or scorpions (Vachon & Heyler 1985).

714

715 **Lifestyle**

716 Although extant millipedes generally live in forest litter (Golovatch & Kime 2009),
717 many of them display adaptations to specific habitats and lifestyles. Kime &
718 Golovatch (2000) and Golovatch & Kime (2009) recognized various ecological
719 morphotypes such as: 1) “bulldozers” (e.g. Juliformia) with a cylindrical body and
720 short walking legs adapted to move relatively deep into the soil; 2) “litter-splitters”

721 (e.g. Polydesmoida) with a flat back adapted to enter crevices and 3) “borers” (e.g.
722 Platydesmoida) similar to morphotype 1 and 2 but with a more flexible body shape
723 and a tapering anterior end, making them well adapted to live within the litter.
724 Additional morphotypes have been proposed such as: 1) “rollers” i.e. short-bodied
725 millipedes that are able to roll up (Pentazonia, pill millipedes) as a defence behaviour
726 and 2) “bark dwellers” represented by bristly Penicillata millipedes that shelter in the
727 small crevices of tree barks.

728 Many ecological morphotypes have been proposed by authors as an attempt to
729 categorize behaviours in relation with habitats and substrates. Most extant diplopods
730 would belong to the “stratobiont” ecotype that encompasses species living within the
731 litter or upper soil layers, whereas juliforms, some glomerids and platydesmoids that
732 preferentially colonize deeper soil layers would fall into the category of
733 “pedobionts/geobionts”. According to this classification, other small (polyxenoids,
734 glomerids) or flat-backed (polydesmoids, platydesmoids) millipedes that conceal
735 themselves under bark fragments should be called “xylobionts”. Other specialized
736 ecotypes refer to millipedes adapted to arborescent life in tropical and subtropical
737 area (“epiphytobiont”; Manton 1977; Enghoff 1983). Applying these precise
738 ecological categories to Palaeozoic myriapods remains a challenge because of the
739 lack of direct information on their habitat.

740

741 [Insert Fig 13 here]

742 ***Amynilyspes fatimae***. Comparisons with pill millipedes (e.g. overlap features such
743 as margins on terga edges, lateral ridges on head) and phylogenetic affinities with
744 Sphaerotheriida (Fig 6) both suggest that *A. fatimae* was a pill-millipede of the “roller”
745 type. *A. fatimae* is likely to have been a stratobiont (Fig 13A) or a epiphytobiont (Fig

746 13B) and possibly lived in the litter and upper soils layers that were probably
747 abundant in the forest-like environments of Montceau. Its spines may have been
748 used to push out coarse detrital elements and should not be considered as a
749 disadvantage for tunnelling into an heterogenous and loosely packed substrate.
750 Some extant Sphaerotheriida species, such as *Zoosphaerium arboreale*
751 (Madagascar), are arboreal (Haacker & Fuchs 1972; Wesener & Sierwald 2005) and
752 live in rainforest environments. They closely resemble *A. fatimae* in their overall
753 morphology. Whether *A. fatimae* was similarly an epiphytobiont remains hypothetical.
754 However, the diplopods from Montceau lived in a highly vegetated environment
755 where arborescent sphenopsids, filicophytes (tree ferns) and pteridosperms
756 (Charbonnier 2014) offered animals potential fresh (in-situ leaves) and decayed
757 (litter) food and also a rich variety of sheltering micro-habitats. It is not inconceivable
758 that some millipedes such as *A. fatimae* had colonized such arboreal niches.

759 ***Blanziulus parriati***. Close morphological similarities with extant Juliformia would
760 suggest that *Blanziulus parriati* belonged to the “bulldozer” type. Indeed, its robust
761 head and body shape seem to have been adapted for digging into soil and litter and
762 possibly move through it. *Blanziulus parriati* had a large collum. This feature protects
763 the head of extant Juliformia when digging into soil (Enghoff 1984). Going back to the
764 ecotype, *B. parriati* may belong to the “stratobiont” or “pedobiont” ecotype (Fig 13C).
765 The mouth apparatus of *B. parriati* is almost identical to that of extant Juliformia. This
766 suggests that *B. parriati* exploited food sources such as decaying leaves or other
767 plant detritus (David 2015) as do extant Juliformia. Most extant burrowing millipedes
768 actually feed on a great variety of detritus. Whether *B. parriati* had such an
769 opportunist feeding mode is hypothetical and would require to be tested by the
770 analysis of gut contents. *B. parriati* and *A. fatimae* are particularly well represented at

771 the Saint-Louis (Fig 1C) fossil site where arborescent flora is particularly abundant
772 and diverse (Charbonnier 2014). This would indicate a possible correlation between
773 myriapod occurrence and food availability.

774 **Relative abundance of millipedes at Montceau.** *B. parriati* is far more abundant than
775 *A. fatimae* with 65 against four specimens found in opened nodules. This might indicate
776 that *B. parriati* was effectively more abundantly represented than *A. fatimae* in the
777 Montceau biota. However, taphonomy should be taken into consideration as a
778 potentially bias. Recent taphonomic scenarios suggest that most animals of the
779 Montceau biota were transported from their original habitat into neighbouring swamps
780 and rivers by landslides and storm-induced water flows, where they were eventually
781 buried (Perrier & Charbonnier 2014). This scenario is consistent with the equatorial
782 and humid climate that supposedly prevailed at Montceau and the presence of
783 potential steep relief and slopes (Hercynian Mountain range e.g. Charbonnier 2014).
784 In this context, small arthropods living in litter and soil such as *B. parriati* would have
785 been more easily swept away by water and mud flows than those possibly inhabiting
786 trees. If we follow our hypothesis of *A. fatimae* inhabiting trees (possible epiphytobiont)
787 instead of litter, then its relative under-representation may be explained by the fact that
788 it was more rarely transported by water and mud. Or *B. parriati* may have simply been
789 more abundant than *A. fatimae* in the Montceau palaeoenvironment. Only a quarter of
790 the 120, 000 nodules collected at Montceau (Sotty 2014) have been split open and
791 observed. One may expect that the study of the whole fossil collection will provide more
792 conclusive results on the relative diversity and numerical abundance of plant and
793 animal species.

794

795 **Conclusion**

796 The non-destructive μ CT analysis of *Amynilyspes fatimae* and *Blanziulus parriati*
797 revealed an array of new morphological features that had been overlooked by
798 previous authors (e.g. Langiaux & Sotty 1976; Racheboeuf *et al.* 2004) and led to
799 unprecedented detailed 3D-reconstructions of these ancient myriapods. Key features
800 (e.g. margins and antennal ridges) involved in the volvation process confirm the
801 placement of *A. fatimae* within the Order Amynilyspedida. *A. fatimae* is seen as a
802 detritus feeder based on its mandibular apparatus similar to that of extant pill
803 millipedes. Its sensory organs (eyes, antennae) were similar to those of extant
804 Sphaerotheriidae. *A. fatimae* had legs adapted to moving on/within litter as in extant
805 millipedes. Its diplopody confirms that *A. fatimae* is a millipede. *A. fatimae* and extant
806 pill millipedes share the same type of sexual dimorphism with presumed males
807 bearing telopods posteriorly. Our study suggests that *A. fatimae* 1) possibly belonged
808 to the “roller” ecological type defined by biologists, based on similarities with modern
809 pill millipedes and 2) was a “stratobiont” or an “epiphytobiont” with a behaviour
810 possibly resembling that of extant tropical Sphaerotheriidae.

811

812 *B. parriati* is placed within the Superorder Juliformia. Its mandibular apparatus points
813 to a detritus feeding mode. Sensory organs and leg morphology are close to those of
814 extant Juliformia. The presence of tracheal openings as in extant Juliformia, confirm
815 that it was adapted to terrestrial environments. Sexually dimorphic appendages close
816 to those of modern Mongoliulidae and Parajulidae shed light on its possible
817 copulatory behaviour. *B. parriati* may belong to the “bulldozer” ecological type and a
818 “stratobiont” or a “pedobiont” ecotype. Its behaviour seems to have been close to that
819 of extant juliforms.

820 Our results added to previous successful microtomographic studies on other
821 arthropod species from Montceau, (e.g. Garwood 2011; Garwood *et al.* 2012, 2016)
822 demonstrate that non-invasive techniques such as μ CT are most suitable for the
823 study of fossils preserved in nodules. μ CT revealed fine morphological details of
824 great importance for taxonomy and ecology such as head appendages, sexual
825 dimorphism and chemical deterrence. This promising technique will soon be applied
826 to other myriapods from Montceau such as *Arthropleura* (Kraus & Brauckmann 2003)
827 and euthycarcinoids (Racheboeuf *et al.* 2008) that are now resolved as stem
828 myriapods in recent phylogenetic trees (Edgecombe *et al.* 2020). μ CT may also be
829 used for scanning the numerous unopened nodules (ca 30,000; see Sotty 2014) that
830 are still awaiting to be studied. This will hopefully lead to the discovery of other
831 myriapods such as chilopods (centipedes) that are found associated with diplopods in
832 coeval deposits such as the Mazon Creek Lagerstätte (Mundel 1979).

833

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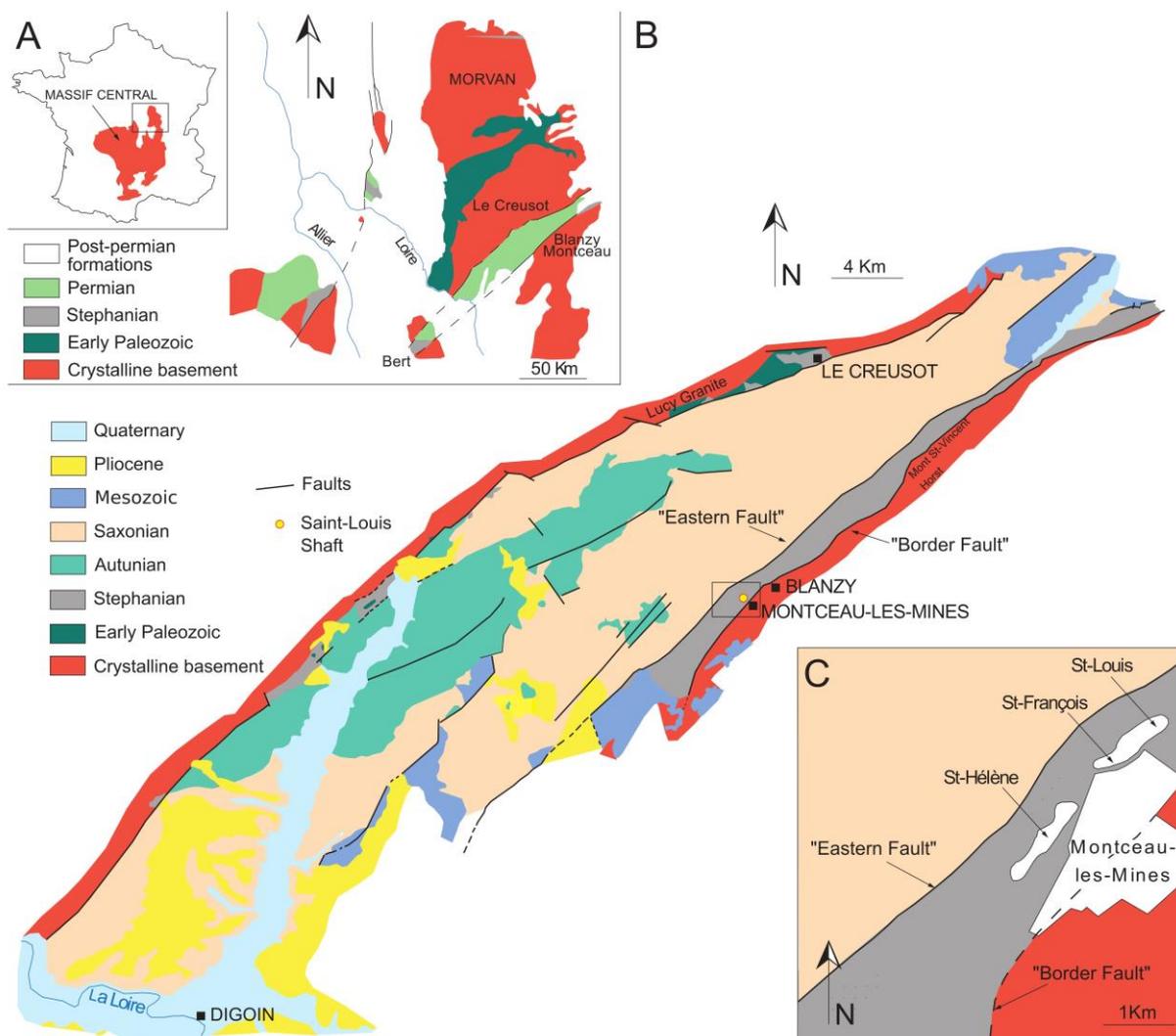
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1184 Figure captions:



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1187 **Fig 1.** Coal basin of Montceau-les-Mines. A: Regional map. B: Location of the coal basin of Montceau in the

1188 Stephano-Permian graben of Blanzay-Le Creusot-Bert. C: Location of the sites with sideritic nodules. From

1189 (Charbonnier 2014) .

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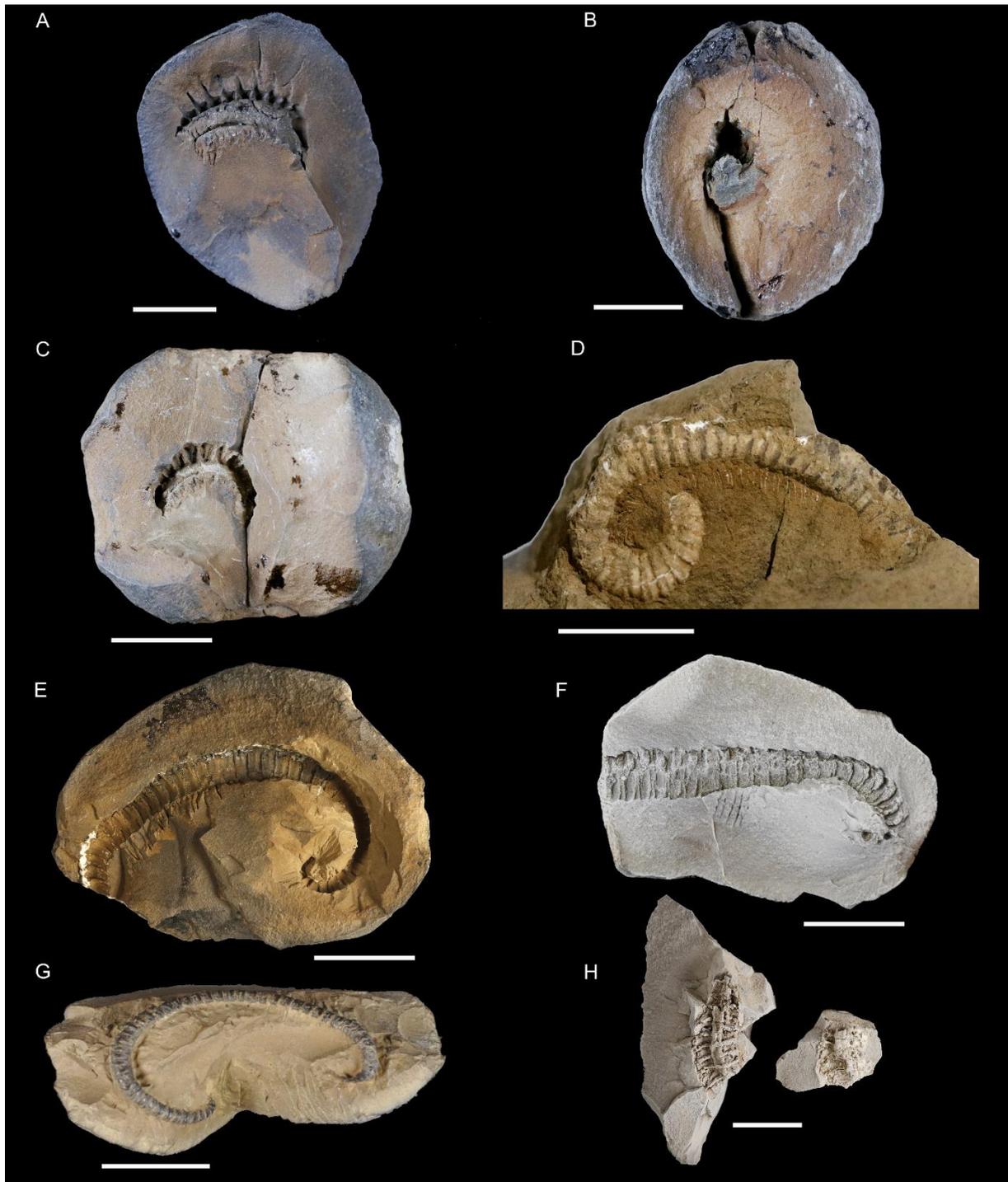
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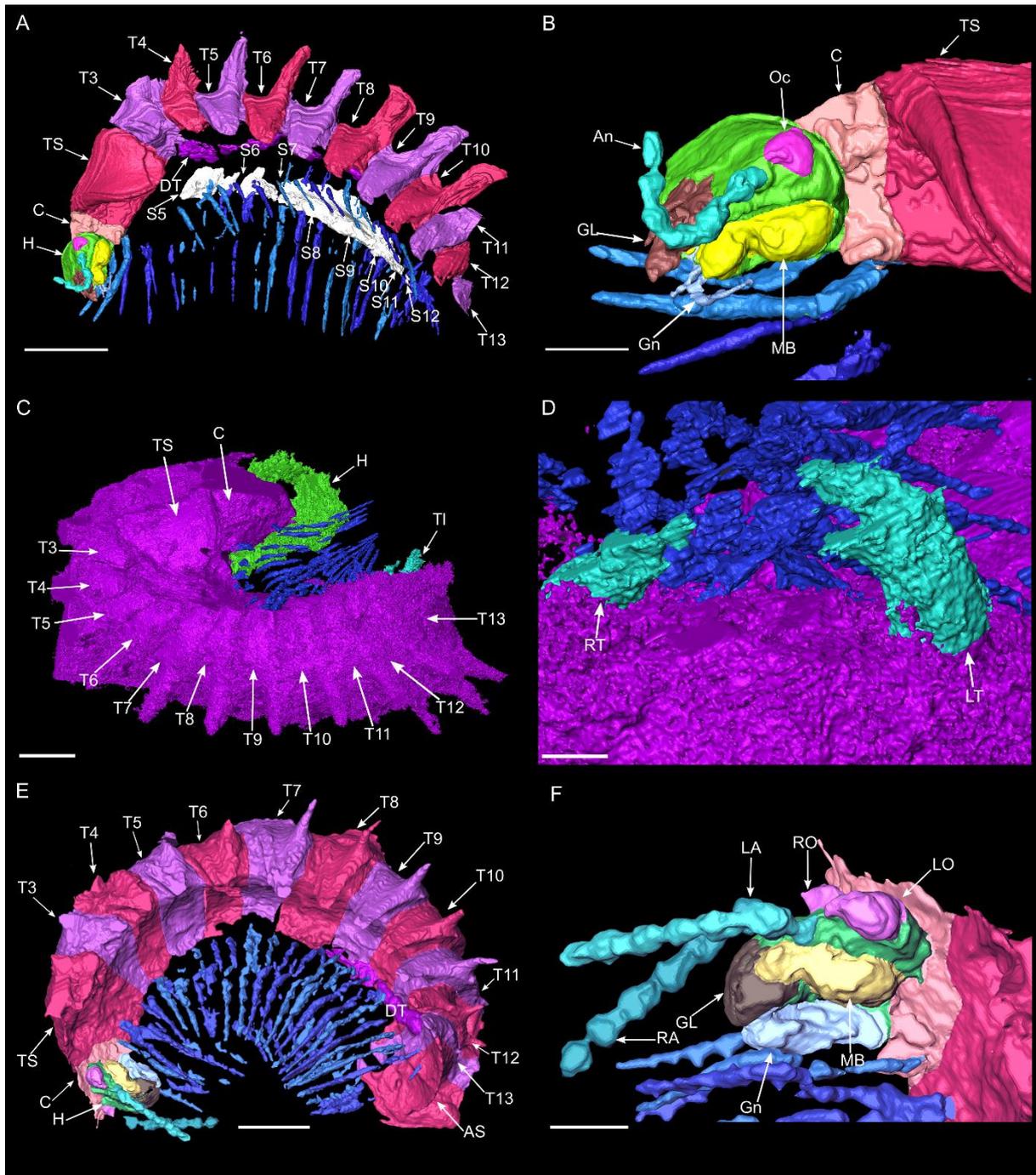
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1199 **Fig 2.** Specimens of *Amynilyspes fatimae* and *Blanziulus parriati*. A-C: *Amynilyspes fatimae*. (A): Holotype
 1200 MNHN.F.SOT.2134. (B): Paratype MNHN.F.SOT.14983. (C): Paratype MNHN.F.SOT.2129. D-H: *Blanziulus*
 1201 *parriati*. (D): Holotype MNHN.F.SOT.76-H-1-A. (E): MNHN.F.SOT.2114a. (F): MNHN.F.SOT.5148. (G):
 1202 MNHN.F.SOT.81522. (H): MNHN.F.SOT.2113. Scale bars represent: 1 cm (A-G); 3 mm (H).

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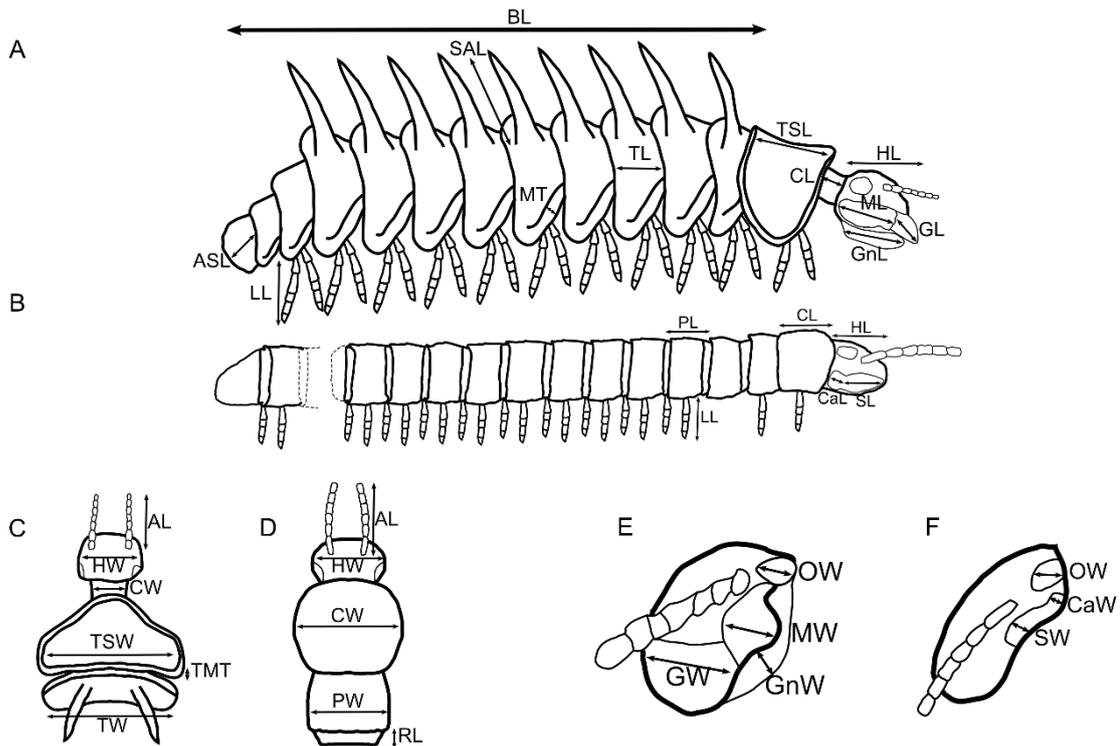
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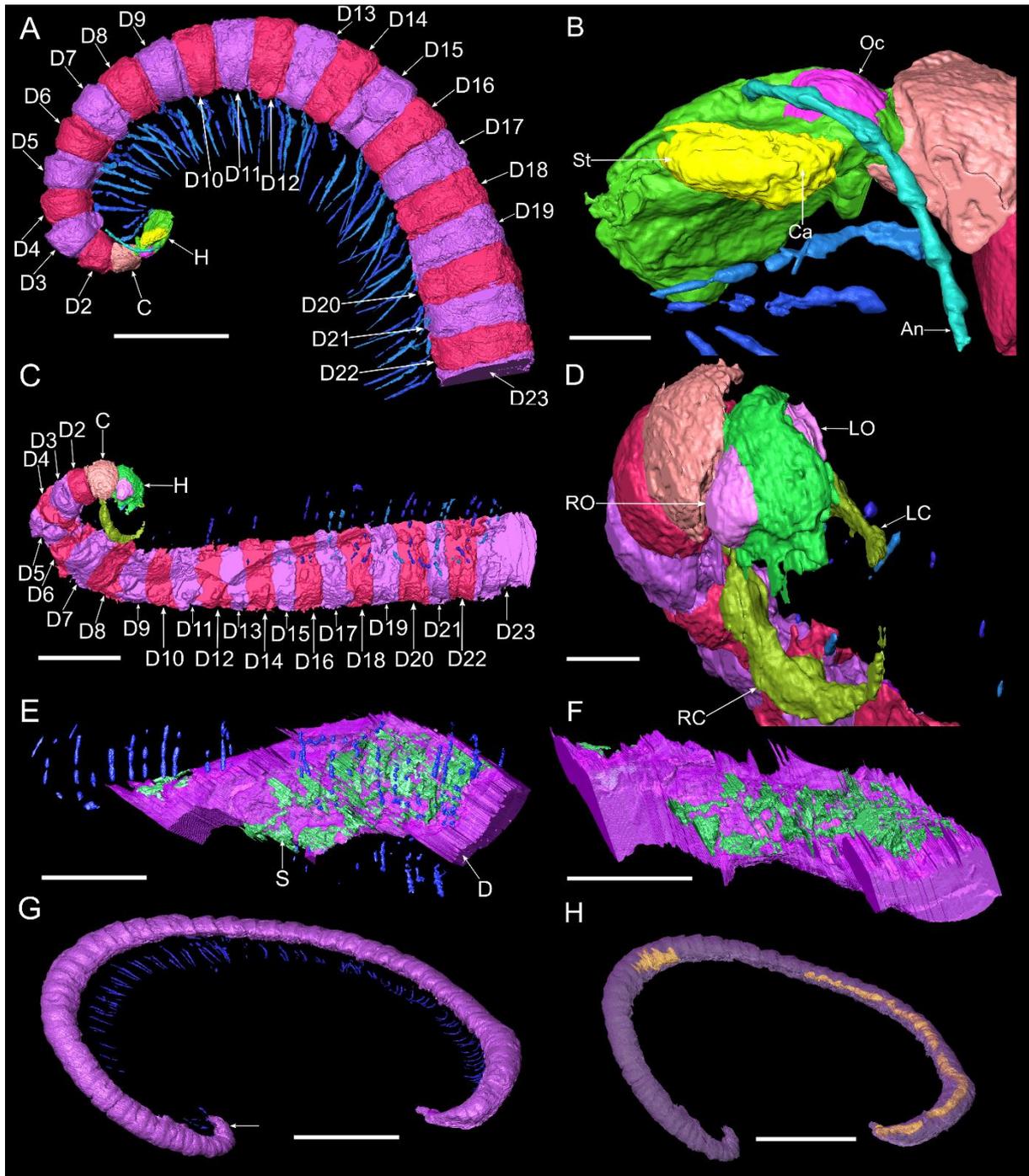
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Fig 3. 3D reconstructions of *Amynilyspes fatimae*. A-B: Holotype MNHN.F.SOT.2134. (A) Left lateral view. (B) Details on the head. C-D: Paratype MNHN.F.SOT.14983. (C) Oblique postero-dorsal view. (D) Details on the telopods. E-F: Paratype MNHN.F.SOT.2129. (E) Left lateral view. (F) Details on the head. An, antenna; AS, anal shield; C, collum; DT, digestive tube; GL, gnathal lobe; Gn, gnathochilarium; H, head; LA, left antenna; LO, left ocular field; LT, left telopod; MB, mandibular base; Oc, ocular fields; RA, right antenna; RO, right ocular field; RT, right telopod; S#, sternite number #; T#, tergum number #. Scale bars represent: 3 mm (A); 2 mm (E); 1mm (B-C); 500 μ m (F); 100 μ m (D). The reconstructions of MNHN.F.SOT.14983 are made from the scans of the μ CT SKyscan 1272. All the other reconstitutions are made from the scans of the Phoenix X-ray Phoenix v|tome|x CT-scan.



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Fig 4. Schematic diagrams of *A. fatimae* and *B. parriati* indicating main morphological parameters. (A) Right lateral view of *A. fatimae*. (B) Right lateral view of *B. parriati*. (C) Dorsal view of *A. fatimae*. (D) Dorsal view of *B. parriati*. (E) Three-quarter view of *A. fatimae*. (F) Three-quarter view of *B. parriati*. AL, antenna length; ASL, anal shield length; BL, body length; CL, collum length; CW, collum width; CaL, mandibular cardo length; CaW, mandibular cardo width; GL, gnathal lobe length; GW, gnathal lobe width; GnL, gnathochilarium length; GnW, gnathochilarium width, HL, head length; HW, head width; LL, leg length; ML, mandibular base length, MT, margin thickness; MW, mandibular base width; OW, ocular field width; PL, pleurotergum length; PW, pleurotergum width; RL, ridge length; SAL, spine axial length; SL, mandibular stipes length; SW, mandibular stipes width; TL, tergum length; TMT, thoracic shield margin thickness; TSL, thoracic shield length; TSW, thoracic shield width; TW, tergum width.



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Fig 5. 3D reconstructions of *Blanziulus parriati*. A-B: MNHN.F.SOT.2114a. (A) Left lateral view. (B) Details on the

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head. C-D: MHNHN.F.SOT.5148. (C) Right lateral view. (D) Details on the head and front part. E-F:

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MNHN.F.SOT.2113. (E) Ventro-dorsal view. (F) Lateral view. G-F: MNHN.F.SOT.81522. (G) Left lateral view.

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Whiter arrow point the anterior part. (H) Highlighting of the digestive tube. An, antenna; C, collum; Ca, mandibular

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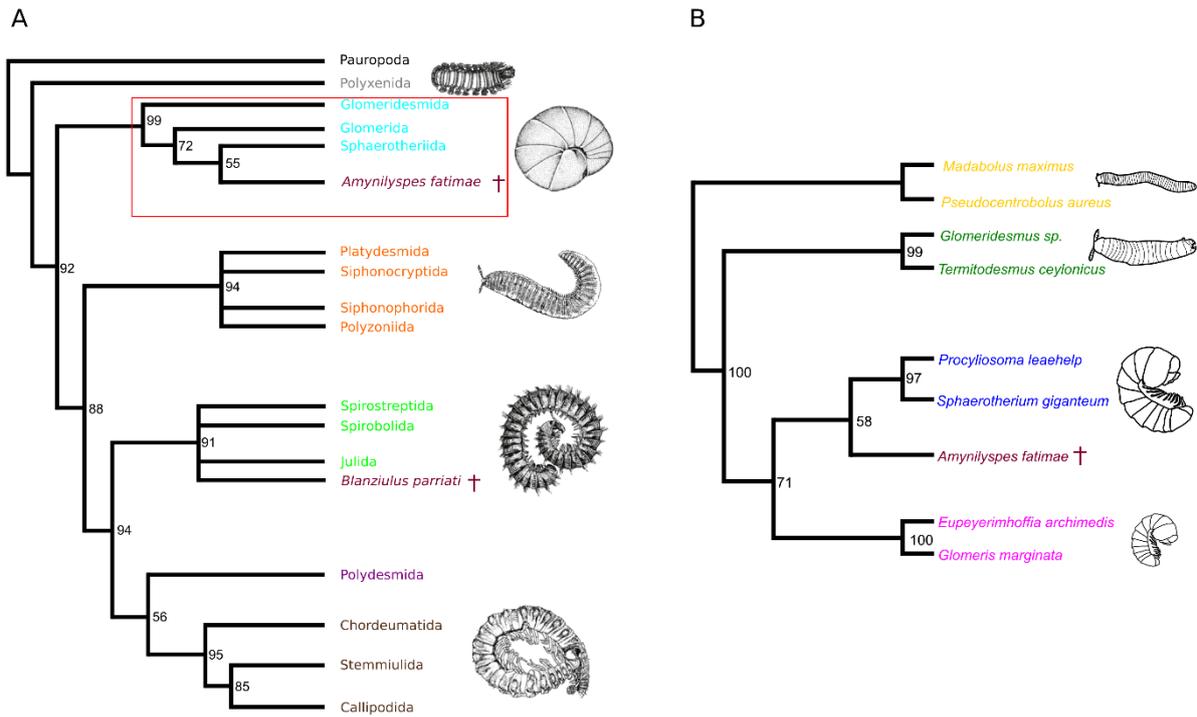
cardo; D#, Diplotergum number #; H, head; LC, left clasper; LO, left ocular field; ; Oc, ocular field; RC, right clasper;

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Ro, right ocular field; S, sternite; St, mandibular stipes. Scale bars represent: 5 mm (A, C, E-F, G-H); 1 mm (D);

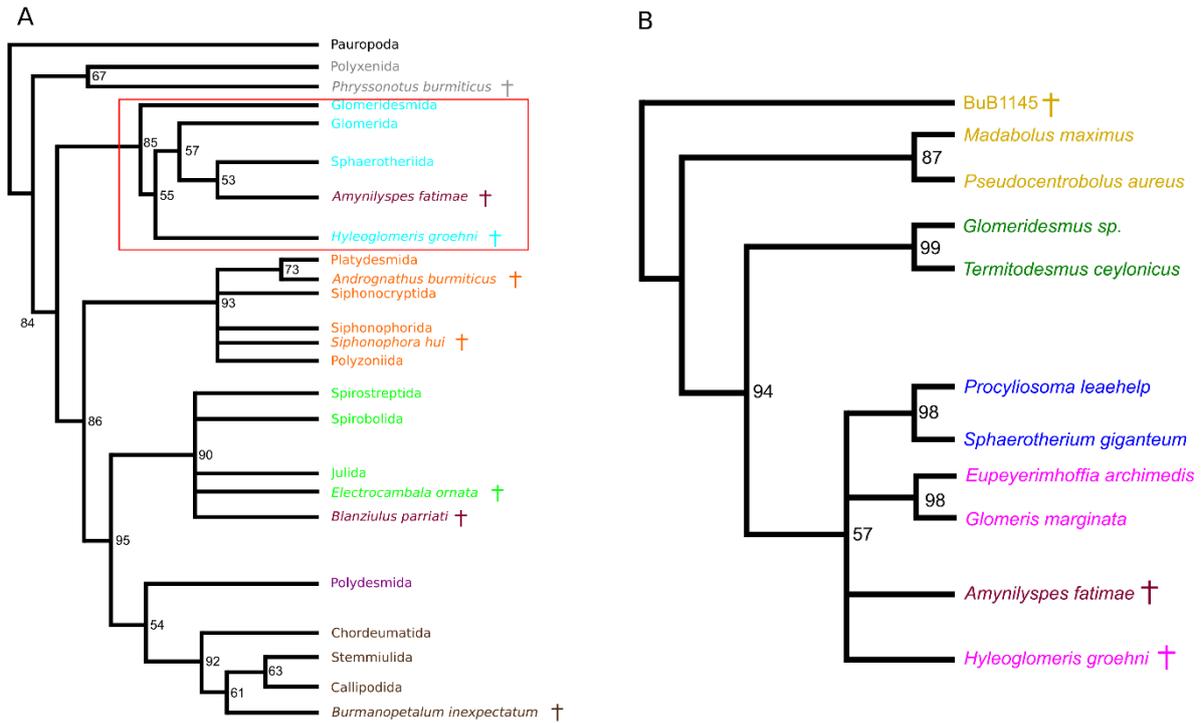
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Fig 6. Consensus of maximum parsimony morphological phylogeny for the two Montceau species and extant Diplopoda orders/species. (A) Consensus for *A. fatimae*, *B. parriati* and extant orders of the class Diplopoda. Pauropoda = black; Polyxenida = grey; Pentazonia = light blue; Colobognatha = orange; Juliformia = light green; Polydesmida = purple; Nematophora = brown; fossil species from Montceau = dark red. Red rectangle show the subclass Pentazonia. Drawings from Blanke & Wesener 2014. (B) Consensus for *A. fatimae* and extant species of the subclass Pentazonia. Spirobolida = yellow; Glomeridesmida = dark green; Sphaerotheriida = blue; Glomerida = pink; *A. fatimae* = dark red. (A) and (B) Branch and Bound bootstraps scores = node value.



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1266 **Fig 7.** Consensus of maximum parsimony morphological phylogeny for the two Montceau species, extant Diplopoda

1267 orders/ species and other extinct Diplopoda species. (A) Consensus for *A. fatimae*, *B parriati*, extant orders and six

1268 extinct species of the class Diplopoda. (B) Consensus for *A. fatimae*, extant species and two extinct species of the

1269 subclass Pentazonia. (A) and (B) Same colour code and node values as in Fig. 6.

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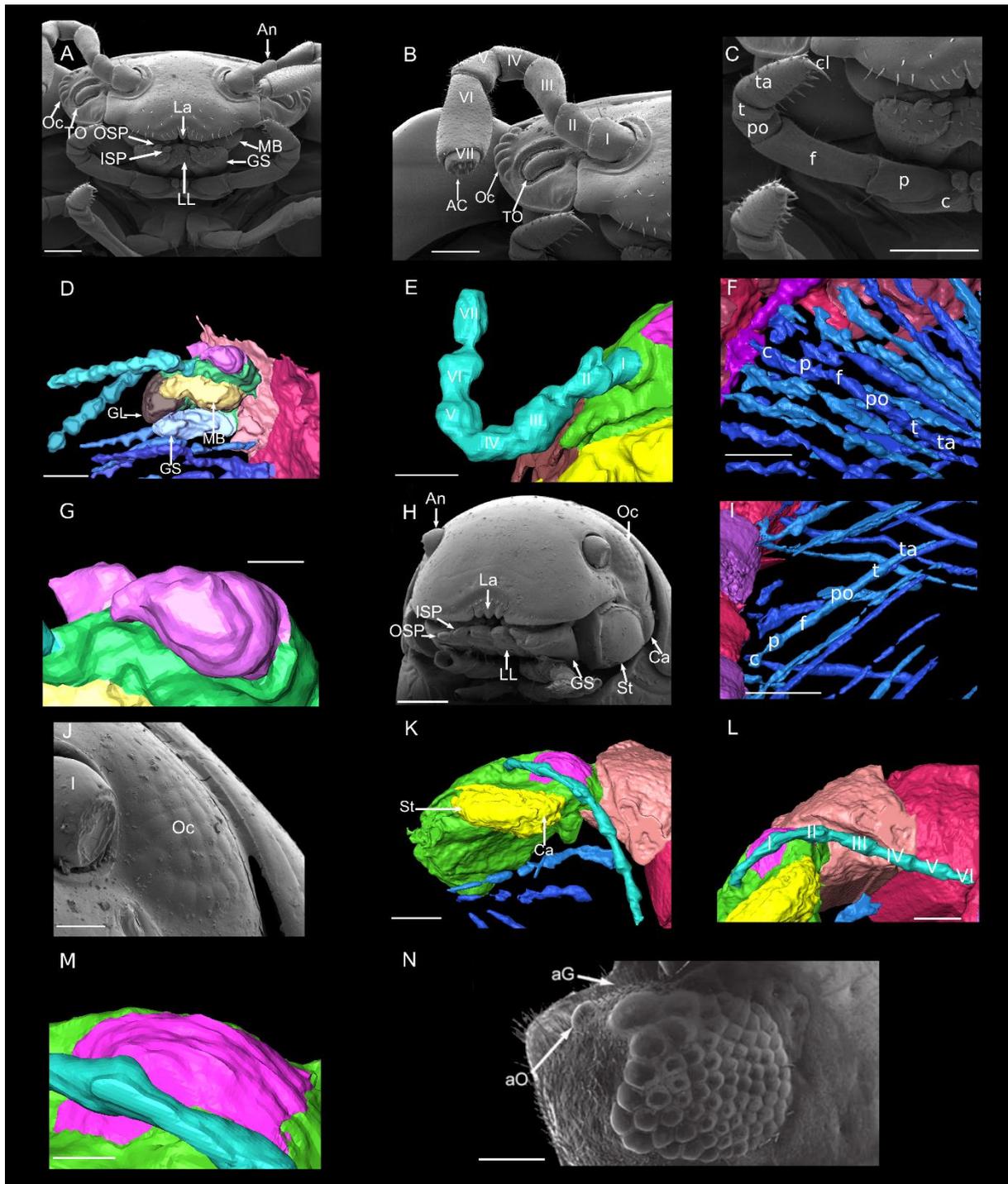
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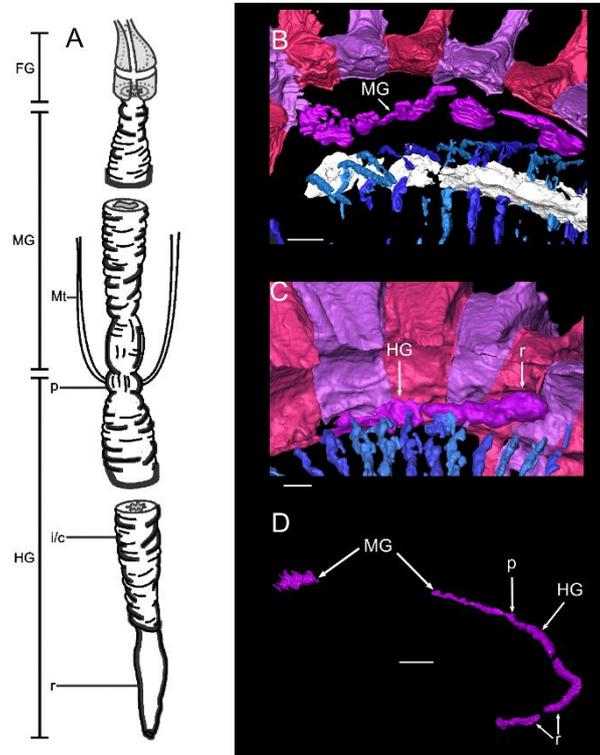
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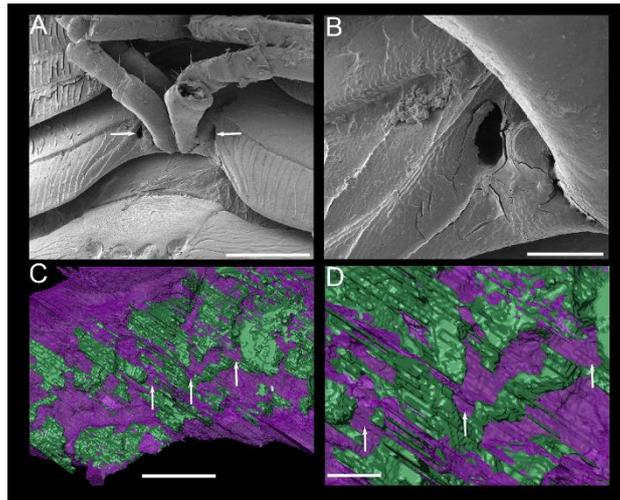
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Fig 8. Comparisons between *Amynilylspes fatimae* and *Glomeris marginata* and between *Blanziulus parriati* and an extant Juliformia. (A) Head of *G. marginata*. (B) Sense organs of *G. marginata*. (C) Leg of *G. marginata*. (D) Head of *A. fatimae*. (E) Antenna of *A. fatimae*. (F) Legs of *A. fatimae*. (G) Ocular fields of *A. fatimae*. (H) Head of an unidentified Juliformia. (I) Legs of *B. parriati*. (J) Sense organs of an unidentified Juliformia. (K) Head of *B. parriati*. (L) Antenna of *B. parriati*. (M) Ocular field of *B. parriati*. (N) Ocular field of *Zoosphaerium* sp. (Wesener 2016b). AC, apical cones; aG, antennal groove; aO, aberrant ocellus; An, antenna; c, coxa; Ca, mandibular cardo; cl, claw; f, femur; GL, gnathal lobe; GS, gnathochilarial stipes; ISP, inner stipital palps, La, labrum; LL, lamellae lingualis; MB,

1293 mandibular base; Oc, ocular field; OSP, outer stipital palps; p, prefemur; po, postfemur; St, mandibular stipes; t,
 1294 tibia, ta, tarsus; Tö; Tömösváry organ. Roman number #, corresponding antenna segment. Scale bars represent: 1
 1295 mm (F, I); 500 μ m (A-E, H, K-L, N); 250 μ m (G); 150 μ m (J); 100 μ m (M). Specimens: MNHN.F.SOT. 2134 (E);
 1296 MNHN.F.SOT. 2129 (D, F, G); MNHN.F.SOT. 2114a (I, K, L, M).
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 1300 **Fig 9.** Digestive system of extant and extinct diplopods. A: schematic illustration of a diplopod digestive tube
 1301 (Fontanetti et al. 2015). B-C: Digestive tubes of *Amynilyspes fatimae*. (B) MNHN.F.SOT.2134. (C)
 1302 MNHN.F.SOT.2129. (D) Digestive tube of *Blanziulus parriati*, specimen MNHN.F.SOT.81522. FG, foregut; HG,
 1303 hindgut; i/c, ileo/colon; MG, midgut; Mt, Malpighian tubule; p, pylorus; r, rectum. Scale bars represent: 2 mm (D); 1
 1304 mm (B); 500 μ m (C).
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1315 **Fig 10.** Respiratory apparatus of Juliformia. A-B: tracheal openings of an unidentified Juliformia. (B) Details on one
1316 opening. C-D: possible tracheal openings on *Blanziulus parriati*, specimen MNHN.F.SOT.2113. (D) Details on the
1317 openings. White arrows indicate the openings on the extant Juliformia and the presumed ones on *Blanziulus parriati*.

1318 Scale bars represent: 2 mm (C); 500 μm (A, D); 100 μm (B).

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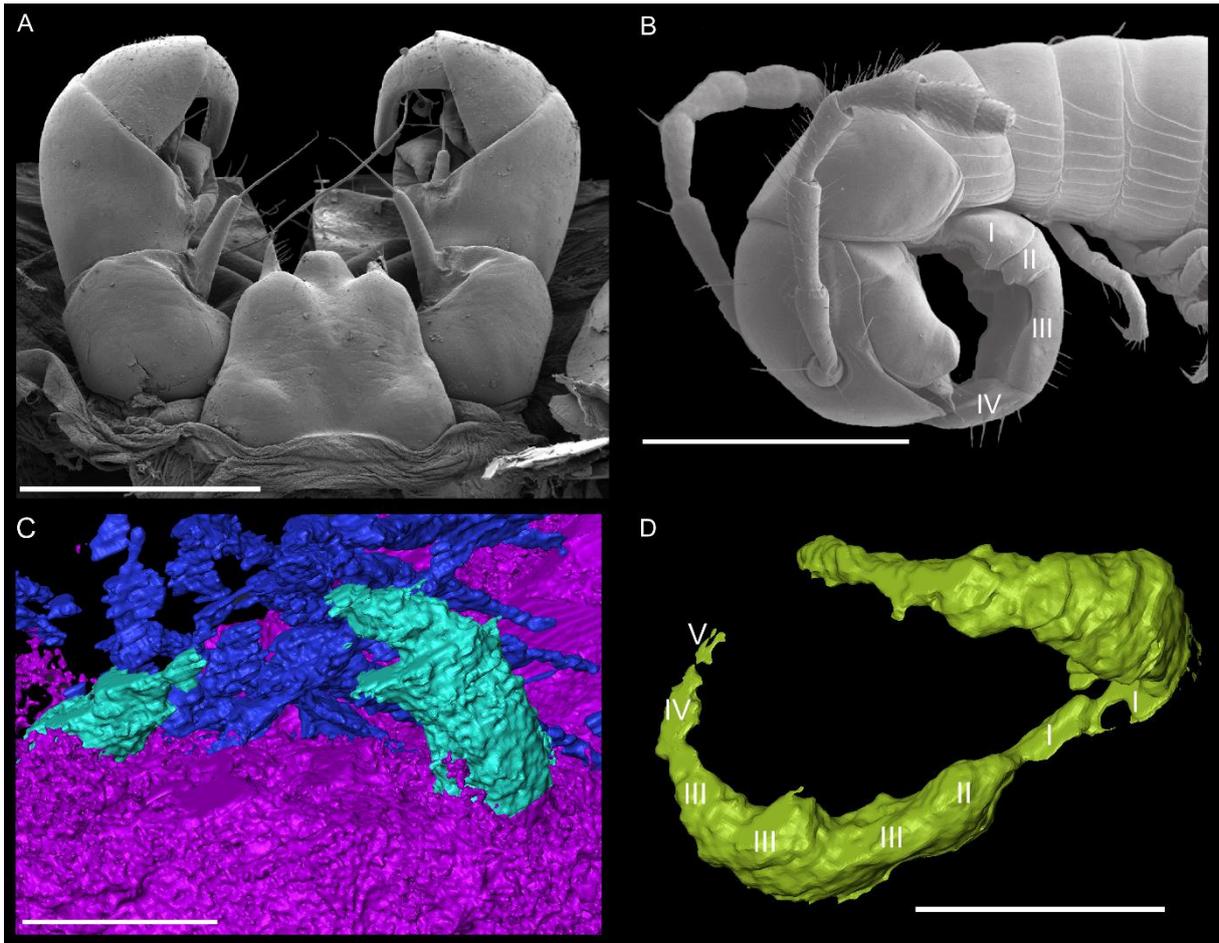
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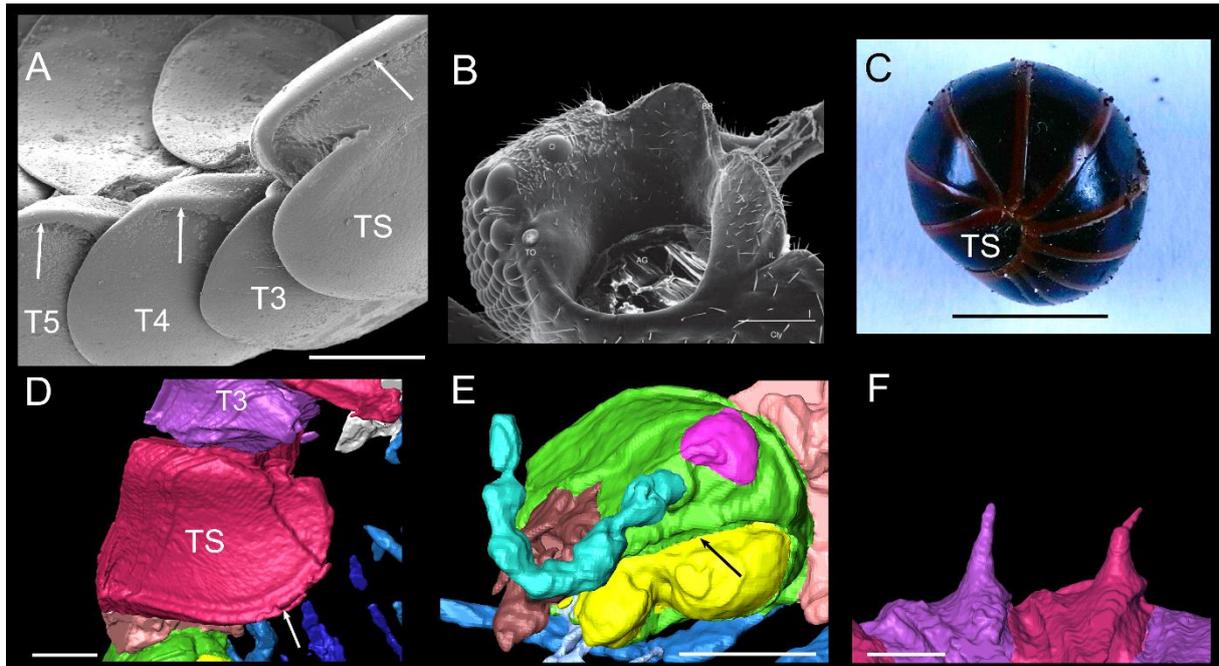
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Fig 11. Sexual appendages of pill millipedes and Juliformia. (A) Outer telopods of *Glomeris marginata* (Glomerida). (B) Front part of *Koiulus interruptus* (Enghoff, Jensen & Mikhaljova, 2017) (Julida: Mongoliulidae), from Enghoff *et al.* 2017. (C) Inner telopods of *Amynilyspes fatimae*, specimen MNHN.F.SOT.14983. (D) Details on claspers of *Blanziulus parriati*, specimen MNHN.F.SOT.2113. Roman number #, corresponding clasper segment. Scale bars represent: 2 mm (D); 1 mm (A, C); 100 μ m (B).



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1357 **Fig 12.** Morphological defences of pill millipedes. A-C: extant pill millipedes. (A) Details on margins of *Glomeris*
 1358 *guttata*. (B) Antennal groove (antenna removed) of *Cryxus ovalis* (Linnaeus, 1758) (Sphaerotheriida), from
 1359 Golovatch *et al.* 2012. (C) *Glomeris marginata* in volvation. D-F: *Amynilyspes fatimae*, specimen
 1360 MNHN.F.SOT.2134. (D) Details on margins. (E) Details on the head. (F) Details on spines. AG, antennal groove;
 1361 BR, brim of head; Cly, clypeus; IL, incisura lateralis; O, isolated ocellus; TO; organ of Tömösváry; TS, thoracic
 1362 shield; T#, tergite number #. White arrows on (A) and (D) indicate margins. Black arrow on (E) indicate lateral ridge.
 1363 Scale bars represent: 5 mm (C); 1 mm (D-F); 500 μ m (A); 400 μ m (B).

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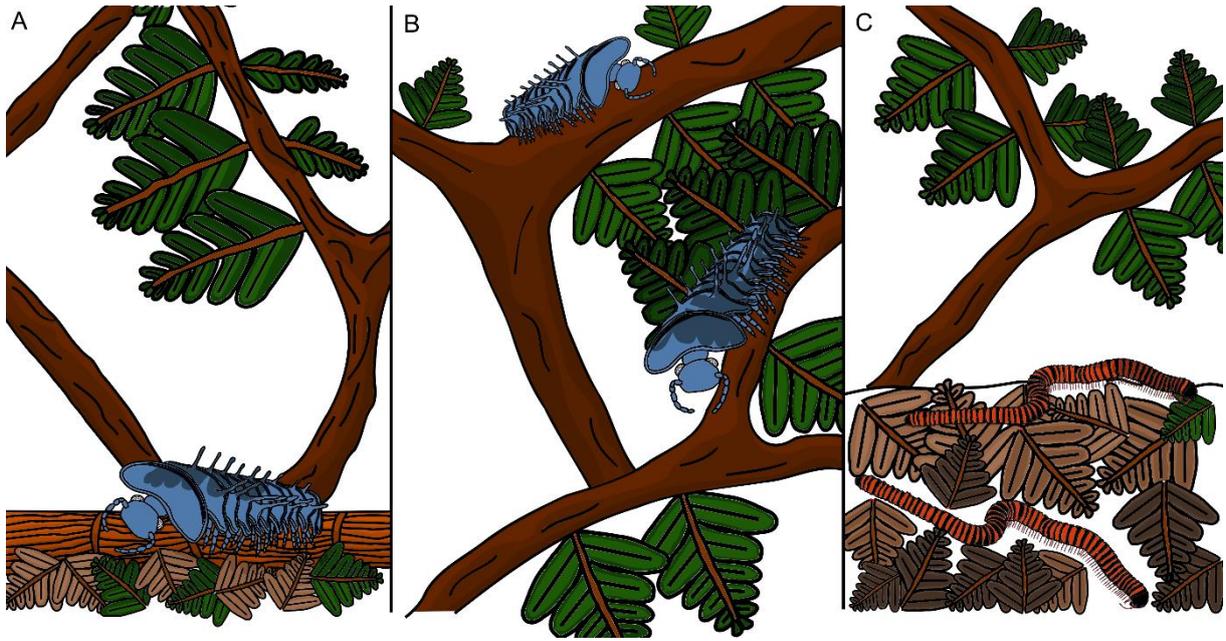
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1379 **Fig 13.** Reconstruction of possible ecotypes of *Aynilyspes fatimae* and *Blanziulus parriati* in in their supposed

1380 environment. (A) *Aynilyspes fatimae* with a stratobiont strategy. (B) *Aynilyspes fatimae* with an epiphytobiont

1381 strategy. (C) *Blanziulus parriati* with stratobiont and pedobiont strategies.

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