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1 **The wing venation of a new fossil species, reconstructed using**
2 **geometric morphometrics, adds to the rare fossil record of Triassic**
3 **Gondwanian Odonata**

4

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6

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15

16 **Keywords :** Wing venation – Molteno Formation – Stem-Odonata – Reconstruction

17

18 **Abstract**

19 Probably, the most common rock imprint fossil insect remain is an incomplete, isolated
20 wing. This pitfall has been traditionally addressed by manually reconstructing missing parts,
21 which is not ideal to comprehend long-term evolutionary trends in the group, in particular
22 for morphological diversity (i.e., disparity) approaches. Herein we describe a new Triassic
23 relative of dragon- and damselflies (Odonata), *Moltenophlebia lindae* gen. et sp. nov., from

24 the Molteno Formation (Karoo Basin, South Africa), on the basis of three incomplete,
25 isolated wings. In order to provide a reconstruction of the complete wing venation of the
26 species, we formalized and applied a repeatable method aiming at inferring the missing parts
27 of a given specimen. It is based on homologous veins automatically identified thanks to a
28 standardized color-coding. The dedicated script can be applied broadly to the fossil record of
29 insect wings. The species occurs to be a member of the Zygophlebiida, within the
30 Triadophlebiomorpha. This discovery therefore represents the first ascertained occurrence of
31 the latter group in Gondwana, an area where the fossil record of Odonata is depauperate.

32

33 **1. Introduction**

34 Although the fossil record of Odonata (dragon- and damselflies, and their stem-relatives) is
35 composed of about a thousand species (Paleobiology Database, 2019), many of the known fossils
36 are represented by incomplete wings. Moreover, particular periods and geographical areas
37 remain under-studied. This situation makes it difficult to comprehend long-term evolutionary
38 trends in the group, using either taxonomic or morphological diversity (i.e., disparity)
39 approaches.

40 Herein we describe a new species from the Molteno Formation (Triassic, South Africa). The
41 species is represented by three incomplete, isolated wings. In order to provide a reconstruction of
42 the entire wing venation of the species, we applied a standardized and repeatable method aiming
43 at reconstructing missing parts. We used Thin Plate Splines (TPS), mathematical basis for
44 deformation grids (Bookstein, 1989), to deform a reference shape onto a target shape using
45 homologous landmarks and semi-landmarks subsampled along veins identified thanks to a
46 standardized color-coding.

47

48 The new species adds to the fossil record of Odonata during the Triassic. Indeed it represents
49 the first well ascertained occurrence of Triadophlebiomorpha in the Southern Hemisphere, a
50 group previously known from Europe and Asia only (Nel et al., 2001; Pritykina, 1981; Zheng et
51 al., 2017).

52

53 2. Terminology and materials

54 2.1. Nomenclature and abbreviations

55 We follow the serial insect wing venation ground pattern (Lameere, 1923, 1922). The
56 corresponding wing venation nomenclature is repeated for convenience: ScP, posterior Subcosta;
57 R, Radius; RA, anterior Radius; RP, posterior Radius; RP1+2, anterior branch of RP (to be
58 further divided into RP1 and RP2); RP3+4, posterior branch of RP (to be further divided into
59 RP3 and RP4); MA, anterior Media; MP, posterior Media; Cu, Cubitus; CuA, anterior Cubitus;
60 CuP, posterior Cubitus; AA, anterior Analis. Based on this ground pattern we follow homology
61 conjectures for total-Odonata proposed by Riek and Kukalová-Peck (1984), Bechly (1996) and
62 Béthoux (2015; and see references therein). We follow Deregnaucourt et al. (2017) for the
63 terminology to apply to intercalary veins. In details, $I_{rp1-rp2}$ is the intercalary vein occurring
64 between RP1 and RP2 (also termed 'IR1'), and $I_{rp1+2-rp3+4}$ that occurring the RP1+2 and RP3+4
65 (also termed 'IR2'). In addition to this standard terminology, we propose to use additional terms,
66 as follows. For the strongly convex, oblique cross-vein located between MA and MP and aligned
67 with RP+MA/MA, we propose the term 'pons' ('bridge' in Latin; also termed 'MAB', e.g. by
68 Nel et al., 1996); for the strongly convex and aligned cross-veins located between MP and the
69 posterior wing margin, or CuA and the posterior wing margin, we propose the term 'pillar'.

70 Whether its portion located between CuP and the posterior wing margin AA (or one of its
71 branches) or a strengthened cross-vein is addressed in the Discussion.

72

73 *2.2. Documentation of fossil material*

74 The studied specimens are housed at the Evolutionary Studies Institute (PRE/F/; formerly
75 ‘Bernard Price Institute for Palaeontology’), University of the Witwatersrand, Johannesburg,
76 South Africa.

77 Draft drawings were prepared with the aid of a Zeiss SteREO Discovery V8
78 Stereomicroscope equipped with a pair of W-PL 10x/23 eye pieces, a Plan Apo S 1.0x FWD
79 objective, and a drawing tube (Jena, Germany). Photographs were taken using a Canon EOS 5D
80 Mark III equipped with Canon 50 mm or MP-E 65 mm macro lenses. The light-mirror technique
81 was used to provide positive views of the specimens. Photographs were optimized [i.e. features
82 (e.g. contrast) uniformly adjusted to maximize information content] using Adobe Photoshop CS6
83 (Adobe Systems, San Jose, CA, USA). Vector line drawings were made using Adobe Illustrator
84 CS6 (Adobe Systems, San Jose, CA, USA) based on both scans of draft drawings and
85 photographs. The drawing of the wing base of the holotype of *Zygophlebia tonchuanensis*
86 Zheng, Nel, Wang, Jarzembowski, Chang and Zhang, 2017 was prepared based on published
87 data and photographs provided by D. Zheng.

88

89 **3. Reconstruction of missing parts**

90 *3.1. Methodology*

91 In the literature, reconstructing non-conserved part of a fossil, for example a wing, is usually
92 achieved following the author's appreciation, i.e., a non- repeatable, unstandardized method. The

93 material at hand, composed of several conspecific wings preserving different areas, was suitable
94 for exploring methodologies aiming at reconstructing missing parts.

95 Several standardized reconstruction methods have already been developed and tested in the
96 field of palaeoanthropology for 3D models of cranium (Gunz et al., 2009; Ogihara et al., 2015),
97 including bilateral symmetry, multivariate regression and/or thin-plate spline (TPS)
98 interpolation. Bilateral symmetry is not appropriate for our model (there is no inner symmetry in
99 an isolated wing). Multivariate regression requires a sample of complete specimens, which is not
100 available for our case. We therefore resorted to semi-landmarks and TPS deformation.

101 TPS deformation mimics the deformation of an infinitely thin metal plate (Bookstein, 1989).
102 Therefore, it minimizes the bending energy of the transformation from a reference shape (here
103 the wing used to infer the missing parts of the incomplete one) to a targeted shape (the wing to
104 be reconstructed). As a consequence, the whole plan of the reference shape will be deformed. In
105 practice, the entire reference drawing will be affected by the deformation in such a way that the
106 placed points of reference (landmarks and semi-landmarks) fit perfectly the ones on the targeted
107 shape. Thus, the missing parts of the targeted shape will be inferred by those deformed from the
108 reference shape.

109 The two most complete specimens of *Moltenophlebia lindae*, PRE/F/20522 and
110 PRE/F/10626 (Fig. 2A, B), have largely overlapping parts. Therefore, each can be used as
111 reference shape to infer the missing parts of the other (Fig. 1A). Unfortunately, both specimens
112 lack the wing apex. Thus, a second TPS deformation was performed using data on *Zygophlebia*
113 *ramosa* Pritykina, 1981, the closest relative known from a complete wing, to reconstruct the
114 missing apex (Fig. 1B).

115 For details, the missing parts of the specimen PRE/F/20522 (light lines in Fig. 2A) were
116 inferred based on the specimen PRE/F/10626 (dark lines in Fig. 2B), and vice-versa. A drawing
117 of the main veins and wing margin was first vectorized with Adobe Illustrator CS6. A specific
118 color-code was applied to each vein. The vector files were then imported on R using grImport
119 v.0.9-1 (Murrell, 2009).

120 Selection of sliding semi-landmarks was then performed (orange block in Fig. 1A). Fourteen
121 homologous vein portions present on both specimens were automatically selected thanks to their
122 color-coding. They were then sub-sampled to generate sets of landmarks with geomorph v.3.0.7
123 (Adams and Otárola-Castillo, 2013). For details, for each curve, the subsampling procedure
124 generates two landmarks (considered homologous) at its beginning and end, and 3 to 49 semi-
125 landmarks between them (proportionally to the curve's length and complexity). Semi-landmarks
126 were allowed to slide using the minimum Bending Energy criterion. This method is more
127 suitable than minimizing Procrustes distances when there is large shape variation (Gunz and
128 Mitteroecker, 2013; Schlager, 2017), which is the case for the second step of the reconstruction
129 (see below; Fig. 1B). The actual disposition of landmarks and the rationale for placing them are
130 provided as Supplemental Data 1 (Appendix A.).

131 A Procrustes superimposition (GPA) was then performed to correct for the effects of
132 rotation, translation and size (Rohlf and Slice, 1990). Finally, a TPS deformation was applied to
133 the specimen PRE/F/10626 (reference shape) so that its homologous points' coordinates fit those
134 of the specimen PRE/F/20522 (targeted shape). The same deformation is applied to each pixel of
135 the original drawing in order to obtain the image of PRE/F/20522 complemented by
136 PRE/F/10626 original parts. The wing was almost completely reconstructed at that point, except
137 for the apex.

138 To reconstruct this last area we applied the same procedure using data on *Zygophlebia*
139 *ramosa* which, among the Zygophlebiida, to which *Moltenophlebia lindae* belongs (see
140 Systematic Paleontology section), is the only species for which a complete wing is documented
141 (Fig. 1B). However this specimen, like others excavated in the corresponding locality, is
142 assumed to have been uniformly deformed by tectonics (Sharov, 1971, 1968; Voigt et al., 2006).
143 To take that bias into account, we added a ‘retrodeformation’ step (blue block in Fig. 1B): the
144 wing of *Zygophlebia ramosa* was submitted to 37 rotations (over 180°) and 11 elongations (from
145 100% to 200%) to create 407 retro-deformed wings (see examples in Supplemental Data 1,
146 Appendix A). The Procrustes superimposition was then performed. The retro-deformed drawing
147 selected for reconstruction was the one minimizing distances between landmarks coordinates and
148 those of the previously reconstructed wing (purple wing in Fig. 1). The TPS deformation was
149 then realized on this retro-deformed wing so that its homologous points' coordinates fit those of
150 the previously reconstructed wing (penultimate step in Fig. 1B). A fully reconstructed wing was
151 then obtained (main script, functions and functions description are available as Supplemental
152 Data 2, 3 and 4 respectively, Appendix A.).

153 The same procedure was used to reconstruct the wing of the specimen PRE/F/10626 (but
154 using the specimen PRE/F/20522 as reference shape for the first step).

155

156 3.2. Method limitations

157 Several sets of main veins were tested for reconstruction. Notably, the pertinence of using
158 semi-landmarks on RP2, for the second part of the process (aiming at reconstructing the wing
159 apex; Fig. 1B), was examined. Indeed, the area between RP3 and the anterior branch of RP2 is
160 very dissimilar in the reference and targeted shapes: RP2 is branched more basally than RP3+4

161 in *Zygophlebia ramosa* whereas in *Moltenophlabia lindae* RP2 is forked close to the posterior
162 wing margin. Additionally, RP3+4 has many more branches in *Moltenophlabia lindae*. In a first
163 attempt, RP2 was not used because of this important variation between the two wing shapes.
164 However, the obtained reconstructed wing was not realistic: it was very elongated and the apex
165 had a marked posterior bending. This reconstructed wing could have hardly flown.

166 In a second attempt, semi-landmarks were placed on the portion of RP2 before its first split
167 on each wing shape, assuming that this variable area would be more constrained so as to better fit
168 the targeted shape. The obtained reconstruction, more realistic, is the one presented here (Fig.
169 2A). However, given the remarkable differences in this area between the two wings (viz. the
170 reconstructed *Moltenophlabia lindae* and the retro-deformed *Zygophlebia ramosa*), the TPS
171 deformation generated unrealistic distortions of some vein portions. These distortions were not
172 taken into account for the final reconstruction because they affected parts which were preserved
173 in the targeted shape. The proposed reconstruction (Fig. 2A) is therefore a smoothed version of
174 the R output to fit the fossil's preserved parts. R outputs are provided in Supplemental Data 1
175 (Appendix A.).

176 Unrealistic distortions were probably due to shape differences too important to be managed
177 by the method. Indeed, semi-landmarks are allowed to slide along a curve, while only the first
178 and last points are homologous landmarks (i.e., are not allowed to slide). Some semi-landmarks
179 slid away from the original curve, not fitting anymore the original wing shape, probably because
180 of the constraint induced by the use of RP2 curve for such a different area. The use of a more
181 closely related species as reference shape might fix this issue. An additional improvement would
182 be to consider more than one closely related species as reference shapes. Indeed, Gunz et al.

183 (2009) used several references to reconstruct their target and obtained different results. However,
184 for now, there is no other complete wing appropriate for such a reconstruction.

185 Other issues can also be mentioned. It was not always possible to delimit vein portions based
186 on well-defined points such as vein branching. We therefore resorted to a manual pre-alignment
187 of the two sub-complete wings, inducing some degree of subjectivity. As arose by Gunz et al.
188 (2009) and Ogihara et al. (2015), other parameters are susceptible to lead to differing
189 reconstructions, such as the number of landmarks and semi-landmarks. In our case, a minimal
190 number of semi-landmarks is needed to faithfully quantify a vein curvature, but too many render
191 the sliding computation more complicated, time-consuming and prone to generate unrealistic
192 crossings of semi-landmarks (due to their proximity).

193 Also, we ignore whether the two specimens of *Moltenophlebia lindae* used in the first step
194 (Fig. 1A) belonged to homologous thoracic segments (i.e., were both forewings, or hind wings),
195 or to individuals of the same sex. Some of the observed differences could reflect fore- vs. hind
196 wing differentiation and/or sexual dimorphism, both variations occurring among extant Odonata.
197 Indeed, i.e., hind wings are commonly broader and shorter than forewings in these insects. This
198 differentiation is much less conspicuous in those possessing petiolated wings (*Zygoptera* and
199 *Anisozygoptera*; i.e., damselflies and *Epiophlebia* spp., respectively), as *Moltenophlebia lindae*
200 does. In *Calopterygidae* (i.e., broad-winged damselflies) females commonly have wings more
201 elongated than those of males. However, leaving apart purely shape-related aspects, the main
202 veins pattern remains essentially unchanged, especially in the distal two-thirds of the wing. This
203 general appreciation was confirmed by Blanke (2018) who, on the basis of a broad-scale
204 morphometric analysis of *Anisoptera* wing venation, demonstrated that fore- and hind wings
205 correlate with each other in their shape variation. It can then be expected that our reconstruction

206 method will satisfactorily account for fore- vs. hind wing differentiation and/or sex-related shape
207 differences. This is indeed exemplified by the fact that the obtained reconstruction of the
208 specimen PRE/F/20522 (Fig. 2A) is broader than the used reference shape, which likely
209 represents a genuine differentiation.

210 The obtained reconstructions are based on a standardized repeatable method which could be
211 used on any wing that needs to be reconstructed for comparative analysis, or any fossil
212 equivalent to a 2D model lacking bilateral symmetry. Gunz et al. (2009) tested several aspects of
213 the reconstruction approach (e.g. error induced by reconstruction against intra-specific variability
214 within an inter-specific framework) and highlight the relevance of the TPS deformation for cases
215 such as the one presented here. We proposed an adaption of this method to insect wings and
216 detailed it step by step to ensure a complete transparency. However, further testing could be
217 valuable focusing on our model, for the reconstruction and also the retro-deformation step.

218 A possible venue would be to simulate missing parts on extant species and comparing the
219 obtained reconstructions with the original wing shape. The number and distribution of missing
220 areas, as well as their extents, likely are critical elements. For example, the reconstruction of a
221 wing apex, as we endeavored herein, is likely to be less reliable than that of an inner part. Indeed,
222 we performed an extrapolation, i.e., constraints were only applied on one side of the
223 reconstructed part. That could explain why the firstly reconstructed wing apex was
224 unrealistically elongated. In contrast, the reconstruction of a part located in the middle of a wing
225 could be more accurate because it is an interpolation, i.e., with constraints on several sides. Also,
226 phylogenetic closeness between the reference and target shapes is likely another prevalent factor
227 to be tested. The number of landmarks and semi-landmarks also needs to be tested. Ultimately,
228 the error induced by the reconstruction could be tested against intra-specific variability, within an

229 inter-specific framework (Gunz et al., 2009). Considering additional constraints, for example in
230 relation with flight biomechanics (Wootton and Kukalová-Peck, 2000) and developmental
231 modelling (Hoffmann et al., 2018), could further help obtaining more reliable reconstruction.

232

233 **4. Systematic paleontology**

234

235 ORDER ODONATA FABRICIUS, 1793

236 TAXON PANDISCOIDALIA NEL ET AL., 2001

237 TAXON DISCOIDALIA BECHLY, 1996

238 TAXON TRIADOPHLEBIOMORPHA PRITYKINA, 1981

239 TAXON ZYGOPHLEBIIDA NEL ET AL., 2001

240

241 *Emended diagnosis*

242 RP2 and $Irp_{1+2-rp_{3+4}}$ fused for some distance shortly after the origin of the former, and Irp_1-
243 rp_2 and RP2 fused for some distance; CuA without posterior branches; and, occurrence of a pillar
244 (ranging either from CuA to the posterior wing margin, or from MP to the posterior wing
245 margin).

246

247 *Included families*

248 Zygophlebiidae, Xamenophlebiidae, Permophlebiidae and Kargalotypidae.

249

250 *Remarks*

251 Nel et al. (2001) listed six character states as diagnostic of the taxon Zygophlebiida. Two of
252 them relate to the particular organisation of Irp_1-rp_2 , RP2, and $Irp_{1+2}-rp_{3+4}$. We provide a
253 tentative interpretation of the corresponding area (Fig. 2) consistent with statements made by
254 Bechly (1996) and Nel et al. (2001), positing that (1) in the basal part, RP2 briefly fuses with
255 $Irp_{1+2}-rp_{3+4}$, and, (2) in the distal part, Irp_1-rp_2 , briefly fuses with RP2. These two states might
256 have been acquired concurrently as a consequence of the relocation of the bases of Irp_1-rp_2 , RP2,
257 and $Irp_{1+2}-rp_{3+4}$ towards the wing base. Therefore we propose to treat them as a single character
258 state, which is obviously derived, as it is absent in the most remote stem-Odonata (Riek and
259 Kukalová-Peck, 1984). Note that, as indicated by Nel et al. (2001), this character state was
260 acquired convergently within Protomyrmeleontidae, belonging to the Stigmoptera
261 (Deregnacourt et al., 2021, and references therein), a group therefore only remotely related to
262 the Zygophlebiida.

263 Other character states listed by Nel et al. (2001) are present in various other Pandiscoidalia,
264 such as the Triadotypomorpha (Nel et al. 2001; Deregnacourt et al., 2017). In other words, these
265 states form a corpus relevant only if observed jointly. The most relevant is ‘CuA simple’,
266 allowing Zygophlebiida to be distinguished from other Triadophlebiomorpha. However, it might
267 represent the apomorphy of a larger group, including all extant forms.

268 Whether the posterior-most portion of the pillar is composed of AA (or one of its branches)
269 or a strengthened cross-vein, as favored herein, is addressed in the Discussion. Regardless of its
270 nature, the occurrence of the pillar itself is a putative diagnostic trait of Zygophlebiida, or of a
271 subset within this group, as pointed out by Nel et al. (2001).

272

273 FAMILY UNCERTAIN

274 GENUS *MOLTENOPHLEBIA* GEN. NOV.

275

276 *Type species*

277 *Moltenophlebia lindae* gen. et sp. nov.

278

279 *Diagnosis*

280 By monotypy, as for the type species

281

282 *Etymology*

283 The name derives from that of the geological Formation and from ‘phlebia’, itself derived

284 from the Ancient Greek ‘phlebos’ (vein).

285

286 *Remarks*

287 The genus *Moltenophlebia* can be confidently assigned to the Discoidalia owing to the

288 occurrence of the pons. It can be further assigned to the Zygophlebiida owing to the occurrence

289 of the diagnostic character states of this taxon (see above).

290

291 *MOLTENOPHLEBIA LINDAE* GEN. ET SP. NOV.

292 (FIGS. 2–4)

293

294 *Type specimens*

295 Holotype: PRE/F/20522 (negative imprint). Paratypes: PRE/F/10626 (negative and positive

296 imprints), PRE/F/10615 (negative and positive imprints).

297

298 *Diagnosis*

299 CuA-CuP fork located basal to the pillar (i.e., CuP not capturing the pillar; putative
300 plesiomorphy within Zygophlebiida; see section 5.1); RP4 branched (putative plesiomorphy
301 within Zygophlebiida; see *Remarks* section).

302

303 *Occurrence*

304 All the specimens are from Aasvoëlberg locality (locality code "Aas 411"; see Anderson and
305 Anderson, 1984), Karoo Basin, South Africa; Molteno Formation; Carnian, Triassic (Anderson
306 et al., 1998).

307

308 *General description*

309 Wing total length and maximum width unknown (about 98 mm, and 23 mm respectively when
310 considering the reconstructions); wing broad with numerous small cells, slightly petiolate,
311 narrowing from the second third of the wing to the apex; ScP fused with the anterior wing
312 margin at the first third of the wing; many antenodal cross-veins; RA parallel to the anterior wing
313 margin distal to the nodus, with a single row of cell between the two; RP+MA diverging
314 obliquely from RA basal to the second antenodal cross-vein; RP+MA divided in RP and MA
315 distal to the second antenodal cross-vein; RP divided into RP1+2 and RP3+4 basal to the nodus
316 (inferred from preserved parts of the holotype); Irp₁₋₂, RP2 and Irp_{1+2-rp3+4} fused for some
317 distance, forming a 'rectilinear convex stem' parallel to RP1 and seemingly diverging from this
318 vein just distal to the nodus; Irp₁₋₂ and RP2 diverging shortly after the wing mid-length;
319 Irp_{1+2-rp3+4} diverging obliquely from the 'rectilinear convex stem' at wing mid-length; RP2

320 diverging obliquely from the 'rectilinear convex stem' further distally; areas between RP1 and
321 Irp_1-rp_2 , and between RP2 and $Irp_{1+2}-rp_{3+4}$ with a single row of cells; RP2 with at least two
322 branches (some of the concave veins located between Irp_1-rp_2 and RP2, visible in PRE/F/10626,
323 might actually be branches of RP2, as in Zygophlebiidae); RP3+4 divided in RP3 and RP4 at the
324 two-third of the wing length, each with at least two branches; area between RP4 and MA with a
325 single row of cells; MA with a strong angle when dividing from RP; presence of a convex pons
326 aligned with the RP+MA and the basal portion of MA; MA and MP close and parallel to each
327 other basal to the nodus, diverging distal to it, and converging close to their endings; area
328 between MA and MP ranging from one row of cells up to four; a cross-vein occurring in the area
329 between R+MA and MP, basal to the first antenodal cross-vein; MP with no evident fork, but
330 delimiting a large area filled with several concave branches (intercalaries?) and convex
331 intercalaries, subparallel; Cu close to the posterior wing margin at the end of the petiole; Cu
332 divided into CuA and CuP at the level of the point of divergence of RA and RP+MA; CuA and
333 CuP parallel with one row of cells between them, occasionally divided into two cells in a same
334 wing; CuP with no evident fork, but delimiting an area filled with several concave branches
335 (intercalaries?) and convex intercalaries, subparallel.

336

337 *Specimen description*

338 Holotype specimen PRE/F/20522 (Figs. 2A and 3A): Left wing, almost complete, apex and
339 posterior wing margin missing; preserved length 79.6 mm, maximum width 19.6 mm; CuA and
340 CuP more bent than in the specimen PRE/F/10626.

341 Paratype specimen PRE/F/10626 (Figs. 2B, 3B): Two-third of a right wing, antero-basal
342 third and apex missing; preserved length 74.7 mm, maximum width 20.6 mm; posterior wing
343 margin and distal portions of RP2, RP3 and RP4 branches preserved.

344 Paratype specimen PRE/F/10615 (Figs. 2C, 3C): Two broken segments of a left wing, the
345 base and a part of the third quarter; preserved length 19.2 mm, maximum width 34 mm.

346

347 *Etymology*

348 The name is dedicated to Linda Terblanche, who allowed access to the site where the fossils
349 were discovered.

350

351 *Remarks*

352 There is virtually no doubt that the specimens PRE/F/20522 (holotype) and PRE/F/10626
353 (paratype) are conspecific. Our reconstruction suggests that the former is slightly broader, but
354 this could represent differences between a hind wing and a forewing, and/or sexual dimorphism.
355 The specimen PRE/F/10615 can be attributed to the same species thanks to the presence of a
356 convex pons aligned with the RP+MA and the basal portion of MA, and also the CuA-CuP split
357 located basally (at the level of the point of divergence of RA and RP+MA). It is also very similar
358 in size with the two other specimens.

359 The occurrence of a cross-vein in the area between R+MA and MP near the wing base,
360 observed in the holotype specimen is unusual for the group. It is not unlikely that it represents a
361 rare, uncommon feature for the species (it could then be an atavism).

362 In the Zygophlebiida and more generally in Triadophlebiomorpha MP is distinct from Cu at
363 the wing base (the two veins then remaining fused for some distance). This character state is

364 plesiomorphic, being observed in the earliest odonates (Riek and Kukalová-Peck, 1984). In our
365 reconstruction we therefore assumed that *Moltenophlebia lindae* displayed this state.

366 Within the Zygophlebiida, the new species can neither be attributed to the
367 Xamenophlebiidae nor to the Permophlebiidae, as it lacks the diagnostic characters of these
368 families as delimited by Nel et al. (2001). The family Zygophlebiidae currently lacks a diagnosis
369 (Bechly, 1996; Nel et al., 2001). The family currently contains four genera, from which
370 *Moltenophlebia lindae* differs in many aspects, including a RP2 branched close to the posterior
371 wing margin (whereas RP2 is widely developed in known Zygophlebiidae genera). Also, in the
372 new species both RP3 and RP4 are branched (as in Triadotypomorpha, suggesting that this state
373 is a plesiomorphy; see Pritykina, 1981; Nel et al., 2001). The resulting wide area (between RP3
374 and RP4) is also present in *Mixophlebia mixta* Pritykina, 1981, but RP4 is simple in this species.
375 The observed differences justify the erection of a new genus. However, given uncertainties on
376 the occurrence of several character states in various genera of Zygophlebiidae, and on the
377 polarity of several character states, we refrained from erecting a new family to accommodate
378 *Moltenophlebia*.

379

380 5. Discussion

381

382 5.1. Nature of the pillar

383 In Zygophlebiidae, the portion of the pillar located between CuP and the posterior wing
384 margin has been interpreted as a branch of AA by Pritykina (1981) and Bechly (1996), and AA
385 by Nel et al. (2001) and Zheng et al. (2017) (Fig. 4A). It implies that CuP and AA (or one of its
386 branches) form a composite stem from the CuA-CuP split. However, the condition displayed by

387 *Moltenophlebia lindae*, previously undocumented for Zygophlebiida, provides a new perspective
388 on this particular aspect of wing venation homology conjectures. Instead of possessing a single,
389 convex stem in the area delimited by MP, the pillar and the posterior wing margin,
390 *Moltenophlebia lindae* displays a convex stem but also another, conspicuously concave one
391 (green arrow in Fig. 4B; and see Fig. 3C), the latter likely being CuP free from any other vein (a
392 configuration similar to that of Archizygoptera; Nel et al., 2012). It strongly suggests that the
393 pillar, in *Moltenophlebia lindae*, is exclusively composed of strengthened cross-veins (as
394 represented in Fig. 4D).

395 In turn, an alternative interpretation of the wing venation homology of other Zygophlebiidae,
396 consistent with this observation, can be proposed. In the petiole of *Zygophlebia tongchuanensis*,
397 a short vein-like element occurs in the area between the posterior wing margin and the vein
398 immediately anterior to it, between the point of fusion of MP with Cu+AA and the point of
399 divergence of MP. It was interpreted as a cross-vein by Zheng et al. (2017; Fig. 4A) but another
400 plausible interpretation is that it is AA (Fig. 4C), which would then end earlier than previously
401 assumed. It must be emphasized here that such early ending of AA has been conjectured for
402 many other members of Discoidalia, including members of the triasolestid assemblage, regarded
403 as closely related to the crown-group of Odonata (Nel et al., 2002; Tierney et al., 2020) . In other
404 words, this conjecture is very plausible. Then, the pillar is composed of (i) a very oblique portion
405 of CuP and (ii) a strengthened cross-vein. With respect to the configuration in *Moltenophlebia*
406 *lindae* (Fig. 4D), it can then be hypothesized that the CuA-CuP split is located more distally in
407 *Zygophlebia tongchuanensis* (Fig. 4E) and in other Zygophlebiidae, to the point where CuP fuses
408 with the portion of the pillar previously located between it and CuA (i.e., CuP captures the first
409 cross-vein forming the pillar). Cross-veins forming the pillar being overall convex (Fig. 4B), this

410 elevation was likely imposed to CuP. This interpretation likely applies to the entire
411 Zygophlebiida. The state ‘CuA-CuP split located basally’ is present in stem-Odonata more
412 ancient than Zygophlebiida, including the Meganisoptera (see (Nel et al., 2009)) and the
413 ‘geropteromorphs’ (see Riek and Kukalová-Peck, 1984).

414

415

416

417 5.2. *Triassic Gondwanian Odonata*

418 Within early-diverging stem-Odonata (and, more specifically, within the Discoidalia), the
419 Triadophlebiomorpha were greatly diversified and widely distributed across Europe and Asia
420 during the Triassic (Nel et al., 2001; Pritykina, 1981; Zheng et al., 2017). The new species,
421 *Moltenophlebia lindae*, can be confidently assigned to one of the main lineages of this taxon,
422 namely the Zygophlebiida. It therefore represents the first ascertained occurrence of the
423 Triadophlebiomorpha in the Gondwana. This discovery concurs with previous accounts
424 suggesting that major groups of Triassic Odonata had a worldwide distribution. The Triassic,
425 Australian *Iverya averyi* Béthoux and Beattie, 2010, initially regarded as a Triadotypomorpha
426 (see original description) but which actually occupies an uncertain position within the
427 Discoidalia (Deregnacourt et al., 2017), already indicated similarities between Laurasian and
428 Gondwanian faunas of stem-Odonata. Moreover, a representative of another group of stem-
429 Odonata, the Triadotymorpha, well-documented from Europe and Asia (Bechly, 1997; Béthoux
430 et al., 2009; Laurentiaux-Vieira et al., 1952; Pritykina, 1981; Reis, 1909) also occurred at
431 Molteno (Deregnacourt et al., 2017). Even the gracile, damselfly-like Protomyrmeleontoidea
432 Handlirsch, 1906, which dispersal capabilities might have been more limited than those of larger,

433 contemporaneous stem-Odonata, have been documented from Triassic outcrops in Australia
434 (Henrotay et al., 1997; Tillyard, 1922) and also from Molteno (Deregnacourt et al., 2021). In
435 summary, this South African outcrop testifies to a great diversity of Triassic Odonata in the
436 Gondwana, and to a widespread distribution of the main lineages of Odonata during this period.

437

438 **Authors contributions**

439 **Isabelle Deregnacourt:** Conceptualization, Data curation, Formal analysis, Investigation,
440 Methodology, Visualization, Writing — original draft. **Jérémie Bardin:** Conceptualization,
441 Formal analysis, Investigation, Methodology, Supervision, Writing — review & editing. **John**
442 **M. Anderson:** Resources, Writing — review & editing. **Olivier Béthoux:** Conceptualization,
443 Investigation, Funding acquisition, Supervision, Visualization, Writing — review & editing.

444

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459

460 **References**

461 Adams, D.C., Otárola-Castillo, E., 2013. geomorph: an R package for the collection and analysis
462 of geometric morphometric shape data. *Methods in Ecology and Evolution* 4, 393–399.

463 Anderson, J.M., Anderson, H.M., 1984. The fossil content of the Upper Triassic Molteno
464 Formation, South Africa. *Palaeontologia Africana* 25, 39–59.

465 Anderson, J.M., Anderson, H.M., Cruickshank, A.R.I., 1998. Late Triassic Ecosystems of the
466 Molteno/Lower Elliot Biome of Southern Africa. *Palaeontology* 41, 387–421.

467 Bechly, G., 1996. Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und
468 deren Stammgruppenvertreter (Insecta; Pterygota; Odonata) unter besonderer
469 Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata
470 [revised edition including appendix in English]. *Petalura Special Volume* 2, 1–402.

471 Bechly, G., 1997. New fossil odonates from the Upper Triassic of Italy, with a redescription of
472 *Italophlebia gervasuttii*, and a reclassification of Triassic dragonflies (Insecta: Odonata).
473 *Rivista del Museo civico di Scienze Naturali "Enrico Caffi"* 19, 31–70.

474 Béthoux, O., 2015. The Late Carboniferous *Triplosoba pulchella* is not a fly in the ointment but a
475 stem-mayfly. *Systematic Entomology* 40, 342–356.

476 Béthoux, O., Beattie, R.G., 2010. *Iverya averyi* gen. nov. & sp. nov., a new triadotypomorphan
477 species from the Middle Triassic at Picton, New South Wales, Australia. *Acta Geologica*
478 *Sinica* 84, 688–692.

479 Béthoux, O., de la Horra, R., Benito, I.M., Barrenechea, J.F., Galán, A.B., López-Gómez, J.,
480 2009. A new triadotypomorphan insect from the Anisian (Middle Triassic),
481 Buntsandstein facies, Spain. *Journal of Iberian Geology* 35, 179–184.

482 Bookstein, F.L., 1989. Principal warps: thin-plate splines and the decomposition of
483 deformations. *IEEE Transactions on Pattern Analysis and Machine Intelligence* 11, 567–
484 585.

485 Deregnacourt, I., Wappler, T., Anderson, J.M., Béthoux, O., 2017. A new triadotypid insect
486 from the Late Triassic of South Africa. *Acta Palaeontologica Polonica* 62, 613–618.

487 Deregnacourt, I., Wappler, T., Anderson, J.M., Béthoux, O., 2021. The wing venation of the
488 *Protomyrmeleontidae* (Insecta: Odonoptera) reconsidered thanks to a new specimen
489 from Molteno (Triassic; South Africa). *Historical Biology* 33, 306–312.

490 Fabricius, J.C., 1793. *Entomologia systematica emendata et aucta. Secundum classes, ordines,*
491 *genera, species adjectis synonymis, locis, observationibus, descriptionibus. Tome 2.* Proft,
492 C. G., Copenhagen.

493 Gunz, P., Mitteroecker, P., 2013. Semilandmarks: a method for quantifying curves and surfaces.
494 *Hystrix It. J. Mamm.* 24, 103–109.

495 Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G.W., Bookstein, F.L., 2009. Principles for the
496 virtual reconstruction of hominin crania. *Journal of Human Evolution* 57, 48–62.

497 Handlirsch, A., 1906. *Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein*
498 *Handbuch für Paläontologen und Zoologen.* Wilhelm Engelmann, Berlin.

499 Henrotay, M., Nel, A., Jarzembowski, E.A., 1997. New *Protomyrmeleontidae* damselflies from
500 the Triassic of Australia and the Liassic of Luxembourg. *Odonatologica* 26, 395–404.

501 Hoffmann, J., Donoughe, S., Li, K., Salcedo, M.K., Rycroft, C.H., 2018. A simple
502 developmental model recapitulates complex insect wing venation patterns. PNAS 115,
503 9905–9910.

504 Lameere, A., 1922. Sur la nervation alaire des insectes. Bulletin de la Classe des Sciences de
505 l’Académie Royale de Belgique 8, 138–149.

506 Lameere, A., 1923. On the wing-venation of insects. Psyche 30, 123–132.

507 Laurentiaux-Vieira, F., Ricour, J., Laurentiaux, D., 1952. Un Protodonate du Trias de la Dent de
508 Villard. Bulletin de la Société Géologique de France, (6) 1, 319–324.

509 Murrell, P., 2009. Importing vector graphics: The grImport package for R. Journal of Statistical
510 Software 30, 1–37.

511 Nel, A., Béthoux, O., Bechly, G., Martínez-Delclòs, X., Papier, F., 2001. The Permo-Triassic
512 Odonoptera of the “protodonate” grade (Insecta: Odonoptera). Annales de la Société
513 Entomologique de France (N.S.) 37, 501–525.

514 Nel, A., Fleck, G., Garrouste, R., Gand, G., Lapeyrie, J., Bybee, S.M., Prokop, J., 2009. Revision
515 of Permo-Carboniferous griffenflies (Insecta: Odonoptera: Meganisoptera) based upon
516 new species and redescription of selected poorly known taxa from Eurasia.
517 Palaeontographica Abteilung A 289, 89–121.

518 Nel, A., Marie, V., Schmeissner, S., 2002. Revision of the Lower Mesozoic dragonfly family
519 Triassolestidae Tillyard, 1918 (Odonata: Epiproctophora). Annales de Paléontologie 88,
520 189–214.

521 Nel, A., Papier, F., Stamm-Grauvogel, L., Gall, J.-C., 1996. Voltzialesstes triasicus, gen. nov., sp.
522 nov., le premier Odonata Protozygoptera du Trias inférieur des Vosges (France).
523 Paleontologia Lombarda, (N.S.) 5, 25–36.

- 524 Ogihara, N., Amano, H., Kikuchi, T., Morita, Y., Hasegawa, K., Kochiyama, T., Tanabe, H.C.,
525 2015. Towards digital reconstruction of fossil crania and brain morphology.
526 *Anthropological Science* 123, 57–68.
- 527 Pritykina, L.N., 1981. Novye triasovye strekozy srednej Azii. In: Vishniakova, V.N., Dlussky,
528 G.M., Pritykina, L.N. (Eds.), *Novye Iskopaemye Nasekomye s Terrotorii SSSR. Trudy*
529 *Paleontologicheskogo instituta, Akademiya Nauk SSSR*, 183, Moscow, pp. 5–42.
- 530 Reis, O.M., 1909. *Handlirschia gelasii* nov. gen. et spec. aus dem Schaumkalk Frankens.
531 *Abhandlungen der Koeniglich Bayerischen Akademie der Wissenschaftern,*
532 *Mathematisch-Physikalischen Klasse* 23, 659–694.
- 533 Riek, E.F., Kukalová-Peck, J., 1984. A new interpretation of dragonfly wing venation based
534 upon Early Upper Carboniferous fossils from Argentina (Insecta, Odonatoidea) and basic
535 character states in pterygota wings. *Canadian Journal of Zoology* 62, 1150–1166.
- 536 Rohlf, F.J., Slice, D., 1990. Extensions of the Procrustes Method for the Optimal
537 Superimposition of Landmarks. *Syst Biol* 39, 40–59.
- 538 Schlager, S., 2017. Morpho and Rvcg – Shape Analysis in R. In: *Statistical Shape and*
539 *Deformation Analysis*. Elsevier, pp. 217–256.
- 540 Sharov, A.G., 1968. Filogeniya orthopteroidnykh nasekomykh. *Trudy Paleontologicheskogo*
541 *instituta, Akademiya Nauk SSSR* 118, 1–216.
- 542 Sharov, A.G., 1971. *Phylogeny of the Orthopteroidea*. Israel Program for Scientific Translations,
543 Jerusalem.
- 544 Tierney, A., Deregnacourt, I., Anderson, J.M., Tierney, P., Wappler, T., Béthoux, O., 2020. The
545 Triassic Mesophlebiidae, a little closer to the crown of the Odonata (Insecta) than other
546 ‘triassolestids.’ *Alcheringa: An Australasian Journal of Palaeontology* 44, 279–285.

- 547 Tillyard, R.J., 1922. Mesozoic insects of Queensland. No. 9. Orthoptera, and additions to the
548 Protorthoptera, Odonata, Hemiptera and Plannipennia. Proceedings of the Linnean
549 Society of New South Wales 47, 447–470.
- 550 Voigt, S., Haubold, H., Meng, S., Krause, D., Buchantschenko, J., Ruckwied, K., Götz, A.E.,
551 2006. Die Fossil-Lagerstätte Madygen: ein Beitrag zur Geologie und Paläontologie der
552 Madygen-Formation (Mittel- bis Ober-Trias, SW-Kirgisistan, Zentralasien). Hallesches
553 Jahrbuch für Geowissenschaften 22, 85–119.
- 554 Wootton, R.J., Kukalová-Peck, J., 2000. Flight adaptations in Palaeozoic Palaeoptera. Biological
555 Review 75, 129–167.
- 556 Zheng, D.R., Nel, A., Wang, B., Jarzembowski, E.A., Chang, S.-C., Zhang, H.C., 2017. The first
557 Triassic ‘Protodonatan’ (Zygophlebiidae) from China: stratigraphical implications.
558 Geological Magazine 154, 169–174.

559

560 **Figures and Figure Captions**

561

562 **Fig. 1.** Flow-chart explaining the standardized method used to reconstruct the wing of specimen
563 PRE/F/20522. **A**, first step, reconstruction of specimen PRE/F/20522 with specimen
564 PRE/F/10626. **B**, second step, reconstruction of the firstly reconstructed wing of specimen
565 PRE/F/20522 with the holotype of *Zygophlebia ramosa* PIN 2785/20. GPA = generalised
566 Procrustes analysis; TPS = thin plate splines; squares correspond to process and circles to data.

567

568 **Fig. 2.** *Moltenophlebia lindae* gen. et sp. nov., from Carnian (Triassic) of Aasvoëlberg locality,
569 Molteno Formation, Karoo Basin, South Africa, line drawings. **A**, specimen PRE/F/20522 (left

570 wing; holotype). **B**, specimen PRE/F/10626 (right wing; paratype). **C**, specimen PRE/F/10615
571 (left wing). RA = anterior Radius; RP = posterior Radius; RP1+2 = anterior branch of RP (to be
572 further divided into RP1 and RP2); RP3+4 = posterior branch of RP (to be further divided into
573 RP3 and RP4); Irp₁₋₂ = intercalary vein between RP1 and RP2; Irp_{1+2-rp3+4} = intercalary vein
574 between RP1+2 and RP3+4; MA = anterior Media; MP = posterior Media; CuA = anterior
575 Cubitus; CuP = posterior Cubitus. Light lines were reconstructed.

576

577 **Fig. 3.** *Moltenophlebia lindae* gen. et sp. nov., from Carnian (Triassic) of Aasvoëlberg locality,
578 Molteno Formation, Karoo Basin, South Africa, photographs. **A**, specimen PRE/F/20522, left
579 wing (light-mirrored; holotype). **B**, specimen PRE/F/10626a, right wing (light-mirrored, flipped
580 horizontally; paratype). **C**, specimen PRE/F/10615a left wing (flipped horizontally). White frame
581 refers to Fig. 4B.

582

583 **Fig. 4.** Detail of the area of the pillar. **A**, *Zygophlebia tonchuanensis* Zheng, Nel, Wang,
584 Jarzembowski, Chang and Zhang, 2017, detail of holotype, homology conjectures by Zheng et al.
585 (2017). **B**, *Moltenophlebia lindae* gen. et sp. nov., detail of specimen PRE/F/20522, left wing
586 base (light-mirrored; holotype). **C**, as in **A**, except for the course of AA, following the homology
587 conjecture we favoured herein. **D–E**, simplified schemes of the respective positions of CuP and
588 of the pillar as in **B** and **D**, as favored herein. RA = anterior Radius; RP = posterior Radius; MA
589 = anterior Media; MP = posterior Media; CuA = anterior Cubitus; CuP = posterior Cubitus; AA
590 = anterior Analis; small white arrows (bordered in green -gray in grayscale version) indicate the
591 CuA-CuP split; in **A–C**, large black arrow indicates the pons, white arrows indicate the pillar; in

592 **B**, very large green arrow (grey in grayscale version) indicates the portion of CuP basal to the
593 pillar (and see Fig. 3A).







