

1 The evolution of Zoraptera

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19 20 Abstract

21 Zoraptera is one of the most enigmatic and least understood orders in insects. Based on
22 a wide taxon sampling from all continents where the group is known, we applied a
23 phylogenetic approach using multiple DNA sequences to elucidate species-level
24 relationships. The resulting phylogeny shows that Zoraptera is divided into three major
25 clades, and that two comprise species distributed on different continents. The
26 monophyly of these clades is at least partly supported by shared derived morphological
27 features. The divergence age estimation and ancestral distribution area reconstruction
28 suggest an ancient origin and early radiation initiated in the Permian. Plate tectonics
29 theory suggests that the present distribution of Zoraptera was mainly established by
30 vicariance, rather than dispersal. The three major clades likely originated on the
31 Pangaea supercontinent, or alternatively on the Gondwana and Laurasia
32 supercontinents. Their ancient origin explains previously found conspicuous
33 interspecific variation of the genital apparatus, sperm structure, and mating behaviour,
34 in striking contrast to a highly conserved general body morphology. We compiled data
35 of available reproductive features and reconstructed the character evolution. Our
36 analyses revealed repeated acquisitions and/or losses of a hyper-elongated intromittent
37 organ, mating hooks, and tergal protuberances.

38 39 Introduction

40 Zoraptera is the third smallest order in Insecta after Mantophasmatodea and
41 Grylloblattodea. The group is mainly distributed in subtropical and tropical regions
42 (Grimaldi & Engel, 2005; Beutel *et al.*, 2014; Mashimo *et al.*, 2014c; Choe, 2018). Its
43 phylogenetic position has been controversial (reviewed in Mashimo *et al.*, 2014c; Kjer
44 *et al.*, 2016; Beutel *et al.*, 2017), with consensus apparently reached recently with
45 Zoraptera being placed in a monophyletic Polyneoptera based on different sources of
46 evidence (Yoshizawa, 2011; Mashimo *et al.*, 2014a, 2015; Misof *et al.*, 2014; Wipfler &
47 Pass, 2014; Matsumura *et al.*, 2015; Wipfler *et al.*, 2019). Recently, Wipfler *et al.*
48 (2019) reconstructed the morphology of the common ancestor of Polyneoptera and

49 subsequent evolutionary developments, based on a robust phylogenetic hypothesis
50 congruent with Misof *et al.* (2014). They recovered Zoraptera as the sister group of
51 Dermaptera, and both orders were placed as sister to the rest of the polyneopteran
52 orders. They also postulated that the last common ancestor of Polyneoptera was ‘a
53 ground-dwelling insect with a largely unmodified body relative to the last common
54 ancestor of winged insects’ (Wipfler *et al.*, 2019). Considering the winged morphs of
55 Zoraptera (e.g., Friedrich & Beutel, 2008; Mashimo *et al.*, 2014c; Matsumura *et al.*,
56 2015), it is reasonable to postulate that extant species are relatively similar in their
57 morphology to the aforementioned ‘ancestral’ polyneopteran. The combination of
58 mostly plesiomorphic morphological features with few autapomorphies partly explains
59 the difficulty of placing this order phylogenetic context (Mashimo *et al.*, 2014c).

60 In contrast to the species diversity found in major polyneopteran orders (e.g.,
61 Phasmatodea, Mantodea, Blattodea, Orthoptera), to date only 44 extant species and 14
62 extinct species are described in Zoraptera (Mashimo *et al.*, 2018; Chen & Su, 2019).
63 Kukalová-Peck & Peck (1993) proposed six genera within Zoraptera based on the wing
64 venation. However, this character complex is known to vary even within a species
65 (Choe, 1989). Consequently, these genera were synonymized with *Zorotypus* by Engel
66 (2000) who considered ‘their homologies tenuous and their system unstable’. Likewise,
67 a genus described by Chao & Chen (2000) was similarly synonymized with *Zorotypus*
68 (Engel, 2000). Since then, Engel’s monogeneric classification has been widely accepted
69 (Rafael & Engel, 2006; Terry & Whiting, 2012; Mashimo *et al.*, 2013; Yin *et al.*, 2015;
70 Wang *et al.*, 2016; Choe, 2018). The described species of *Zorotypus* are relatively
71 small, typically less than 3 mm and live cryptically mainly in rotten trees. They lack any
72 conspicuous features with the exceptions of a very distinct dimorphism (apterous and
73 alate morphs) and extremely varying genitalia (Mashimo *et al.*, 2014c; Choe, 2018).
74 Considering the assumed reconstructed common ancestor of Polyneoptera (Wipfler
75 *et al.*, 2019), Zoraptera apparently have acquired a life style characterized by cryptic
76 habitats, gregarious behaviour and miniaturization. However, their evolutionary origin
77 and morphological transformations over time are still largely obscure.

78 The striking diversity of genital structures is in strong contrast to the external
79 homogeneity among species. The highly diversified male genitalia have been
80 investigated intensively, with detailed anatomical reconstructions (Hünefeld, 2007;
81 Matsumura *et al.*, 2014), but also in the framework of taxonomic studies (e.g., Gurney,
82 1938). In some species a spiral-shaped elongated male genital structure was reported
83 (e.g., Gurney, 1938; New, 1978, 2000; Mashimo *et al.*, 2013). To our best knowledge
84 this is a unique character state in Polyneoptera. Different types of elongation of the
85 intromittent organs are also known within Zoraptera, looped for instance in *Z.*
86 *zimmermani* (Gurney, 1939) and straight in *Z. barberi* (Gurney, 1938). Some species
87 possess asymmetrical genitalia (Gurney, 1938; Paulian, 1949, 1951; Hwang, 1974,
88 1976; Rafael & Engel, 2006; Hünefeld, 2007; Rafael *et al.*, 2008; Mashimo *et al.*, 2013,
89 2018; Wang *et al.*, 2016; Kočárek *et al.*, 2017; Yin & Li, 2017), in some species
90 remarkably differing in their specific features. Another conspicuously diversified
91 character system is the structure of elements of the terminal abdominal segment, the
92 presence or absence and size of spines and mating hooks (e.g., Gurney, 1938). This
93 variation may be related to the mating posture to some extent. Males are probably
94 connected to females by these terminal structures, laying in an upside-down position in
95 the majority of the species, in which the mating posture is known (Shetlar, 1978; Choe,
96 1994, 1995; Mashimo *et al.*, 2011; Dallai *et al.*, 2013). The disparity between a far-
97 reaching uniformity of the general morphology and an extreme diversity of genital

98 features is obviously a fascinating phenomenon and a challenging topic in evolutionary
99 biology. However, a reliable evaluation was not possible so far due to the lack of formal
100 phylogenetic analyses on the species level (see Engel, 2003).

101 The primary aim of our study is to reconstruct the phylogeny within Zoraptera
102 using molecular data. The taxon sampling covers species from all continents. The
103 evolutionary history is evaluated by means of divergent time estimation and based on
104 the plate tectonics theory (see Seton *et al.*, 2012). The character evolution with a special
105 focus on reproductive structures was reconstructed based on the phylogenetic trees.

106

107 **Materials and methods**

108

109 Most of the specimens were collected for this study and fixed with 80 – 99.5 % ethanol
110 (Fig. 1). Type specimens of *Z. novobritannicus* were borrowed from Arthropod
111 Collection, Brigham Young University, Provo, UT, USA. In total 31 individuals
112 belonging to 21-22 species were included (Fig. 2). We failed to trace the identity of
113 sample YK16-10 collected from Ecuador and named it as *Z. sp. 6*. We collected only *Z.*
114 *huxleyi* and *Z. hamiltoni* from the same locality at the same time, and *Z. sp. 6* likely
115 belongs to the latter species. Outgroups were selected from all polyneopteran orders and
116 some species from Psocodea, Hemiptera, Ephemeroptera, Odonata, Zygentoma and
117 Archaeognatha. The tree was rooted with Archaeognatha. The sequences of the
118 outgroup taxa were obtained from GenBank (metadata of the samples are listed in
119 Tables S1 and S2).

120

121 ***DNA extractions, amplifications, sequences and alignment***

122 Partial sequences of the following genes were used: nuclear 18S rRNA and Histone 3,
123 mitochondrial 16S rRNA and 12S rRNA. The following primers were used for
124 amplifying 18S (18S-Zora-f: 3'-ATT AAG CCA TGC AAG TGT CAG-5'; 18S-Zora-r:
125 3'-TTA RYA TAT GCT ATT GGW GCT GG-5'), Histone 3 (His3-Embryo-f: 3'-AAR
126 GCY CCW MGM AAR CAR CT-5'; His3-Embryo-r: 3'-TGR ATR GCR CAV AGR
127 TTR GTR TCY TC-5'), 16S (16Sbr: 3'-CCG GTC TGA ACT CAG ATC ACG T-5';
128 16Sar-Locust: 3'-CGC CTG TTT ATC AAA AAC AT-5') and 12S (12S-Zora-f: 3'-TGG
129 CGG YRW DWW RWT YTW TYR GRG G-5'; 12S-Zora-r: 3'-TTA CTM TYA AAT
130 CCA CCT TC-5'). Methods for DNA extraction, polymerase chain reaction
131 amplification, and sequencing followed Yoshizawa & Johnson (2008). Some faintly
132 amplified gene fragments were cloned prior to sequencing using the pGem-T Easy
133 Vector system (Promega, Madison, Wisconsin) following manufacturer protocols.
134 Alignment of protein coding genes was straightforward as no gap was identified in the
135 sequences. Ribosomal RNAs were aligned using MAFFT 6.5 (Katoh & Standley, 2013)
136 with the Q-INS-i option, in which secondary structure information of RNA is
137 considered. Apparent misalignments were corrected manually, and poorly aligned
138 regions were excluded from the analyses.

139

140 ***Model selection and phylogenetic estimation***

141 The best substitution models and partition schemes were estimated using
142 PartitionFinder 2.3.3 (Lanfear *et al.*, 2017), with the greedy algorithm. The codon
143 positions for Histone 3 (3 partitions) and rRNA (3 partitions) were predefined for the
144 PartitionFinder analyses. The best fit partition scheme and models were described in the
145 nexus formatted data matrix (Supplementary Data).

146 Previous studies showed that the phylogenetic relationships of polyneopteran
147 orders cannot be estimated accurately using a limited number of gene sequences (e.g.,
148 Kjer, 2004; Yoshizawa & Johnson, 2005; Ishiwata *et al.*, 2011; Misof *et al.*, 2014;
149 Wipfler *et al.*, 2019). Therefore, we constrained the phylogenetic relationships among
150 orders according to Misof *et al.*, (2014) and Wipfler *et al.*, (2019) for the following
151 phylogenetic analyses. In addition, unconstraint analyses were also performed to test the
152 monophyly of Zoraptera (see Supplementary Data).

153 We estimated a maximum likelihood tree using IQ-Tree 1.6.3 (Nguyen *et al.*,
154 2015), with 10,000 replicates of an ultrafast likelihood bootstrap with -bnni option
155 (Hoang *et al.*, 2018) to obtain bootstrap branch support values. To see the stability of
156 results, ten independent IQ-Tree analyses were performed. All the analyses resulted in a
157 concordant result, and we selected the tree obtained from the last run for Fig. 3. A
158 Bayesian analysis was performed using MrBayes (Ronquist & Huelsenbeck, 2003). We
159 performed two runs each with four chains for 1,000,000 generations, and trees were
160 sampled every 1,000 generations. The first 10% of sampled trees was excluded as burn-
161 in, and a 50% majority consensus tree was computed to estimate posterior probabilities.
162 Tracer in the BEAST software package (Bouckaert *et al.*, 2014) was used to check that
163 the MCMC runs reached a state of convergence.

164

165 ***Divergence time estimation***

166 For divergence date estimation, a Bayesian method was adopted using the software
167 MCMCtree in the PAML 4.8 software package (Yang, 2007) and BEAST 2.6
168 (Bouckaert *et al.*, 2014). The following fossil ages were used as soft minimum bounds
169 according to Misof *et al.* (2014) and Tong *et al.* (2015): 160 MYA for the deepest
170 divergence of Plecoptera; 130 MYA for the deepest divergence of Isoptera; and 99
171 MYA for the deepest divergence of Embioptera (Table 1). For all fossil calibrations, the
172 age of Rhynie chert (412 MYA) was used as the hard maximum bound according to
173 Evangelista *et al.* (2019). In addition, the hard maximum bound 450 MYA was also
174 adopted for Zygentoma-Pterygota divergence age according to Misof *et al.* (2014) and
175 Tong *et al.* (2015).

176 For the MCMCtree analysis, we first estimated the substitution rate prior using the
177 divergence date 419 MYA for the Polyneoptera - Paraneoptera branching according to
178 Tong *et al.* (2015). Based on the result, a gamma prior for the substitution rate was
179 estimated using baseml in the PAML software package. The GTR+G model was
180 adopted with an alpha = 0.5, which was a close approximation of the best substitution
181 model estimated by jModeltest (Posada, 2008) for entire dataset. We performed a run
182 for 1,000,000 generations, and the values were sampled every 50 generations. The first
183 10% of the obtained values were excluded for burn-in. We ran two independent
184 analyses to check that the MCMC runs reached a state of convergence (dos Reis *et al.*,
185 2017).

186 For the BEAST analysis, we used the Clade Ages package (Matchiner *et al.*, 2017).
187 The following options were selected: BEAST Model Test for the site model, Relaxed

188 clock Log Normal for the clock model, Birth-Death model for the priors. We performed
189 a run for 20,000,000 generations, and the first 10% of the obtained values were
190 excluded for burn-in. Tracer in the BEAST software package (Bouckaert *et al.*, 2014)
191 was used to check that the MCMC runs reached a state of convergence.

192

193 ***Biogeographical analysis***

194 Ancestral area reconstruction was performed using the dated tree obtained from the
195 MCMCtree analysis. Outgroup samples were excluded from the analysis. We used a
196 Dispersal-Extinction-Cladogenesis (DEC) model (from Lagrange: Ree & Smith, 2008)
197 as implemented in the software RASP 3.2 (Yu *et al.*, 2015). Dispersal-Vicariance
198 Analysis (DIVA: Ronquist, 1997) was a potential alternative to the DEC model.
199 However, a previous study showed that DIVA wrongly identifies ancestral areas with
200 complex patterns of dispersals and within-area speciation events (Kodandaramaiah,
201 2010). Five geographical realms were defined: Afrotropical, Indomalaysian, Nearctic,
202 Neotropical and Australasian. The maximum number of areas allowed for ancestral
203 distributions at each node was set to two, and dispersal between all pairs of
204 distributional areas was equally weighted. For extant species, there are no species
205 distributed in two or more biogeographical regions. The biogeographical region coding
206 of each sample was based on the known distributional range of the species.

207

208 ***Character evolution***

209 We focussed on the following eight features, (1) absence or presence of an elongated
210 intromittent organ, (2) symmetry of genitalia, (3) absence or presence of basal plate, (4)
211 absence or presence and size of mating hook, (5) absence or presence of records of
212 males, (6) absence or presence and size of protuberances on abdominal tergites 9-12, (7)
213 modifications of subgenital plate, and (8) absence or presence of hairy patch on vertex
214 ('fontanelle gland' in the literature). The relevant data are provided in many taxonomic
215 studies, and most of the information was obtained from the literature. If necessary, we
216 examined specimens under a stereomicroscope Olympus SZX12 (Olympus Corporation,
217 Tokyo, Japan) to obtain additional information. For an overview of the diversity focus
218 stacking images of the caudal view were taken using a stereomicroscope Leica M205 A
219 equipped with a camera Leica DFC420 and the software LAS 3.8 (Leica Microscopy
220 GmbH, Wetzlar, Germany). Relevant information for the outgroups was obtained from
221 the following studies: Tuxen (1970), Helm *et al.* (2011), and Klass *et al.* (2013).
222 Character evolution was reconstructed with the software Mesquite 3.6 (Maddison &
223 Maddison, 2018).

224

225 **Results**

226 ***Phylogeny, dating, and biogeography***

227 The aligned sequences consisted of 1753 bp (of which 75 bp were excluded from the
228 analyses), and the obtained maximum likelihood (ML) and Bayesian trees (Fig. 3,
229 suppl. Figs. 1 – 3) were congruent except for one weakly supported branch. Both
230 analyses, with and without constraining phylogenetic relationship among outgroup
231 orders (Misof *et al.*, 2014 and Wipfler *et al.*, 2019), did not yield different phylogenetic
232 relationships within Zoraptera (Fig. 3, Figs. S1 – S3). Therefore, the influence of the

233 analytical methods on the evolutionary history discussion is negligible, and we focussed
234 on the ML tree thereafter.

235 The monophyly of the order Zoraptera was strongly supported (100 % bootstrap
236 (BS), 1 posterior probability (PP)) (Figs. S1, S3) and it can be divided into three major
237 clades (Fig. 3). Clade 1 comprises five species from different continents: *Z. hubbardi*
238 (Nearctic: NA), *Z. impolitus* (Indomalaysia: IM), *Z. shannoni* (Neotropic: NT), *Z.*
239 *asymmetristernum* (Afrotropic: AF), and *Z. sp. 1* (AF) (Fig. 3). The ancestral
240 distribution areas of Zoraptera and clade 1 were not convincingly estimated (Fig. 4).
241 Clade 1 is estimated to have split around 270 Mya (210 – 385 Mya) from the rest and
242 diverged around 224 Mya (163 – 285 Mya) (Fig. 4). Within clade 1, *Z. hubbardi* (NA)
243 and *Z. impolitus* (IM) separated 155 Mya (89 – 225 Mya) (Fig. 4), and the ancestral area
244 remains uncertain (Fig. 4) as in the previous cases. *Z. shannoni* (NT) derived 85 Mya
245 (42 – 143 Mya) from a common ancestor with *Z. asymmetristernum* (AF). The ancestral
246 distribution of the clade including *Z. sp.1* (Afrotropic: AF) was presumed as either
247 Afrotropic + Neotropic (77.15 %) or only Afrotropic (22.85 %) (Fig. 4).

248 Clades 2 and 3 were estimated to have diverged around 236 Mya (179 – 295 Mya)
249 (Fig. 4), presumably in an area corresponding with the contemporary Neotropic region
250 (100 %). Clade 3 includes only *Z. barberi* (SA) among the included species, while clade
251 2 comprises the majority of species evaluated in our study (Fig. 3). Clade 2 diversified
252 around 183 Mya (134 – 238 Mya) (Fig. 4). The ancestral distribution was estimated as
253 either Neotropical (74.47 %) or the Indomalaysia + Neotropic regions (25.53 %) (Fig.
254 4). Clade 2 comprises three major lineages (Fig. 3). The first emerging clade 2c
255 comprises *Z. weidneri* (NT), *Z. brasiliensis* (NT), and *Z. huxleyi* (NT) (Fig. 3), with a
256 subclade of *Z. weidneri* and *Z. brasiliensis*. These species were estimated to have
257 diverged around 128 Mya (86 – 180 Mya) (Fig. 4) in the Neotropical region (Fig. 4).
258 The rest of clade 2 was estimated to have split 161 Mya (114 – 214 Mya). One
259 subgroup (clade 2a) diverged in the Neotropical region and the other (clade 2b) in
260 continents corresponding to the current Indomalaysian region + Australasia (35.33 %),
261 Indomalaysia (33.21 %), Indomalaysia + Neotropical region (26.23 %), or only the
262 Neotropical region (5.24 %) (Figs. 3, 4). The Neotropical clade (c2a) diverged around
263 103 Mya (64 – 155 Mya), and *Z. mexicanus* (NA) arose 30 Mya (14 – 56 Mya) (Fig. 4).
264 The origin of *Z. mexicanus* was estimated as the Nearctic + Neotropical regions.
265 *Zorotypus novobritannicus* (Australasian) was placed as sister to the Indomalaysian
266 group, and their divergence date was estimated as 138 Mya (94 – 190 Mya). The rest
267 diverged around 104 Mya (64 – 155 Mya) in the Indomalaysian region (Fig. 4).

268 The divergence age estimation based on a BEAST model (Fig. S4) showed very
269 similar results. The divergence ages of each node were estimated slightly older than
270 those obtained from a MCMCtree analysis, while the estimated divergence ages of clade
271 1 were younger. However, in all cases they largely overlapped.

272

273 ***Evolution of reproductive character states***

274 Based on our original observations and a literature survey, mainly from taxonomic
275 studies, information on the above mentioned eight characters related to reproduction
276 was available for the majority of the described species and is summarized in Table S3.
277 Consensus on structural homologization in zorapteran genitalia was not evident, and
278 researchers used different terminologies based on varying interpretations in the
279 literature. A reliable assessment of homologies is still pending, a point also emphasized

280 in Boudinot's (2018) first comprehensive synthesis of insect male genitalia. As this
281 turned out as too ambiguous for characters (3) and (6), they were not scored for
282 terminals outside of Zoraptera.

283 The maximum likelihood reconstruction was performed to estimate evolutionary
284 histories of the eight features (Figs. 5 and 6). Hyper-elongation of the intromittent organ
285 occurred at least twice, possibly even three times (Fig. 5A). Since clade 2a includes
286 many species with unknown character states, the independent occurrence of the spiral in
287 clades 2a and 2b is not conclusive. An asymmetric configuration of the genitalia is a
288 commonly observed feature in Polyneoptera (Huber *et al.*, 2007), but a symmetrical
289 condition is considered as ancestral for the group (Helm *et al.*, 2011; Boudinot, 2018).
290 The ancestral state of Zoraptera was likely symmetric according to our estimate (Fig.
291 5B). The asymmetric state was likely acquired in the ancestor of clade 1.

292 The last common ancestor of Zoraptera had likely acquired a mating hook, or at
293 least a small mating hook was present in the common ancestor of clades 2 + 3. Its
294 enlargement and modifications occurred independently in several lineages (Fig. 5C).
295 Modifications of the marginal area of the subgenital plate are known in some species
296 that form the monophyletic subunit *Z. shannoni* (NT) + *Z. asymmetristernum* (AF) + *Z.*
297 *sp. 1* (AF) of clade 1 (Fig. 5D). It is likely that a bifurcated margin has evolved in the
298 common ancestor, with subsequent transformation of the subgenital plate in *Z.*
299 *asymmetristernum*.

300 The presence or absence of a basal plate in the zorapteran ground-plan remains
301 equivocal (Fig. 6E), as the identity of the basal plate observed in species of clades 2 and
302 3 is not confirmed yet. However, it is clearly shown that the character states separate
303 clades 1 from 2 + 3. This implies that this character was either lost or completely
304 modified in clade 1, or alternatively newly developed in clade 2 + 3. The high diversity
305 among species is usually visible in caudal view of the abdomen (Fig. 7). Easily visible
306 differences among species are the presence or absence of protuberances of tergites 9-12,
307 and also different sizes of these structures. The homology of these protuberances was
308 completely unclear, and the evolutionary history was reconstructed based on data only
309 acquired from Zoraptera. Varying conditions of these surface structures were found in
310 different clades, and it seems that repeated acquisitions and losses occurred in Zoraptera
311 (Fig. 6F).

312 The lack of any records of males does not necessarily mean that the concerned
313 species are parthenogenetic. However, it is confirmed that females of *Z. brasiliensis*
314 (NT, c2c) and *Z. gurneyi* (NT) can reproduce parthenogenetically (Silvestri, 1947;
315 Choe, 1997). Our results must be considered as preliminary. However, it appears that
316 species with unknown males are not closely related, suggesting possible independent
317 losses (Fig. 6G), with parthenogenesis evolving several times independently in
318 Zoraptera. Courtship feeding through a hairy patch on the vertex is known in *Z. barberi*
319 (NT, c3) (Choe, 1995). The setal patches are known from several additional species
320 (Table S3). Although the presence of a gland is not confirmed, we mapped the
321 externally visible character state on the phylogeny. The ancestral state was likely absent,
322 and it appears likely that acquisitions occurred repeatedly (Fig. 6H).

323

324 Discussion

325 The present study confirms the monophyly of Zoraptera by means of formal
326 phylogenetic analyses based on a broad sampling of zorapteran species, as previously

327 shown by Yoshizawa & Johnson (2005). Traditionally, the following features including
328 reductions were considered as potential autapomorphies of the order Zoraptera: (1)
329 distinct dimorphism (apterous and alate morphs), (2) strongly simplified wing venation
330 and a capability of dropping the wings, (3) two-segmented tarsi without adhesive
331 structures, and (4) correlations of presence/absence of compound eyes, ocelli, and
332 distinct pigmentation (Beutel and Gorb, 2001; Beutel *et al.*, 2014; Mashimo *et al.*,
333 2014c). Holocentric chromosomes reported from *Z. hubbardi* (Nearctic: NA)
334 (Kuznetsova *et al.*, 2002) could also be another autapomorphy of Zoraptera. Comparing
335 with the reconstructed ground dwelling ancestor of Polyneoptera (Wipfler *et al.*, 2019),
336 which intuitively resembles a grasshopper, distinct miniaturization and partial structural
337 simplification must have occurred in the common ancestor of Zoraptera, possibly due to
338 the habitat specialization, a preference for subcortical spaces (under bark) of fallen trees
339 where spatial size is extremely limited. Our molecular phylogenetic approach revealed
340 the further evolutionary history of Zoraptera.

341

342 *Phylogeny, Dating & Biogeography*

343 The results of our analyses of molecular data suggest that extant Zoraptera form three
344 major clades. The early splits presumably occurred in the early Permian (Fig. 3) or
345 possibly the Carboniferous period (Fig. S5), when the continents were united as
346 Pangaea, or at least a connection existed between the supercontinents Gondwana and
347 Laurasia (Smith *et al.*, 2004). The heterogeneous distribution ranges found in clades 1
348 and 2 may be mainly due to their old origin and subsequent vicariance between the
349 contemporary continents.

350 Most species of clade 1, i.e., *Z. hubbardi*: (Nearctic: NA), *Z. impolitus*
351 (Indomalaysia: IM), *Z. shannoni* (Neotropic: NT), *Z. sp.1* (Afrotropic: AF), and *Z.*
352 *asymmetristernum* (AF), presumably originated before the continents rifted around 80-
353 100 Mya (Seton *et al.*, 2012). The split of *Z. hubbardi* (NA) and *Z. impolitus* (IM)
354 occurred in the early Jurassic, when Laurasia still existed (Seton *et al.*, 2012). The rest
355 of clade 1 diverged in the late Cretaceous, and the ancestral distribution was estimated
356 to be Afrotropic + Neotropic, which corresponds to Gondwana (Seton *et al.*, 2012). The
357 break-up of Pangaea probably took place in the Jurassic and Cretaceous (100 – 160
358 Mya: Seton *et al.*, 2012), and this may explain the split of the two lineages of clade 1.
359 The split of *Z. shannoni* (NT) and *Z. asymmetristernum* (AF) (85 Mya) is possibly also
360 a result of vicariance. Although the contemporary Neotropical and Afrotropical regions
361 had probably rifted around 100 Mya (Seton *et al.*, 2012), the estimated divergence age
362 contains an estimation error. However, it is also possible that the two species arose in
363 the Afrotropical region and *Z. shannoni* dispersed by drifting through the South Atlantic
364 Ocean, and indeed the divergence age estimated by a BEAST analysis was relatively
365 young (24 MYA).

366 The split between clades 2 and 3 was estimated around 236 Mya, and clade 2
367 diverged around 183 Mya. The first split likely occurred in the regions corresponding to
368 the contemporary Neotropical region. This happened before the separation of
369 Gondwana and Laurasia (Smith *et al.*, 2004; Seton *et al.*, 2012). Therefore, it is
370 conceivable that the ancestral species was distributed in the corresponding southern part
371 of Pangaea. Clade 2 includes three major lineages (c2a, c2b, and c2c), and clade 2b
372 comprises solely of Indomalaysian and Australasian species. This lineage arose
373 presumably 161 Mya and diverged 138 Mya. During this period, it is assumed that the
374 Indian subcontinent + Australasia started to rift from Gondwana, and Australasia started

375 to separate from the Indian subcontinent 120 Mya (Seton *et al.*, 2012). The time of the
376 zorapteran radiation and continental breakup is an estimation and prone to errors. Our
377 estimations did not always suggest that speciation and lineage splits occurred before the
378 estimated continental breakup. However, considering the above-mentioned
379 comprehensive information, the species distribution can be explained by vicariance
380 rather than by dispersal. Consequently, it can be assumed that the speciation mainly
381 occurred on individual continents. The only exception among the studied species is *Z.*
382 *mexicanus* (Nearctic: NA, c2a), whose origin was dated as 30 Mya. The formation of
383 the Panama-Costa Rica Arc is estimated around 60 – 90 Mya (different hypotheses are
384 discussed in Seton *et al.*, 2012). This suggests that *Z. mexicanus* (NA) is derived from
385 the South American lineage, which invaded into the Central America after the formation
386 of the Arc.

387 The early Permian origin of the major zorapteran lineages explains the enormous
388 disparity of the mating behaviour (Choe, 1994, 1995; Dallai *et al.*, 2013) as well as the
389 impressive variation in the genitalia and sperm morphology among species (Dallai *et*
390 *al.*, 2011, 2012, 2014a, b). The recently observed external sperm transfer of *Z. impolitus*
391 (IM, c1) (Dallai *et al.*, 2013) was the first report for a pterygote insects. The exceptional
392 divergence of characters linked to reproduction stands in stark contrast to a far-reaching
393 uniformity in the general body morphology, which is preserved since the late Palaeozoic
394 for reasons not yet understood. Similar phenomena did not evolve in other groups with
395 an origin in the same period, for instance in the presumptive sister taxon Dermaptera.
396 Sperm morphology can be useful for estimation of phylogenetic relationships in some
397 cases (Gottardo *et al.*, 2016). Dallai *et al.* (2014a, b) proposed a hypothesis for sperm
398 evolution in Zoraptera suggesting that (i) those species used in Dallai *et al.* (2011, 2012,
399 2014a, b) arose before the fragmentation of Gondwana in the mid Cretaceous period
400 (the time was estimated due to available fossil records, e.g., Poinar Jr, 1988; Engel &
401 Grimaldi, 2002; Kaddumi, 2005), (ii) that *Z. caudelli* (IM, c2b), *Z. magnicaudelli* (IM,
402 c2b), *Z. huxleyi* (NT, c2c), and *Z. weidneri* (NT, c2c) form a monophyletic unit, and (iii)
403 that *Z. shannoni* (NT, c1), *Z. hubbardi* (NT, c1), and *Z. impolitus* (IM, c1) definitely
404 belong to different lineages. Mashimo *et al.* (2015) also found a possible
405 synapomorphic feature of eggs of *Z. impolitus* (IM, c1) and *Z. hubbardi* (NA, c1). These
406 interpretations are congruent with our molecular phylogeny and corroborate our
407 evolutionary hypotheses.

408

409 *Classification*

410 All extant species of Zoraptera are now classified under the single genus *Zorotypus*. The
411 ancient origin, genetic divergence, and the unusual diversity of genitalia and sperm
412 arguably suggest a division into several supraspecific subunits. As mentioned in the
413 introduction, Kukalová-Peck & Peck (1993) established six genera based on the wing
414 venation and biogeographic distribution (Old v.s. New World). However, only one Old
415 World zorapteran was included in their study, and phylogenetic relationships among the
416 studied species was not reconstructed with a formal approach (Kukalová-Peck & Peck,
417 1993). In addition to this, Chao & Chen (2000) established another Old World genus
418 from Taiwan due to an unusual appearance. The taxonomic treatments of Kukalová-
419 Peck & Peck (1993) and Chao & Chen (2000) did not meet the criteria for the erection
420 of supraspecific taxa outlined by Komarek & Beutel (2006), especially the claim that all
421 supraspecific units (not only the newly erected one) should be monophyletic. Our
422 results also clearly reject the idea that the biogeographic distribution of Zoraptera is

423 useful for the classification of the order. Nevertheless, the concept of Kukalová-Peck &
424 Peck (1993) appears at least partly justified. Four of the six included species were also
425 analyzed in our study, i.e. *Z. barberi* (NT, c3), *Z. brasiliensis* (NT, c2c), *Z. caudelli*
426 (IM, c2b), and *Z. hubbardi* (NT, c1), each of them designated as type species of a
427 separate genus in Kukalová-Peck & Peck (1993). These species were recovered each in
428 different lineages in our analyses, and clade 1 including *Z. hubbardi* (NT, c1) showed
429 specific trends of character state evolution as discussed below in detail. Clade 1 features
430 asymmetric genitalia, without a hyper-elongated intromittent organ and without a basal
431 plate. The asymmetric condition of this subunit is apparently an autapomorphy, and the
432 remaining species are also monophyletic. Therefore, we consider it is a potential option
433 to resurrect one of the genera proposed by Kukalová-Peck & Peck (1993).

434 For a further taxonomic step, the position of the type species of the genus
435 *Zorotypus*, i.e., *Z. guineensis* (AF, not included here) would have to be clarified. The
436 original description of Silvestri (1913) is relatively concise, but we cannot extract
437 sufficient information from it. Dallai *et al.* (2014b) re-evaluated Silvestri's study and
438 the original histological samples. They confirmed that males lack an elongated
439 intromittent organ. Although it is not explicitly mentioned, the figures show neither
440 asymmetric genital sclerites found in species of clade 1, nor any basal plate-like
441 structure typical of species of clade 2 + 3. Furthermore, Dallai *et al.* (2014b) discussed
442 that the male reproductive system (documented with histological sections) displays
443 features likely similar to conditions found in *Z. magnicaudelli* (IM, c2b), *Z. caudelli*
444 (IM, c2b) and *Z. huxleyi* (NT, c2c), rather than in *Z. hubbardi* (NA, c1) and *Z. impolitus*
445 (IM, c1). However, there are also features resembling those of species of clade 1. For
446 instance, features of the hind femur of *Z. guineensis* are very similar to that found in *Z.*
447 *shannoni* (NT, c1) (see Silvestri, 1913; Gurney, 1938), similarly the hairy area on the
448 vertex. Based on the evidence at hand *Z. guineensis* (AF) could belong to any clade
449 recognized in our study. Therefore, we refrain from further taxonomic steps in our
450 study.

451

452 *Morphological evolution*

453 Our analyses suggest independent origins of hyper-elongated intromittent organs, and
454 that these derived states originated from symmetric genitalia. From a morphological
455 point of view, this is also supported by obvious differences between the straight
456 elongated intromittent organ of *Z. barberi* (NT, c3) (Gurney, 1938) and the spiral-
457 shaped elongated one found in many species of Zoraptera (Table S3). However,
458 considering the very specific and complex anatomy of the male genital apparatus of *Z.*
459 *caudelli* (IM, c2b), studied in detail by Matsumura *et al.* (2014), it appears unlikely that
460 the type with a complex, spiral-shaped element has evolved several times
461 independently. The entire apparatus is exceptionally complicated, with structures of
462 unclear homology (e.g., *Z. hubbardi* (NA, c1)) (Hünefeld, 2007). Moreover, it is highly
463 unlikely that complex structures with very specific and complicated configurations have
464 repeatedly evolved in the same way in different species. The ambiguity of the scenario
465 is increased by species of clades 2a and 2b with males not known yet. Recently Rafael
466 *et al.* (2017) reported a gynandromorph of *Z. brasiliensis* (NT, c2c), whose males were
467 previously unknown, containing both male and female characteristics. They discussed
468 possible thelytokous parthenogenesis, with unfertilized eggs yielding females but not
469 males. As another example, *Z. gurneyi* produces males, but parthenogenetically
470 reproducing populations also occur (Choe, 1997). As Choe (2018) stated in a recent

471 review, divergent mating systems are exhibited even between sympatric species.
472 Therefore, it is still debatable whether the spiral was present or absent in the ground
473 plan of clade 2a + 2b. Additional lab and field-based observations of reproductive
474 modes from different populations are necessary as pointed out by Rafael *et al.* (2017).

475 Asymmetric genitalia appear to have evolved in clade 1. The homology of the
476 sclerites composing this type of genitalia is not clarified yet. However, using the
477 available literature (Table S3) we identified 14 out of 28 species with an asymmetric
478 genital apparatus. In the present study we treated asymmetric genitalia as one category,
479 even though structural differences were reported between *Z. hubbardi* (NA, c1) and *Z.*
480 *shannoni* (NT, c1) (illustrated in Gurney, 1938). Detailed morphological data on male
481 genitalia including musculature and related membranes are available for only two
482 species, *Z. hubbardi* and *Z. caudelli* (Hünefeld, 2007; Matsumura *et al.*, 2014).
483 Although zorapterans are rather small, technical problems caused by size reduction play
484 a minor role in state-of-the-art insect anatomy if at all (Friedrich *et al.*, 2014). New
485 detailed anatomical studies will likely help to clarify homology issues, and in a second
486 step to unveil the evolution of the genital structures. This also applies to symmetric
487 genitalia, not only to clarify the origin of the elongated intromittent organs, but also the
488 homology of the basal plate. This issue is related to the challenging interpretation of the
489 tergite numbering in Zoraptera, with distinctly different interpretations suggested by
490 various authors, as shown in columns B and F of the Table S3. Mashimo *et al.* (2014a,
491 b) elegantly established the tergite numbering for *Z. caudelli* (IM, c2b). Therefore, this
492 issue should be relatively easy to solve by carefully comparing abdominal segments for
493 representative species.

494 Structural diversity as typically seen in caudal view of the abdomen has seemingly
495 evolved through repeated development, retrogress, or loss of the mating hook and
496 protuberances on tergites 9-12. Presence of the mating hook is estimated as a possible
497 plesiomorphic state in our analyses. Although its function is not yet known, it may
498 indeed work as a hook during copulation. Except for the external sperm transfer of *Z.*
499 *impolitus* (IM, c1), the known mating posture is that males are coupled to a female
500 through the genitalia and lay upside down (*Z. hubbardi*: NA, c1, Gurney, 1938; *Z.*
501 *barberi*: NT, c3, Choe, 1995; *Z. gurnery*: NT, not included, Choe, 1994; *Z. huxleyi* & *Z.*
502 *weidneri*: NT, c2c, JAR, JTC, YM pers. obs.; *Z. caudelli*: IM, c2b, Mashimo *et al.*,
503 2011; *Z. magnicaudelli*: IM, c2b, Dallai *et al.*, 2013). Any clasping structure or hook
504 would probably be helpful for this type of mating posture. Therefore, it is surprising that
505 *Z. impolitus* has one of the most developed mating hooks (Mashimo *et al.*, 2013),
506 although they externally attach sperm to females (Dallai *et al.*, 2013). The mating hooks
507 might have an additional function, for example opening the female genitalia forcefully
508 to deposit a spermatophore in the female genital tract. This needs verification by
509 detailed observations of intertwining male and female genitalia. In addition,
510 characteristic mating behaviour is also reported in *Apachyus chartaceus* (Dermaptera:
511 Apachyidae) (Shimizu & Machida, 2011), it may prove worthwhile to compare their
512 genital coupling with that of zorapterans.

513 A function of the hairy patch on the male vertex in *Z. barberi* (NT, c3) is secreting
514 nutritious fluid for the females as a nuptial gift (Choe, 1995). Superficially similar
515 structures were observed in some studied species, and also in five out of 25 species with
516 information available in the literature (Table S3). Studies using histological sections of
517 the head of the relevant species are necessary to clarify the presence or absence of gland
518 tissue to confirm its function in the other species.

519 The knowledge on Zoraptera has increased rapidly in the last decade. However, for
520 further understanding the evolution of the group additional investigations are necessary.
521 Future studies should have a main focus on the detailed morphology of genital organs,
522 interactions of the male and female genitalia, mating behavior of each species, and
523 sperm morphology of representative species from additional early split clades, also
524 including the type species *Z. guineensis*.

525

526 **Data accessibility.** All supporting data are available as electronic supplementary
527 materials.

528 **Authors' contributions.** Y.M., R.G.B., K.Y. & J.A.R., J.T.C. conceptualized
529 independently, J.A.R., J.T.C., Y.M. and K.Y. collected samples, Y.M., I.Y. and K.Y.
530 performed molecular experiments. K.Y. analyzed molecular data, Y.M. and K.Y.
531 analyzed evolutionary histories, and all authors interpreted the results. Y.M. and K.Y.
532 wrote the draft and R.G.B., J.A.R., S.P.L., J.T.C. and I.Y. revised it. All authors
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560 field trips.

561

562

563

564 **Fig. 1.** Zorapteran species. A, *Z.* sp. from Costa Rica; B, *Z. asymmetristernum* from Kenya; C-
565 F, *Z. caudelli* from Malaysia. Photographs courtesy of T. Kanao (A) and T. Komatsu (B-F).

566

567 **Fig. 2.** Distribution pattern of the species used in our molecular phylogeny. Detailed location of
568 Brazilian samples shown in the inserted map.

569

570 **Fig. 3.** Constrained maximum likelihood tree estimated by IQ-TREE. Non polyneoptera orders
571 were omitted here. Asterisks on nodes indicate that they were constrained. Major clades in
572 Zoraptera highlighted with colored rectangles (see the text for details).

573

574 **Fig. 4.** Ancestral range reconstruction shown in a time-calibrated phylogeny of Zoraptera based on
575 Dispersal-Extinction-Cladogenesis (DEC) model. Topology based on ML analysis. Pie charts on
576 each node indicate the likelihood of the estimated ancestral area. Detailed statistics of the estimated
577 ancestral distribution is available in ES9 Fig. S5.

578

579 **Fig. 5.** Maximum likelihood ancestral state reconstructions of selected traits with a special focus
580 on reproductive characters of Zoraptera.

581

582 **Fig. 6** (continued). Ancestral state reconstructions based on most likelihood method of selected
583 traits with a special focus on reproductive characters of Zoraptera.

584

585 **Fig. 7.** Morphological diversity of the abdomen in caudal view. A, *Zorotypus hubbardi*; B, *Z.*
586 sp. 1. Cameroon YK2; C, *Z. mexicanus*; D, *Z. weidneri* Brazil; E, *Z.* sp. 6 Ecuador alt. 1000-
587 1200 m YK10, possibly *Z. hamiltoni*; F, *Z. huxleyi* Ecuador; G, *Z. cervicornis*; H, *Z. caudalli*; I,
588 *Z.* sp. 2 Vietnam alt. 1900 m YK15; J, *Z. novobritannicus*. Scale bars: 200 μ m.

589

590

591 Electronic supplements

592

593 ES1 Table S1. A list of species included in our molecular phylogeny analyses. BYUC:
594 Arthropod Collection, Brigham Young University, Provo, UT, USA; INPA: National Institute
595 of Amazonian Research, Brazil; YK PC: Y. Matsumura private collection at the Kiel Univ.,
596 Germany.

597

598 ES2 new Table S2. Metadata of the used specimens.

599

600 ES3 Fig. S1. Unconstrained maximum likelihood tree estimated by IQ-TREE. Major clades in
601 Zoraptera highlighted with colored rectangles (see the text for details).

- 602 ES4 Fig. S2. Constrained Bayesian tree. The phylogenetic relationships among the
 603 polyneopteran orders was constrained following Misof *et al.* (2014) and Wipfler *et al.* (2019).
 604
- 605 ES5 Fig. S3. Unconstrained Bayesian tree. Two nodes enclosed with dashed lines were not
 606 resolved into dichotomies.
 607
- 608 ES6 Table S4. A list of characters used in the study and known characters states from extant
 609 species. Species included in the current study highlighted with red.
 610
- 611 ES7. Nexus formatted combined file of molecular data matrix (four genes) used in this study,
 612 obtained ML and Bayesian trees, character matrix and a maximum likelihood tree used for
 613 the character evolution analyses. Characters: (1) presence of elongated intromittent organ,
 614 (2) symmetry of genitalia, (3) presence of basal plate, (4) presence and size of mating hook,
 615 (5) recorded occurrence (or absence) of males, (6) presence and size of protuberances on
 616 tergites 10-12, (7) subgenital plate, and (8) presence of hairy patch on vertex. For each
 617 character state, we used the following coding: **(1)** unknown: ?, elongated (type 1: straight): 1,
 618 elongated (type 2: spiral-shaped): 2, absent: 0, polymorphism (elongated: non categorized +
 619 absent): 3, **(2)** unknown: ?, symmetrical: 1, asymmetric: 0, polymorphism: 2, **(3)**
 620 unknown: ?, present: 1, absent: 0, **(4)** unknown:?, small: 1, relatively long: 2, two elongate
 621 mating hooks: 3, absent: 0, polymorphism: 4, **(5)** unknown: ?, males known: 1, males
 622 unknown: 0, polymorphism: 2, **(6)** unknown: ?, unmodified setae: 1, thick setae: 2, spines: 0,
 623 **(7)** unknown: ?, no modification: 0, bifurcated: 1, depression: 2, processes: 3, polymorphism
 624 (non-categorized protuberances + absent) : 4, **(8)** unknown: ?, present: 1, absent: 0.
 625
 626
- 627 ES8. Fig. S4 A time-calibrated phylogeny of Zoraptera estimated by BEAST analysis.
 628
- 629 ES9. Fig. S5. Ancestral range reconstruction shown in a time-calibrated phylogeny of Zoraptera
 630 based on Dispersal-Extinction-Cladogenesis (DEC) model, topology based on ML analysis. Pie
 631 charts on each node indicate the likelihood of the estimated ancestral area. Detailed statistics of
 632 the estimated ancestral distribution is listed. The main graphic is congruent with Fig. 4.

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886

887

888 Table 1. A list of used calibration fossils, including ages and min/max bounds.

Fossil taxon	Calibrated groups	Age (MYA)
<i>Pronemoura angustithorax</i>	Plecoptera	161.0 – 160.5
<i>Sorellembia estherae</i>	Embioptera	99.9
<i>Valditermes brennenae</i>	Isoptera	136.4 – 130.0

889

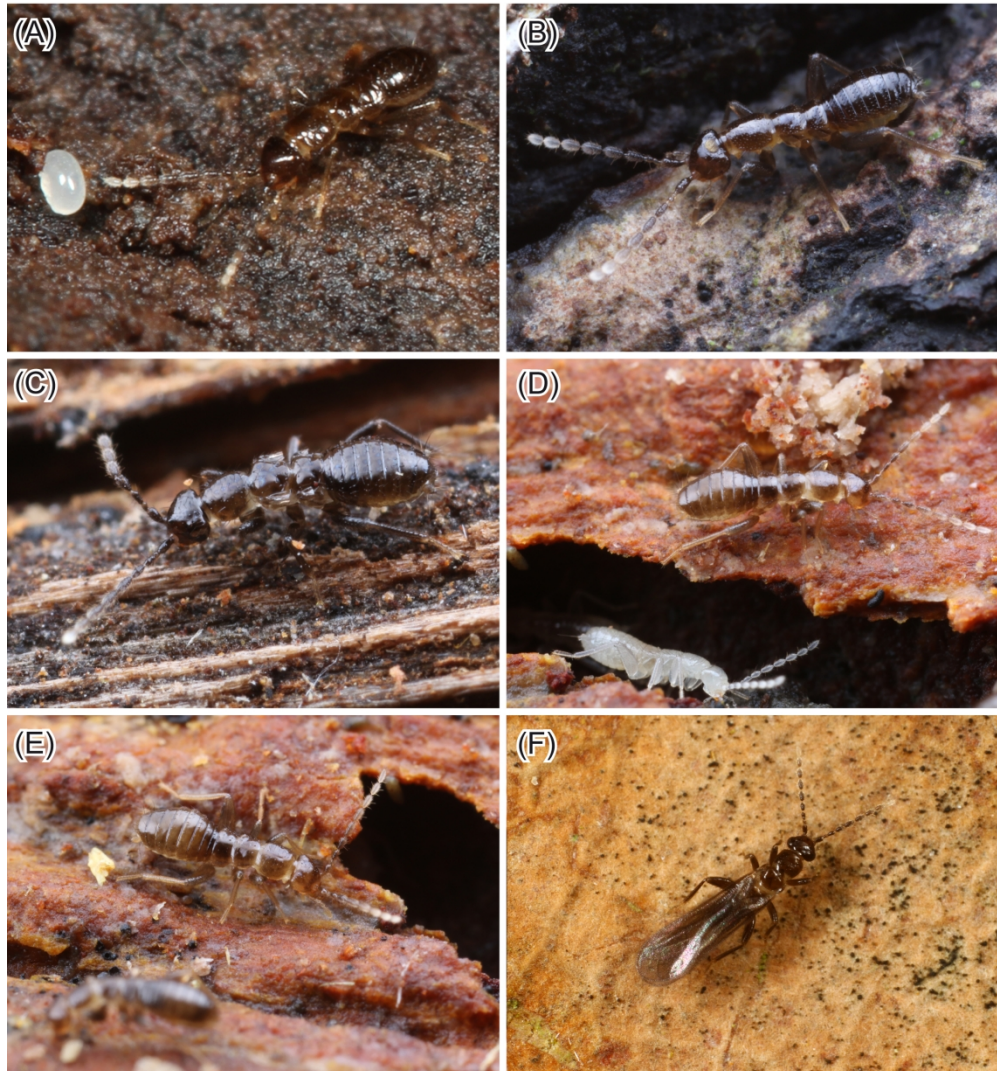


Fig. 1. Zorapteran species. A, *Z. sp.* from Costa Rica; B, *Z. asymmetristernum* from Kenya; C-F, *Z. caudelli* from Malaysia. Photographs courtesy of T. Kanao (A) and T. Komatsu (B-F).

209x225mm (300 x 300 DPI)

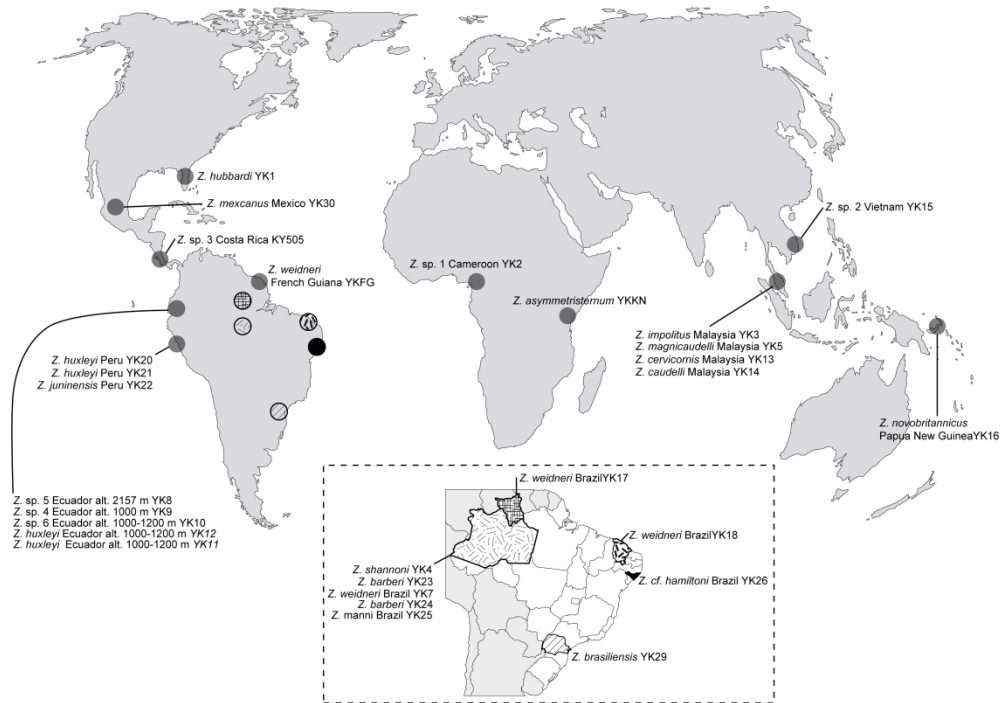


Fig. 2. Distribution pattern of species used in molecular phylogeny. Detailed location of Brazilian samples shown in the inserted map.

294x205mm (300 x 300 DPI)

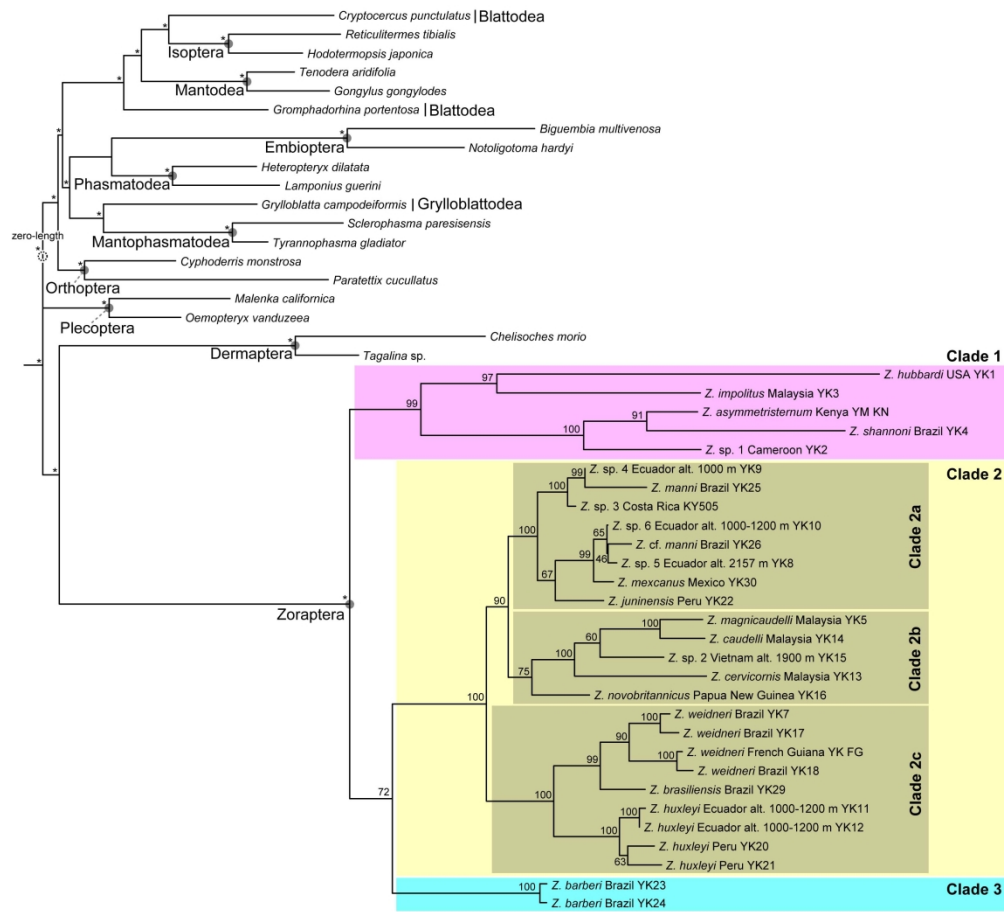


Fig. 3. Constrained maximum likelihood tree estimated by IQ-TREE. Non polyneoptera orders were omitted here. Asterisks on nodes indicate that they were constrained. Major clades in Zoraptera highlighted with colored rectangles (see the text for details).

270x246mm (300 x 300 DPI)

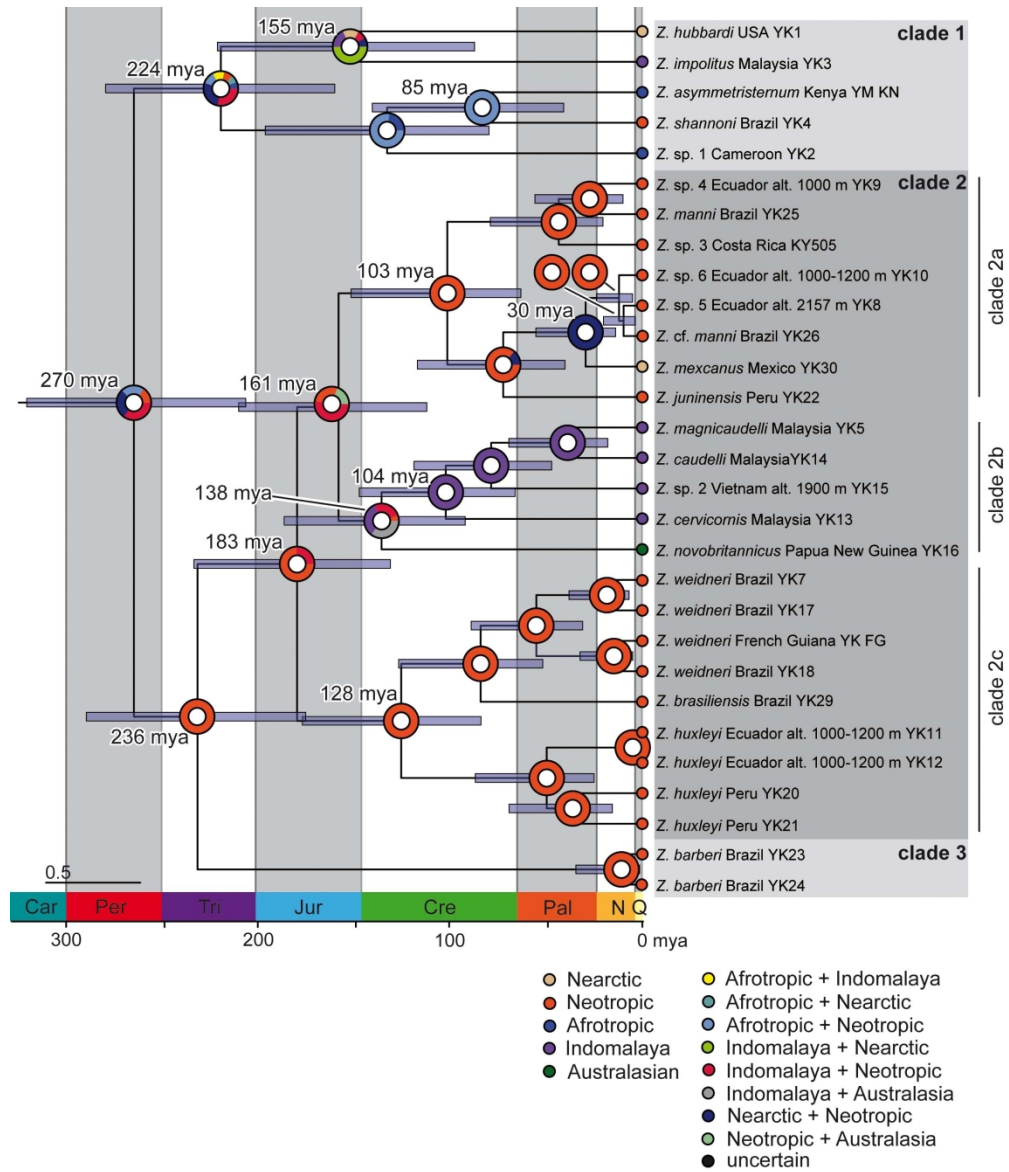


Fig. 4. Ancestral range reconstruction shown in a time-calibrated phylogeny of Zoraptera based on Dispersal-Extinction-Cladogenesis (DEC) model. Topology based on ML analysis. Pie charts on each node indicate the likelihood of the estimated ancestral area. Detailed statistics of the estimated ancestral distribution is available in ES9 Fig. S5.

207x242mm (300 x 300 DPI)

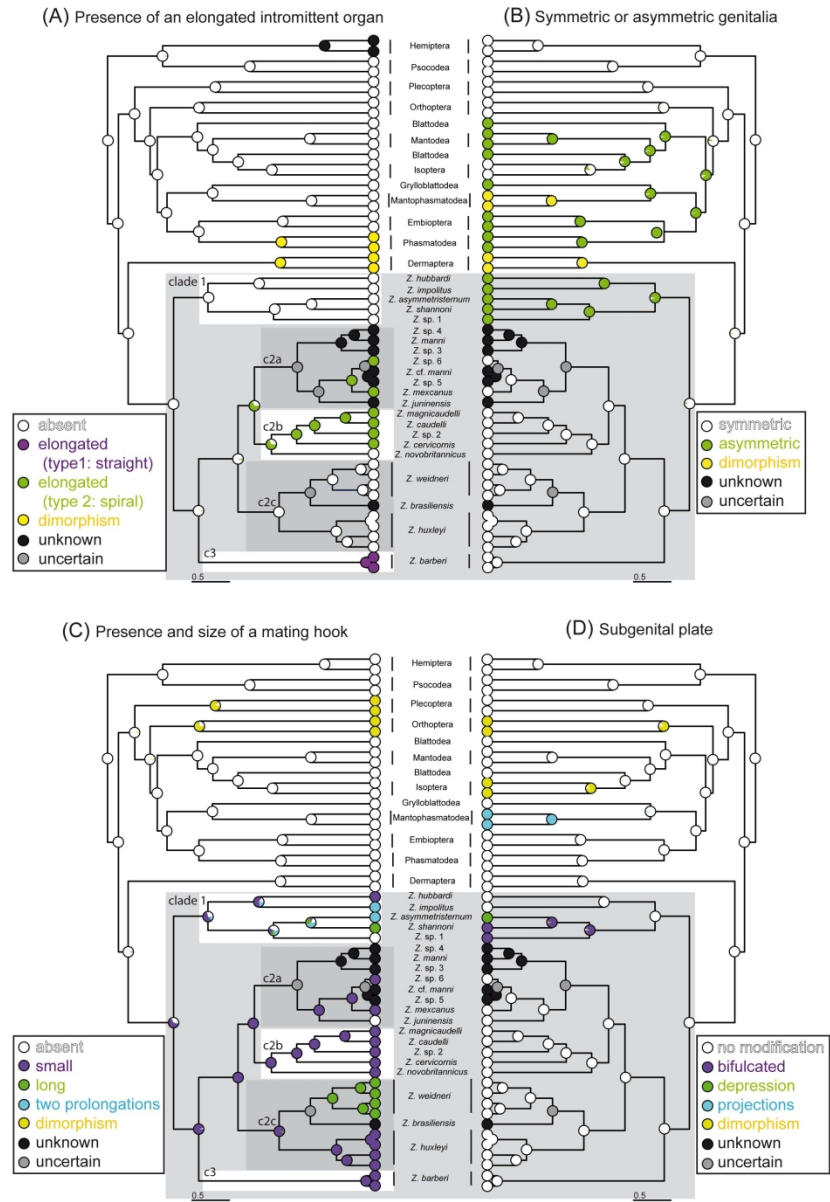


Fig. 5. Maximum likelihood ancestral state reconstructions of selected traits with a special focus on reproductive characters of Zoraptera.

201x292mm (300 x 300 DPI)

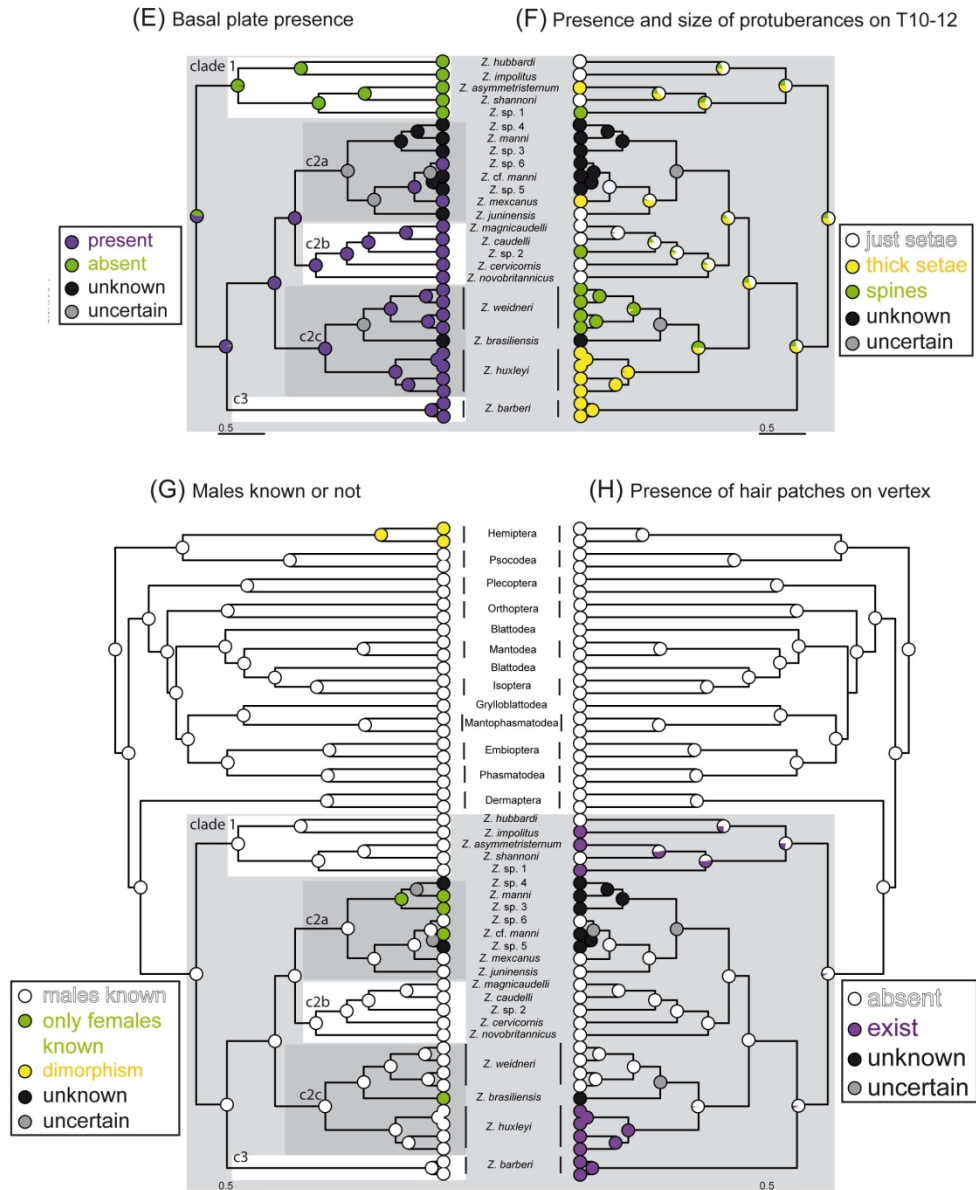


Fig. 6 (continued). Ancestral state reconstructions based on most likelihood method of selected traits with a special focus on reproductive characters of Zoraptera.

195x238mm (300 x 300 DPI)

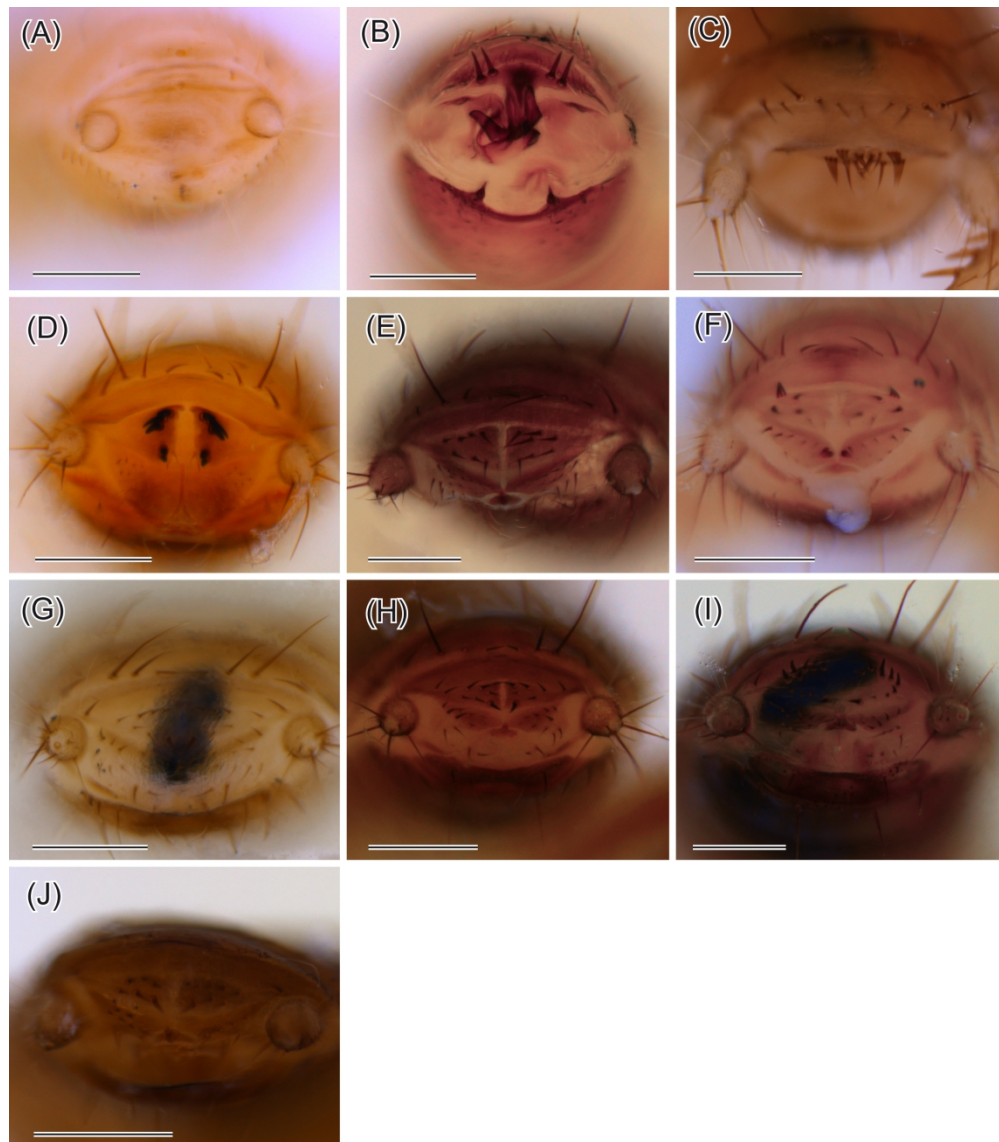


Fig. 7. Morphological diversity of the abdomen in caudal view. A, *Zorotypus hubbardi*; B, *Z. sp. 1.* Cameroon YK2; C, *Z. mexcanus*; D, *Z. weidneri* Brazil; E, *Z. sp. 6* Ecuador alt. 1000-1200 m YK10, possibly *Z. hamiltoni*; F, *Z. huxleyi* Ecuador; G, *Z. cervicornis*; H, *Z. caudalli*; I, *Z. sp. 2* Vietnam alt. 1900 m YK15; J, *Z. novobritannicus*. Scale bars: 200 μ m.

209x238mm (300 x 300 DPI)

Table S1. A list of species included in our molecular phylogeny analyses. BYUC: Arthropod Collection, Brigham Young University, Provo, UT, USA; INPA: National Institute of Amazonian Research, Brazil; YK PC: Y. Matsumura private collection at the Kiel Univ., Germany

Order	Family	Species	ID	Collected locality	Voucher specimens locality	12S	H3	16S	18S
Zoraptera	Zorotypidae	<i>Z. hubbardi</i>	YK1	Florida, USA	YK PC	LC471587	-	LC476731	LC477087
		<i>Z. sp. 1</i>	YK16-2	Cameroon	YK PC	LC471608	-	LC476755	LC477108
		<i>Z. impolitus</i>	YK16-3	Malaysia	YK PC	LC471588	LC477112	LC476732	LC477088
		<i>Z. shannoni</i>	YK16-4	Amazonas, Brazil	YK PC	LC471589	-	LC476733	LC477089
		<i>Z. magnicaudelli</i>	YK16-5	Malaysia	YK PC	LC471595	LC477119	LC476740	LC477096
		<i>Z. weidneri</i>	YK16-7	Amazonas, Brazil	YK PC	LC471600	LC477124	LC476744	LC477101
		<i>Z. sp. 5</i>	YK16-8	Ecuador alt. 2157 m	YK PC	LC471590	LC477113	LC476734	LC477090
		<i>Z. sp. 4</i>	YK16-9	Ecuador alt. 1000 m	YK PC	LC471593	LC477116	LC476737	LC477093
		<i>Z. sp. 6</i>	YK16-10	Ecuador alt. 1000-1200 m	YK PC	LC471591	LC477114	LC476735	LC477091
		<i>Z. huxleyi</i>	YK16-11	Ecuador alt. 1000-1200 m	YK PC	LC471604	LC477129	LC476749	LC477105
		<i>Z. huxleyi</i>	YK16-12	Ecuador alt. 1000-1200 m	YK PC	LC471605	LC477130	LC476750	-
		<i>Z. cervicornis</i>	YK16-13	Malaysia	YK PC	LC471598	LC477122	LC476743	LC477099
		<i>Z. caudelli</i>	YK16-14	Malaysia	YK PC	LC471596	LC477120	LC476741	LC477097
		<i>Z. sp. 2</i>	YK16-15	Vietnam alt. 1900 m	YK PC	LC471597	LC477121	LC476742	LC477098
		<i>Z. novobritannicus</i>	YK16-16	East new Britain Province, Papua New Guinea	BYUC	LC471599	LC477123	-	LC477100
		<i>Z. weidneri</i>	YK16-17	Roraima, Brazil	INPA	LC471601	LC477125	LC476745	LC477102
		<i>Z. weidneri</i>	YK16-18	Ceará, Brazil	INPA	-	LC477126	LC476746	-

		<i>Z. huxleyi</i>	YK16-20	Madre de Dios, Peru	INPA	LC471606	LC477131	LC476751	LC477106
		<i>Z. huxleyi</i>	YK16-21	Quince Mil, Peru	INPA	LC471607	LC477132	LC476752	LC477107
		<i>Z. juninensis</i>	YK16-22	Cusco, Peru	INPA	LC471592	LC477115	LC476736	LC477092
		<i>Z. barberi</i>	YK16-23	Amazonas, Brazil	INPA	-	-	LC476757	LC477110
		<i>Z. barberi</i>	YK16-24	Amazonas, Brazil	INPA	-	-	-	LC477111
		<i>Z. manni</i>	YK16-25	Amazonas, Brazil	INPA	-	LC477117	LC476738	LC477094
		<i>Z. cf. manni</i>	YK16-26	Alagoas, Brazil	INPA	-		LC476754	
		<i>Z. brasiliensis</i>	YK16-29	Paraná, Brazil	INPA	LC471603	LC477128	LC476748	LC477104
		<i>Z. mexicanus</i>	YM16-30	Mexico	YK PC		LC477133	LC476753	
		<i>Z. sp. 3</i>	YM505	Costa Rica	YK PC	LC471594	LC477118	LC476739	LC477095
		<i>Z. weidneri</i>	YM FG	French Guiana	YK PC	LC471602	LC477127	LC476747	LC477103
		<i>Z. asymmetristernum</i>	YM KN	Kenya	YK PC	-	-	LC476756	LC477109
Blattodea	Blaberidae	<i>Gromphadorhina portentosa</i>	-	-	-	AY125216.1	EF623280.1, Z97610.1	EF623123.1, Z97626.1	AY491145.1, Z97592.1
	Cryptocercidae	<i>Cryptocercus punctulatus</i>	-	-	-	AY521698.1	U17779.1	U17780.1	DQ874119.1
Dermaptera	Chelisochoidea	<i>Chelisoches morio</i>	-	-	-	AY125220.1	-	-	AY121133.1
	Pygidicranidae	<i>Tagalina sp.</i>	-	-	-	AY521704.1	-	-	AY521838.1
Embioptera	Embiidae	<i>Biguembia multivenosa</i>	-	-	-	AY521705.1	-	JQ907139.1	JQ907196.1
	Notoligotomidae	<i>Notoligotoma hardyi</i>	-	-	-	EU157030.1	-	EU157038.1	JQ907200.1
Grylloblattodea	Grylloblattidae	<i>Grylloblatta campodeiformis</i>	-	-	-	DQ457398.1, AY125225.1	DQ457227.1	DQ457263.1	DQ457299.1
Isoptera	Rhinotermitidae	<i>Reticulitermes tibialis</i>	-	-	-	-	AY168222.1	FJ226413.1, FJ226412.1, FJ226411.1	AF423782.1

	Termopsidae	<i>Hodotermopsis japonica</i>	-	-	-	AB006580.1	AY521856.1	AF262575.1	AY521856.1
Mantodea	Mantidae	<i>Tenodera aridifolia</i>	-	-	-	GU064799.1	FJ805974.1	AY491097.1, GU064715.1	FJ806336.1
	Empusidae	<i>Gongylus gongylodes</i>	-	-	-	AY521711.1	EF383152.1	EF383312.1	AY521860.1
Mantophasmatodea	Mantophasmatidae	<i>Sclerophasma paretisensis</i>	-	-	-	AY521712.1	-	DQ457265.1	DQ457302.1
	Mantophasmatidae	<i>Tyrannophasma gladiator</i>	-	-	-	AY521713.1	DQ457230.1	DQ457266.1	AY521863.1
Orthoptera	Tetrigidae	<i>Paratettix cucullatus</i>	-	-	-	-	AY338640.1	-	Z97574.1
	Haglidae	<i>Cyphoderris monstrosa</i>	-	-	-	AY521722.1, KF571077.1	Z93279.2	Z93317.2	AF514553.1
Plecoptera	Nemouridae	<i>Malenka californica</i>	-	-	-	AY338642.1	EF623342.1	EF623182.1	AY338724.1
	Taeniopterygidae	<i>Oemopteryx vanduzeei</i>	-	-	-	AY521725.1	EF623432.1	EF623266.1	AY521879.1
Phasmatodea	Bacillidae	<i>Heteropteryx dilatata</i>	-	-	-	AY125241.1	KJ024476.1	KJ024429.1	AY121157.1
	Phsmatidae	<i>Lamponius guerini</i>	-	-	-	AY125261.1	KJ024473.1	KJ024422.1	AY121178.1
Hemiptera	Pentatomoidea	<i>Sastragala esakii</i>	-	-	-	LC099126.1	LC099337.1	LC099179.1	LC099231.1
	Acanthosomatidae	<i>Ditomotarsus hyadesi</i>	-	-	-	LC099154.1	LC099365.1	LC099206.1	LC099259.1
Psocodea	Prionoglarididae	<i>Speleketor irwini</i>	-	-	-	-	DQ104774.1	DQ104747.1	DQ104799.1
	Psocidae	<i>Trichadenotecnum sexpunctatum</i>	-	-	-	LC051951.1	LC052168.1	LC052008.1	LC052067.1
Odonata	Epiophlebiidae	<i>Epiophlebia superstes</i>	-	-	-	EU477631	EU055518	EU477631	EU055226
Ephemeroptera	Baetidae	<i>Centroptilum luteolum</i>	-	-	-	AY749649	AY749710	AY749774	AF461251
	Leptohiphidae	<i>Allenhyphes flinti</i>	-	-	-	AY749677	AY749732	AY749807	AY749880
Zygentoma	Lepismatidae	<i>Thermobia domestica</i>	-	-	-	AY639935	-	AY639935	AF370790

	Lepidotrichidae	<i>Tricholepidion gertschi</i>	-	-	-	AY191994	AF110863	AY191994	AF370789
Archaeognatha	Machilidae	<i>Machilis</i> sp.	-	-	-	-	AY521695	-	AY521826

Table S2. Metadata of the used specimens.

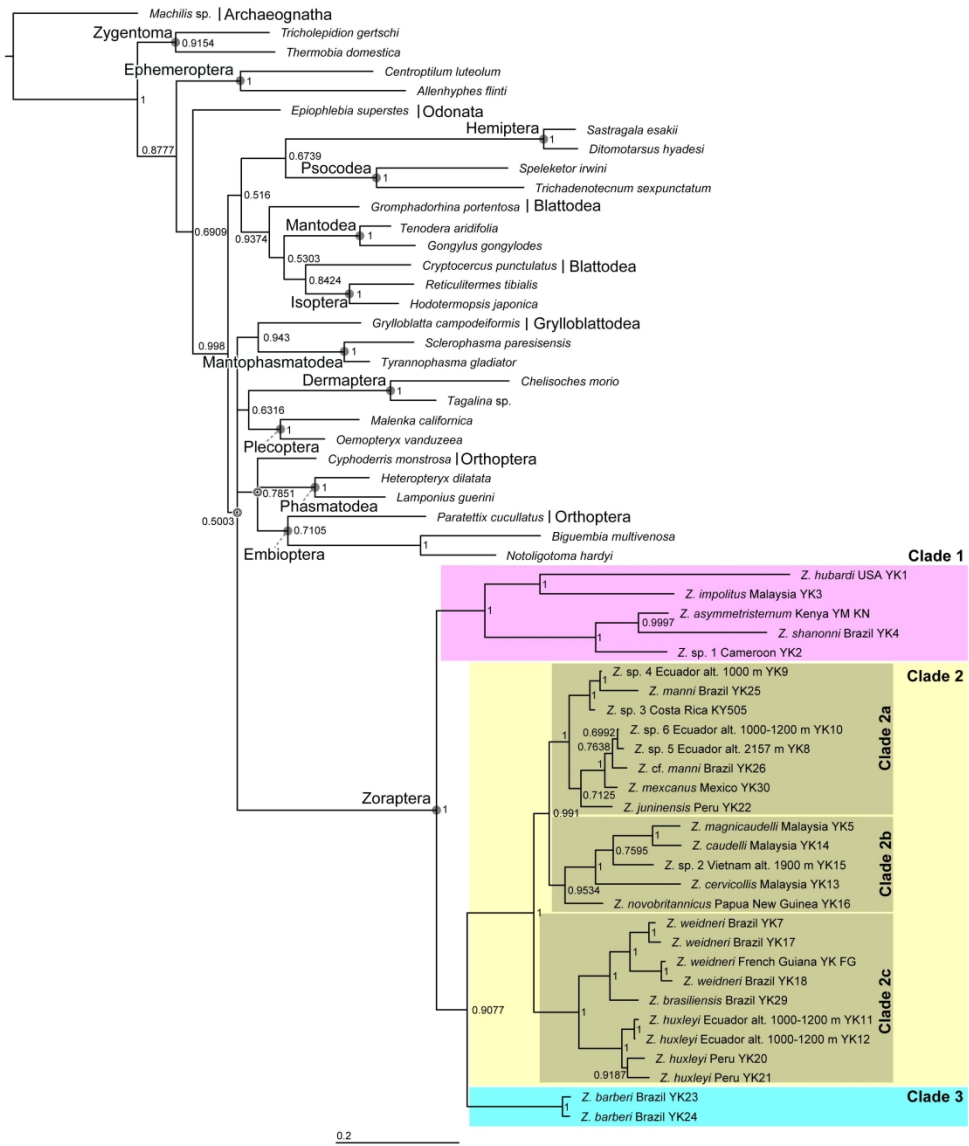
A list of species included in our molecular phylogeny analyses. BYUC: Arthropod Collection, Brigham Young University, Provo, UT, USA; INPA: National Institute of Amazonian Research, Brazil; SEHU: Systematic entomology department of the Hokkaido University; YK PC: Y. Matsumura private collection at the Kiel Univ., Germany

Species	ID	Collected locality	Collected persons	Voucher specimens locality
<i>Z. hubbardi</i>	YK1	USA, Florida, Highlands Hammock state park, 27°35'N, 81°01'W, 07.x.2004	K. Yoshizawa	YK PC
<i>Z. sp. 1</i>	YK16-2	Cameroon, South-west province, Nyasoso, Mt. Kupe, 4°49'N, 9°43'E, 16.v.2015	T. Komatsu	YK PC
<i>Z. impolitus</i>	YK16-3	Malaysia, Selangor, UI Gombak (elevation ca. 200–400 m)	Y. Mashimo & R. Machida	YK PC
<i>Z. shannoni</i>	YK16-4	Brazil, Manaus, Reserva Ducke, am010, km24, 02°45'S-59°51'W, 27.i.2014	J.T. Câmara, F.F. Xavier & Y. Matsumura	YK PC
<i>Z. magnicaudelli</i>	YK16-5	Malaysia, Pahang, Gunung Brinchang, 4°35'N 101°23'E, 11.iii.2015	Y. Matsumura & M. Maruyama	YK PC
<i>Z. weidneri</i>	YK16-7	Brazil, Amazonas, ZF-2, alojam. 02°38'S, 60°09'W, 24.i.2014	J.A. Rafael, J.T. Câmara, Y. Matsumura	YK PC
<i>Z. sp. 5</i>	YK16-8	Ecuador, Zamora-Chinchi, Arcoiris, Montane rainforest, lower slope, alt. 2157 m, 03°59'S, 79°05'W, 12.ii.2013	Y. Matsumura	YK PC
<i>Z. sp. 4</i>	YK16-9	Ecuador, Parque Nacional Podocarpus rainforest, Bombuscaro area, alt. 1025 m, 04°06'S, 78°09'W, 03.ii.2013	Y. Matsumura	YK PC
<i>Z. sp. 6</i>	YK16-10	Ecuador, Zamora-Chinchi, Capalonga lodge reserve rainforest, alt. 1000-1200 m, 04°05'S, 78°57'W, 10.ii.2013	Y. Matsumura	YK PC
<i>Z. huxleyi</i>	YK16-11	Ecuador, Zamora-Chinchi, Capalonga lodge reserve rainforest, alt. 1000-1200 m, 04°05'S, 78°57'W, 10.ii.2013	Y. Matsumura	YK PC
<i>Z. huxleyi</i>	YK16-12	Ecuador, Zamora-Chinchi, Capalonga lodge reserve rainforest, alt. 1000-1200 m, 04°05'S, 78°57'W, 10.ii.2013	Y. Matsumura	YK PC
<i>Z. cervicornis</i>	YK16-13	Malaysia, Pahang, Endau, 2°38'N 103°39'E 9.vii.2003	K. Yoshizawa	YK PC
<i>Z. caudelli</i>	YK16-14	Malaysia, Negeri Selangor, Ulu Gombak (Uni. Malaya field studies centre), alt. 220 m, 3°17'N 101°46'E, 10-18.iii.2015	Y. Matsumura	YK PC
<i>Z. sp. 2</i>	YK16-15	Vietnam, Lam Dong Province, Mt. Lang Biang, alt. 1850 m, 12°02'N 108°26'E, 3.vi.2002	S. Nomura	YK PC
<i>Z. novobritannicus</i>	YK16-16	East New Britain Province, Kerevat, 4° 22'S, 152°02'E, 23.vii.2008	M. Whiting et al. (Terry and Whiting, 2012 Zootaxa 3260: 53–61)	BYUC

<i>Z. weidneri</i>	YK16-17	Brazil, Roraima, Caracará, Parque Nacional Serra da Mocidade, 600 m.a.; 01°36'N 61°54'W, 15-26.i.2016	F.F. Xavier, R. Boldrini & P. Barroso	INPA
<i>Z. weidneri</i>	YK16-18	Brazil, Ceará, Ubajara, Parque Nacional de Ubajara, 03°50'25"S 40°53'53"W, 23.iv.2012, tronco, 840m	J.A. Rafael & J.T. Câmara	INPA
<i>Z. huxleyi</i>	YK16-20	Peru, Madre de Dios, Mazuko, 12°57'14"S 70°1'16"W, 21.viii.2012, tronco caído	J.A. Rafael	INPA
<i>Z. huxleyi</i>	YK16-21	Peru, Cusco, Quincemil, Central Hidrelétrica, 13°17'03"S 70°46'53"W, 26.viii.2012, tronco caído	J.A. Rafael	INPA
<i>Z. juninensis</i>	YK16-22	Peru, Cusco, Quincemille, Rio Areza, 1000 m, 13°21'18"S 70°53'22"W, 22.viii.2012	J.A. Rafael	INPA
<i>Z. barberi</i>	YK16-23	Brazil, Amazonas, Castanho Careiro, Panelão, 03°51'20"S 60°24'58"W, 11- 13.xii.2013	J.A. Rafael, J.T. Câmara & F.F. Xavier	INPA
<i>Z. barberi</i>	YK16-24	Brazil, Amazonas, Guajará, Ramal do Gama, Igarapé Eder, 07°31'26"S 72°40'40"W, 07-18.xi.2006	F.F. Xavier F°	INPA
<i>Z. manni</i>	YK16-25	Brazil, Amazonas, Benjamin Constant, BR 307, km 5, Sítio Ágno, 04°23'35.6"S 70°01'59.7"W, 08-10.iv.2014	F.F. Xavier	INPA
<i>Z. cf. manni</i>	YK16-26	Brazil, Alagoas, Ibateguara, Reserva da Usina Serra Grande, 08°59'58"S 35°51'34"W, 29.v.2007	J.A. Rafael & F.F. Xavier	INPA
<i>Z. brasiliensis</i>	YK16-29	Brazil, Paraná, Serra do Mar, Estrada do Castelhanos, 25°50'52"S 48°56'47"W, 04.vii.2006, tronco caído	J.A.Rafael	INPA
<i>Z. mexicanus</i>	YM16-30	Mexico, 10 km east of Bachil R173, CHIS, 17°01'N, 92°46'E, 7.iii.2013	K. Yoshizawa	YK PC
<i>Z. sp. 3</i>	YM505	Costa Rica, Heredia, Sarapipui, La Selva, 10°25'N 84°00'W, 11.xi.2015	T. Kanao	SEHU
<i>Z. weidneri</i>	YM FG	French Guiana, Guyana, Cayenne, Roura (Amazone nature lodge), alt. 300m, 04°32'N, 52°12'W, 06-18.x.2015	N. Ogawa	YK PC
<i>Z. asymmetristernum</i>	YM KN	Kenya, Kakamega, Kakamega national park, 00°14'N, 34°52'E, 29.v.- 2.vi.2016	Y. Matsumura	YK PC



272x308mm (300 x 300 DPI)



265x306mm (300 x 300 DPI)

species name	A: Existence of an elongated intromittent organ	B: Symmetric or asymmetric genitalia	C: Existence and size of a mating hook	D: modification of subgenital plate
1 <i>Zorotypus amazonensis</i> Rafael & Engel, 2006	absent	asymmetry	small one on T10	margin produced medially
2 <i>Zorotypus asymmetricus</i> Kočárek, 2017	absent	asymmetry	relatively short ones on T10 and T11	no modification
3 <i>Zorotypus asymmetristernum</i> Mashimo, 2018	absent	asymmetry	relatively short ones on T10 and T11	depression
4 <i>Zorotypus barberi</i> Gurney, 1938	exist, type 1 straight	symmetry	small one	no modification
5 <i>Zorotypus brasiliensis</i> Silvestri, 1947	-	-	-	-
6 <i>Zorotypus buxtoni</i> Karny, 1932	-	-	-	-
7 <i>Zorotypus caudelli</i> Karny, 1932	exist, type 2, spiral	symmetry	small one (Mashimo et al 2013)	no modification (Mashimo et al. 2013)
8 <i>Zorotypus caxiuana</i> Rafael et al., 2008	absent	asymmetry	relatively long	margin produced medially
9 <i>Zorotypus cervicornis</i> Mashimo et al., 2013	exist, type 2, spiral	symmetry	small one on T11	no modification
10 <i>Zorotypus ceylonicus</i> Silvestri, 1913	?	?	?	?
11 <i>Zorotypus congensis</i> van Ryn-Tournel, 1971	?	?	?	?
12 <i>Zorotypus cramptoni</i> Gurney, 1938	exist, type 2, spiral	symmetry	small one	no modification
13 <i>Zorotypus delamarei</i> Paulian, 1949	absent	asymmetry	probably absent	probably no modification
14 <i>Zorotypus guineensis</i> Silvestri, 1913	absent	?	?	?
15 <i>Zorotypus gurneyi</i> Choe, 1989	exist, type 2, spiral	symmetry	small one	no modification
16 <i>Zorotypus hainanensis</i> Yin & Li, 2015	exist, type 2, spiral	symmetry	small one	no modification
17 <i>Zorotypus hamiltoni</i> New, 1978	exist, type 2, spiral	symmetry	small one	no modification
18 <i>Zorotypus huangi</i> Yin & Li, 2017	absent	asymmetry	relatively long ones on T10 and T11	no modification
19 <i>Zorotypus hubbardi</i> Caudell, 1918	absent	asymmetry (Hünefeld 2007)	small ones T8 to 10 (Gurney 1938, Hünefeld 2007)	no modification
20 <i>Zorotypus huxleyi</i> Bolivar y Peltain & Coronado, 1963	absent (Dallai et al. 2014)	symmetry	small one on T11	no modification
21 <i>Zorotypus impolitus</i> Mashimo et al., 2013	absent	asymmetry	relatively long ones on T10 and T11	no modification
22 <i>Zorotypus javanicus</i> Silvestri, 1913	-	-	-	-
23 <i>Zorotypus juninensis</i> Engel, 2000	?	?	probably absent	no modification
24 <i>Zorotypus lawrencei</i> New, 1995	-	-	-	-
25 <i>Zorotypus leleupi</i> Weidner, 1967	-	-	-	-

species name	A: Existence of an elongated intromittent organ	B: Symmetric or asymmetric genitalia	C: Existence and size of a mating hook	D: modification of subgenital plate
26 <i>Zorotypus longicercatus</i> Caudell, 1927	-	-	-	-
27 <i>Zorotypus magnicaudelli</i> Mashimo et al., 2013	exist, type 2, spiral	symmetry	small one on T11	no modification
28 <i>Zorotypus manni</i> Caudell, 1923	-	-	-	-
29 <i>Zorotypus medoensis</i> Hwang, 1976	absent	asymmetry	scoop shaped projection on T10	no modification
30 <i>Zorotypus mexicanus</i> Bolivar y Pieltain, 1940	exist, type 2, spiral	symmetry	small one	no modification
31 <i>Zorotypus neotropicus</i> Silvestri, 1916	-	-	-	-
32 <i>Zorotypus newi</i> (Chao & Chen, 2000)	-	-	-	-
33 <i>Zorotypus novobritannicus</i> Terry & Whiting, 2012	absent	symmetry	small one on T11	no modification
34 <i>Zorotypus philippinensis</i> Gurney, 1938	-	-	-	-
35 <i>Zorotypus sechellensis</i> Zampro, 2005	not described	?	exist on 10th, probably small	probably no modification
36 <i>Zorotypus shannoni</i> Gurney, 1938	absent	asymmetry	relatively big	bifurcated
37 <i>Zorotypus silvestrii</i> Karny, 1927	-	-	-	-
38 <i>Zorotypus sinensis</i> Hwang, 1974	absent	asymmetry	scoop shaped projection on T10	no modification
39 <i>Zorotypus snyderi</i> Caudell, 1920	exist, type 2, spiral	symmetry	?	broad medially located depression
40 <i>Zorotypus swezeyi</i> Caudell, 1922	-	-	-	-
41 <i>Zorotypus vinsoni</i> Paulian, 1951	absent	asymmetry	probably absent	probably no modification
42 <i>Zorotypus weidneri</i> New, 1978	absent	symmetry	big	no modification
43 <i>Zorotypus weiweii</i> Wang et al., 2016	absent	asymmetry	relatively long ones on T10 and T11	no modification
44 <i>Zorotypus zimmermani</i> Gurney, 1939	yes type 3 looped dorso-ventrally	symmetry	small	no modification
45 <i>Zorotypus</i> sp. 1 Cameroon	absent	asymmetry	absent	bifurcated
46 <i>Zorotypus</i> sp. 2 Vietnam	exist, type 2, spiral	symmetry	small one on T11	no modification
47 <i>Zorotypus</i> sp. 3 Costa Rica	-	-	-	-
48 <i>Zorotypus</i> sp. 4 Ecuator alt 1000-1200 m	-	-	-	-
49 <i>Zorotypus</i> sp. 5 Ecuador alt. 2157 m	-	-	-	-
50 <i>Zorotypus</i> sp. 6 Ecuator alt 1000-1200 m	probably <i>Z. hamiltoni</i> like individual (see the method in the text)			

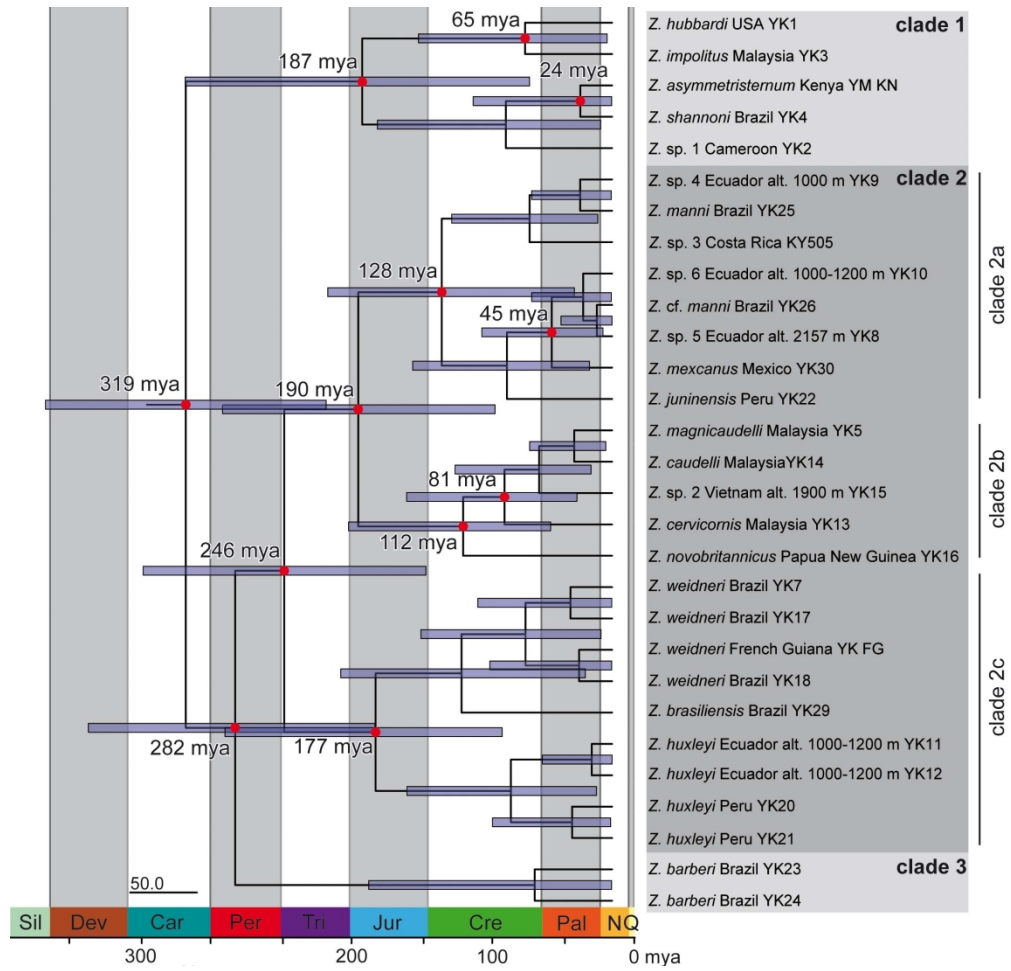
species name	E: Basal plate existence	F: Existence and size of protuberances on T9-12	G: Males known or not	H: Existence of hair patches on vertex
1 <i>Zorotypus amazonensis</i> Rafael & Engel, 2006	absent	thickened, rather oblique setae on T9	males known	longitudinal paramedian setae
2 <i>Zorotypus asymmetricus</i> Kočárek, 2017	absent (However Kočárek et al. 2017 described "spatula-like basal plate present beneath aedeagus")	just setae	males known	absent
3 <i>Zorotypus asymmetristernum</i> Mashimo, 2018	absent	erected setae on T10	males known	exist
4 <i>Zorotypus barberi</i> Gurney, 1938	exist	paired mesal processes on T9	males known	exist (its function is proved by Choe, 1995)
5 <i>Zorotypus brasiliensis</i> Silvestri, 1947	-	-	only female are known (new 1978 and Rafael et al 2006, 2008)	-
6 <i>Zorotypus buxtoni</i> Karny, 1932	-	-	sex is not identified	-
7 <i>Zorotypus caudelli</i> Karny, 1932	exist	just setae	males known	absent
8 <i>Zorotypus caxiuana</i> Rafael et al., 2008	absent	thickened setae on T10	males known	exist
9 <i>Zorotypus cervicornis</i> Mashimo et al., 2013	exist	just setae	males known	absent
10 <i>Zorotypus ceylonicus</i> Silvestri, 1913	?	?	?	?
11 <i>Zorotypus congensis</i> Ryn-Tournel, 1971	?	?	?	?
12 <i>Zorotypus cramptoni</i> Gurney, 1938	exist	just setae	males known	absent
13 <i>Zorotypus delamarei</i> Paulian, 1949	?	probably just setae	males known	absent
14 <i>Zorotypus guineensis</i> Silvestri, 1913	?	?	males known	?
15 <i>Zorotypus gurneyi</i> Choe, 1989	exist	dark-colored setae on T9	males known	absent
16 <i>Zorotypus hainanensis</i> Yin & Li, 2015	exist	just setae	males known	absent
17 <i>Zorotypus hamiltoni</i> New, 1978	exist	just setae	males known	absent
18 <i>Zorotypus huangi</i> Yin & Li, 2017	absent	just setae	males known	absent
19 <i>Zorotypus hubbardi</i> Caudell, 1918	absent (Hünefeld 2007)	just setae	males known	absent
20 <i>Zorotypus huxleyi</i> Bolivar y Pieltain & Coronado, 1963	exist (we confirmed it)	projections on T11 (?), but according to New (1978) they are on T12 and variations in the number.	males known	exist
21 <i>Zorotypus impolitus</i> Mashimo et al., 2013	absent	just setae	males known	exist
22 <i>Zorotypus javanicus</i> Silvestri, 1913	-	-	only females are known (new 1978)	-
23 <i>Zorotypus juninensis</i> Engel, 2000	?	probably just setae	males known	absent
24 <i>Zorotypus lawrencei</i> New, 1995	-	-	only females are known, but New (2000) mentioned it is very similar to <i>Z. caudelli</i>	-
25 <i>Zorotypus leleupi</i> Weidner, 1967	-	-	only females are known (new 1978)	-

	species name	E: Basal plate existence	F: Existence and size of protuberances on T9-12	G: Males known or not	H: Existence of hair patches on vertex
26	<i>Zorotypus longicercatus</i> Caudell, 1927	-	-	only nymphs are known (new 1978)	-
27	<i>Zorotypus magnicaudelli</i> Mashimo et al., 2013	exist	just setae	males known	absent
28	<i>Zorotypus manni</i> Caudell, 1923	-	-	only females are known (new 1978)	-
29	<i>Zorotypus medoensis</i> Hwang, 1976	absent	just setae	males known	absent
30	<i>Zorotypus mexicanus</i> Bolivar y Pieltain, 1940	exist	dark-colored setae	males known	absent
31	<i>Zorotypus neotropicus</i> Silvestri, 1916	-	-	only females are known (new 1978)	-
32	<i>Zorotypus newi</i> (Chao & Chen, 2000)	-	-	only females are known	-
33	<i>Zorotypus novobritannicus</i> Terry & Whiting, 2012	possibly exist from the Figs 14-15 in the original paper	just setae	males known	absent
34	<i>Zorotypus philippinensis</i> Gurney, 1938	-	-	only females are known (new 1978)	-
35	<i>Zorotypus sechellensis</i> Zampro, 2005	?	?	males known	absent
36	<i>Zorotypus shannoni</i> Gurney, 1938	absent (New 1978 had explicitly mentioned not defined basal plate)	just setae	males known	absent
37	<i>Zorotypus silvestrii</i> Karny, 1927	-	-	The sex is not identified	-
38	<i>Zorotypus sinensis</i> Hwang, 1974	absent	just setae	males known	absent
39	<i>Zorotypus snyderi</i> Caudell, 1920	exist	just setae	males known	
40	<i>Zorotypus swezeyi</i> Caudell, 1922	-	-	only females are known (new 1978)	-
41	<i>Zorotypus vinsoni</i> Paulian, 1951	?	probably just setae	males known	
42	<i>Zorotypus weidneri</i> New, 1978	exist (but New 1978 mentioned the genitalia are similar to <i>Z. vinsoni</i> and <i>Z. delamarei</i>)	spines on T10	males known	absent (Beutel and Weide 2005; Matsumura et al. 2015)
43	<i>Zorotypus weiweii</i> Wang et al., 2016	absent	just setae	males known	exist
44	<i>Zorotypus zimmermani</i> Gurney, 1939	exist	just setae	males known	absent
45	<i>Zorotypus</i> sp. 1 Cameroon	absent	spines	a male collected	exist
46	<i>Zorotypus</i> sp. 2 Vietnam	exist	small spines arranged as a ring	males collected	absent
47	<i>Zorotypus</i> sp. 3 Costa Rica	-	-	only females collected	-
48	<i>Zorotypus</i> sp. 4 Ecuator alt 1000-1200 m	-	-	only a nymph collected	-
49	<i>Zorotypus</i> sp. 5 Ecuador alt. 2157 m	-	-	only a nymph collected	-
50	<i>Zorotypus</i> sp. 6 Ecuator alt 1000-1200 m		probably <i>Z. hamiltoni</i> like individual (see the method in the text)		

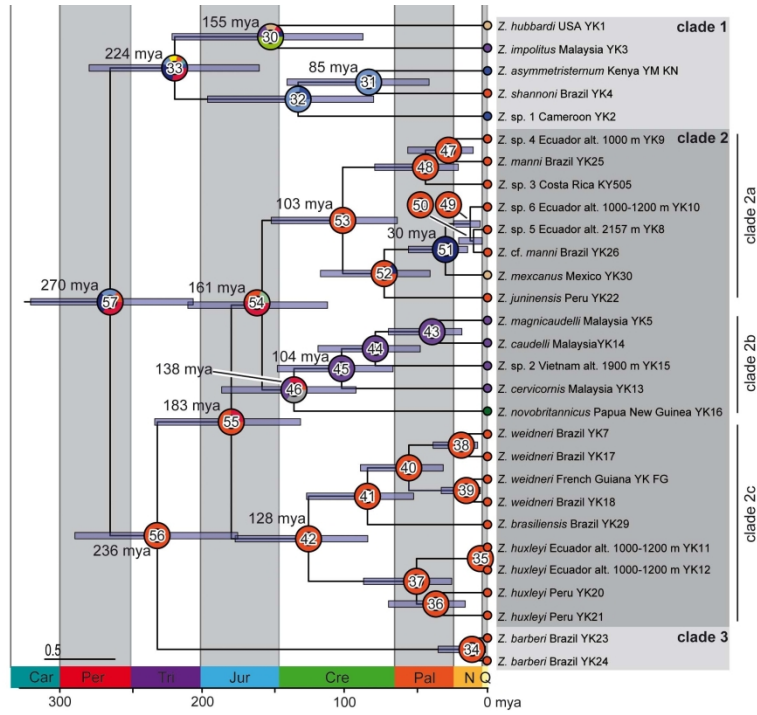
The above listed information were obtained mainly from the original description papers listed below. But in some cases newly describing papers were available and we used those new information, i.e. New (1978) and Rafael et al. (2008) for *Z. brasiliensis*, New (2000) and Mashimo et al. (2013) for *Z. caudelli*, Paulian (1951) for *Z. delamarei*, Dallai et al. (2014) for *Z. guineensis*, Gurney (1938) and Hünefeld (2007) for *Z. hubbardi*, Dallai et al. (2014) and New (1978) for *Z. huxleyi*, Gurney (1938) for *Z. snyderi*.

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202x193mm (300 x 300 DPI)



- Nearctic: C
- Neotropical: D
- Afrotropic: A
- Indomalaya: B
- Australasian: E
- Afrotropic + Indomalaya: A+B
- Afrotropic + Nearctic: A+C
- Afrotropic + Neotropical: A+D
- Indomalaya + Nearctic: B+C
- Indomalaya + Neotropical: B+D
- Indomalaya + Australasia: B+E
- Nearctic + Neotropical: C+D
- Neotropical + Australasia: D+E
- uncertain

DEC result file		
[TAXON]		[RESULT]
1	YK1	C DEC results:
2	YK3	B node 30 (LR): BC 49.76 B 18.23 C 15.36 BD 8.38 CD 8.27
3	YK2	A node 31 (LR): AD 100.00
4	YK4	D node 32 (LR): AD 77.15 A 22.85
5	YKKN	A node 33 (LR): BD 28.09 CD 27.14 AD 11.93 AB 11.31 D 8.74 AC 6.63 A 6.15
6	YK23	D node 34 (LR): D 100.00
7	YK24	D node 35 (LR): D 100.00
8	YK11	D node 36 (LR): D 100.00
9	YK12	D node 37 (LR): D 100.00
10	YK20	D node 38 (LR): D 100.00
11	YK21	D node 39 (LR): D 100.00
12	YK29	D node 40 (LR): D 100.00
13	YK7	D node 41 (LR): D 100.00
14	YK17	D node 42 (LR): D 100.00
15	YK18	D node 43 (LR): B 100.00
16	YKFG	D node 44 (LR): B 100.00
17	YK16	E node 45 (LR): B 100.00
18	YK13	B node 46 (LR): BE 35.33 B 33.21 BD 26.23 D 5.24
19	YK15	B node 47 (LR): D 100.00
20	YK5	B node 48 (LR): D 100.00
21	YK14	B node 49 (LR): D 100.00
22	KY505	D node 50 (LR): D 100.00
23	YK9	D node 51 (LR): CD 100.00
24	YK25	D node 52 (LR): D 86.11 CD 13.89
25	YK22	D node 53 (LR): D 100.00
26	YK30	C node 54 (LR): BD 52.71 D 27.59 DE 19.70
27	YK10	D node 55 (LR): D 74.47 BD 25.53
28	YK8	D node 56 (LR): D 100.00
29	YK26	D node 57 (LR): BD 34.91 CD 27.85 AD 22.15 D 15.09

202x295mm (300 x 300 DPI)