



HAL
open science

Phylogeny and diversification of planthoppers (Hemiptera: Fulgoromorpha) based on a comprehensive molecular dataset and large taxon sampling

Manon Bucher, Fabien L. Condamine, Yang Luo, Menglin Wang, Thierry Bourgoïn

► To cite this version:

Manon Bucher, Fabien L. Condamine, Yang Luo, Menglin Wang, Thierry Bourgoïn. Phylogeny and diversification of planthoppers (Hemiptera: Fulgoromorpha) based on a comprehensive molecular dataset and large taxon sampling. *Molecular Phylogenetics and Evolution*, 2023, 186, pp.107862. <10.1016/j.ympev.2023.107862>. <hal-04260605>

HAL Id: hal-04260605

<https://hal.science/hal-04260605v1>

Submitted on 26 Oct 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

1 ***Title***

2 **Phylogeny and diversification of planthoppers (Hemiptera: Fulgoromorpha) based on a**
3 **comprehensive molecular dataset and large taxon sampling**

4
5 ***Authors***

6 Manon Bucher^{a*}, Fabien L. Condamine^b, Yang Luo^c, Menglin Wang^d, Thierry Bourgoïn^{a*}

7
8 ***Affiliations***

9 ^aInstitut de Systématique, Evolution, Biodiversité (ISYEB), MNHN-CNRS-Sorbonne
10 Université-EPHE-Université des Antilles, Muséum National d'Histoire Naturelle, CP 50, 45
11 rue Buffon, 75005 Paris, France

12
13 ^bInstitut des Sciences de l'Évolution de Montpellier (ISEM), CNRS-Université de Montpellier-
14 IRD-EPHE, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France;
15 fabien.condamine@gmail.com

16
17 ^cHunan Key Laboratory of Green Packaging and Application of Biological Nanotechnology
18 Hunan University of Technology, Zhuzhou 412007, China; amyluo1204@126.com

19
20 ^dKey Laboratory of Southwest China Wildlife Resources Conservation, Ministry of Education,
21 China West Normal University, Nanchong 637009, China; wangmenglin123@126.com

22
23 ****Corresponding authors:***

24 Manon Bucher (manon.bucher@mnhn.fr), Thierry Bourgoïn (thierry.bourgoïn@mnhn.fr)

25

26 **Abstract**

27 Our understanding of the evolution of Fulgoromorpha (Insects, Hemiptera) has relied on
28 molecular studies that have only considered either a limited number of taxa where all the
29 families were not represented simultaneously, or a reduced number of genes. The absence of a
30 global analysis comparing all the available data has thus led to significant biases in the analyzes,
31 as evidenced by the incongruence of the results reported for planthopper phylogeny. Here we
32 provide a phylogenetic and dating analysis of the Fulgoromorpha with a large sampling of 531
33 ingroup taxa, representing about 80% of the currently described suprageneric taxonomic
34 diversity in this group. This study is based on most of the molecular sequences available to date
35 and duly verified, for a set of nuclear and mitochondrial genes from a taxonomic sampling as
36 complete as possible. The most significant results of our study are: (1) the unexpected paraphyly
37 of Delphacidae whose Protodelphacida seem more related to Cixiidae than to other
38 Delphacidae; (2) the group Meenoplidae-Kinnaridae recovered sister to the remaining
39 Fulgoroidea families; (3) the early branching node of Tettigometridae sister of all the other
40 families; (4) the Achilidae-Derbidae clade with Achilidae Plectoderini including Achilixiidae
41 recovered as monophyletic as well as the Fulgoridae-Dictyopharidae clade; and (5) the
42 Tropiduchidae placed sister to the other so called 'higher' families (*sec.* Shcherbakov,
43 2006). Our divergence times analysis, calibrated with a set of duly verified fossils, suggests that
44 the first diversification of planthoppers occurred in the Early Triassic around 240 Mya and those
45 of the superfamilies Delphacoidea and Fulgoroidea in the Middle-Late Triassic around 210 Mya
46 and 230 Mya, respectively. By the end of the Jurassic, all major planthopper lineages were
47 originated, and all families, around 125 Mya, might have been driven in their distribution and
48 evolution (in their first subfamilial divisions) by the geographical constraints of the Gondwanan
49 break-up. Rapid evolutionary radiations occurred particularly in Fulgoridae around 125-130
50 Mya. Our results stress the importance of the good quality of the sequences used in the
51 molecular analyzes and the primordial importance of a large sampling when analyzing the
52 phylogeny of the group.

53

54 **Keywords:** Fulgoromorpha; Molecular phylogeny; Dating analyses; Macroevolution;
55 Diversification

56

57 **1.Introduction**

58

59 Planthoppers (Hemiptera: Fulgoromorpha) constitute a worldwide group of insects, including
60 more than 14,000 described species divided into 37 families, 16 of them being only represented
61 by fossil taxa (Bourgoin, 2023). Aside from this high diversity, which originated about 300
62 million years ago (Mya), they also display a high morphological disparity and a cosmopolitan
63 repartition (Bartlett *et al.*, 2018; Bourgoin, 2023). Except for some species that are major crop
64 pests, their biology remains poorly known as well as does their evolutionary history.

65

66 Fulgoromorpha Evans, 1946, is one of the six sub-orders recognized within the Hemiptera
67 Linnaeus, 1758, traditionally represented by two extant superfamilies (including a few other
68 fossil families and all the extant ones): the Delphacoidea Leach, 1815 and Fulgoroidea Latreille,
69 1807 (Bourgoin & Szwed, 2022, 2023) and three exclusively fossil superfamilies:
70 Coleoscytoidea Martynov, 1935 (Permian), Suriokocixioidea Shcherbakov, 2000 (Permian-
71 Triassic), and the newly recognized Fulgoridioidea Handlirsh, 1939 (Jurassic-Cretaceous).
72 Additionally, a sixth independent fossil lineage, the Moscovian Carboniferous Aviorrhynchidae
73 Nel *et al.*, 2013, was recently added to Fulgoromorpha, as the oldest planthopper representative
74 (Bourgoin & Szwed, 2022). Although Yang & Fang (1993), using phenetic analyses, placed
75 the Tettigometridae Germar, 1821 as the sister position of Membracoidea (sub-order
76 Cicadomorpha), monophyly of Fulgoromorpha is consensually accepted. This monophyly is
77 supported by both the sharing of several morphological synapomorphies (e.g. specialized
78 carinated head capsule, structure of the antennae and tentorium, gut conformations, and
79 conformation of the male genitalia; summarized in Bourgoin and Szwed, 2022) and all
80 molecular phylogenetic analyses (Bourgoin *et al.*, 1997; Yeh *et al.*, 1998, 2005; Yeh & Yang,
81 1999; Urban & Cryan, 2007, 2012; Cryan & Urban, 2012; Song & Liang, 2013; Huang & Qin,
82 2018; Yu & Liang, 2018; Wang *et al.*, 2019; Xu *et al.*, 2019; Kim *et al.*, 2021; Michalik *et al.*,
83 2023).

84

85 Broadly speaking, extant planthopper phylogeny is well accepted on the basis of a fairly good
86 correlation between morphological and molecular approaches, which have mainly followed one
87 by another for the past twenty years. Accordingly, Bartlett *et al.* (2018) summarized the
88 Fulgoromorpha phylogeny based on the results of Urban & Cryan (2007), which remain the
89 most complete to date, dividing them into four large groups (Fig. A) with: (1) an early branching
90 monophyletic group (Delphacidae Leach, 1815 + Cixiidae Spinola, 1839) recently formalized

91 as the superfamily Delphacoidea Leach, 1815 sister clade to the remaining planthopper families
92 all classified within the Fulgoroidea Latreille, 1807 (sec. Bourgoïn & Szwedo, 2022); (2) a
93 paraphyletic group of five families (Kinnaridae Muir, 1925 + Meenoplidae Fieber, 1872),
94 (Achilidae Stål, 1866 + Achilixiidae Muir, 1923) and Derbidae Spinola, 1839; (3) a
95 monophyletic group of so-called 'higher Fulgoroidea' families *sec.* Shcherbakov (2006), with:
96 Acanaloniidae Amyot & Audinet-Serville, 1843, Caliscelidae Amyot & Audinet-Serville, 1843,
97 Flatidae Spinola, 1839, Issidae Spinola, 1839, Nogodinidae Melichar, 1898, Tettigometridae,
98 Tropiduchidae Stål, 1866, Ricaniidae Amyot & Audinet-Serville, 1843 forming a clade sister
99 to (4) an undefined group of the last four extant families (Fulgoridae Latreille, 1807 +
100 Dictyopharidae Spinola, 1839) and (Lophopidae Stål, 1866 + Eurybrachidae Stål, 1862). This
101 topology was updated by Brysz & Szwedo (2019) with the fossil families, although before the
102 recognition of Fulgoridoidea by Bourgoïn et Szwedo (2022, 2023).

103

104 However, behind this conventional agreement, many problems remain as these four divisions
105 form a poorly useful classification not being based on monophyletic units that should offer
106 strong frames of reference in addressing planthopper evolutionary history. Moreover, from the
107 species to the family level, a consensus topology yet remains to emerge. Indeed, recent
108 molecular phylogenies (Song & Liang, 2013; Huang & Qin, 2018; Yu & Liang, 2018; W. Wang
109 *et al.*, 2019; Xu *et al.*, 2019; Kim *et al.*, 2021) have come to challenge the results of Urban &
110 Cryan (2007), to the point that attempting a simple consensus of all the phylogenetic hypotheses
111 would lead to retain only a few polytomous nodes, even for the seemingly well-established
112 sister families. A review of these studies suggests that most of the issues pertain to taxa and
113 characters sampling (Bucher & Bourgoïn, 2019). Indeed, all molecular phylogenies of
114 planthopper families were conducted either on a limited diversity of characters with only a few
115 gene sequences in the pioneer studies (Bourgoïn *et al.*, 1997; Yeh & Yang, 1999; Yeh *et al.*,
116 1998, 2005), or later on a too restricted taxonomic sampling never exceeding ~130 taxa (Cryan
117 & Urban, 2007, 2012; Song & Liang, 2013; Huang & Qin, 2018; Yu & Liang, 2018, Wang *et*
118 *al.*, 2019; Xu *et al.*, 2019; Kim *et al.*, 2021; Michalik *et al.*, 2023), failing to adequately consider
119 the high diversity and disparity of planthoppers. Altogether, this resulted in only partial or
120 biased representations of the planthopper taxonomic diversity and phylogeny, leading to a weak
121 congruence of the different hypotheses proposed until now.

122

123 Consequently, many questions about the phylogenetic relationships and evolutionary patterns
124 of planthoppers, already formulated more than 20 years ago (Bourgoin *et al.*, 1997), still
125 continue to remain and can be summarized in five major issues as follows:

126 (1) What is the first cladogenetic event that splits extant planthoppers? For a long time, the
127 hypothesis of Tettigometridae sister to the rest of planthoppers was consensual for the
128 majority of morphological approaches (Muir, 1923, 1930; Asche 1987; Emeljanov,
129 1990; Chen & Yang, 1995). Later, the Meenoplidae sister to all other planthoppers were
130 supported by some molecular approaches (Yeh *et al.*, 1998; Yeh and Yang, 1999), while
131 the clade Cixiidae+Delphacidae, sister to all other families was finally proposed by most
132 molecular analyses (Bourgoin *et al.*, 1997; Yeh *et al.*, 2005, Urban & Cryan, 2007;
133 Cryan & Urban, 2012; Song & Liang, 2013; Huang & Qin, 2018; Yu & Liang, 2018;
134 Kim *et al.*, 2021). Recent fossil-based analyses (Bourgoin & Szwedo, 2022, 2023; Zhao
135 *et al.*, 2023) led to formalize this early split dividing extant planthopper families into
136 Delphacoidea (Cixiidae+Delphacidae) and Fulgoroidea (all other families).

137
138 (2) Can we recognize large clades among these superfamilies? In addition of the splitting
139 of Delphacoidea and Fulgoroidea, are the general divisions proposed by Bartlett *et al.*
140 (2018) supported, and which families do they include? In particular, is the "issidoid
141 group" proposed by Gnezdilov 2013 (grouping Issidae, Caliscelidae, Acanaloniidae,
142 Tropiduchidae and Nogodinidae) phylogenetically supported?

143
144 (3) Among the supposed monophyletic family pairs traditionally accepted, which ones can
145 we retain: Cixiidae+Delphacidae, Kinnaridae+Meenoplidae, Achilidae+Achilixiidae,
146 Fulgoridae+Dictyopharidae, Lophopidae+Eurybrachidae?

147
148 (4) While the monophyly of most families remain to be confirmed with phylogenetic
149 analyses (Bartlett *et al.*, 2018), should we reconsider the monophyly of Achilidae
150 including Achilixiidae (Liang, 2001)? Likewise, the relatedness of the different lineages
151 within Cixiidae needs to be more closely investigated, as three incongruent evolutionary
152 patterns are now proposed in recent molecular studies with (a) Cixiidae as a
153 monophyletic unit sister to Delphacidae (Song & Liang, 2013; Urban & Cryan, 2007,
154 2012; Yu & Liang, 2018); or (b) Cixiidae as paraphyletic and including Delphacidae
155 (Ceotto *et al.*, 2008; Urban *et al.*, 2010), or (c) Delphacidae as paraphyletic including
156 subfamily Asiracinae Motschulsky, 1863 sister to all Cixiidae (Bucher et Bourgoin,

157 2019; Kim *et al.*, 2021). In addition, a particular attention is needed for the taxonomic
158 value of Nogodinidae that are now repeatedly found to be paraphyletic (Yeh and Yang,
159 1999; Yeh *et al.*, 2005; Urban & Cryan, 2007; Song & Liang, 2013; Bucher *et al.*, 2019),
160 as well as the issue to retain a separate paraphyletic family Kinnaridae including
161 Meenoplidae (Bourgoin, 1993).

162

163 (5) Lastly, questions remain on the placement of some families whose relationships were
164 strongly not consensual in the different phylogenetic inferences *i.e.* Caliscelidae,
165 Lophopidae, Tettigometridae and Tropicuchidae (Bourgoin *et al.*, 1997; Bucher *et al.*,
166 2019; Song & Liang, 2013; Urban & Cryan, 2007; Yeh *et al.*, 2005).

167

168 The weakness of current phylogenetic results is also attested by several molecular dating
169 studies, which suggested conflicting hypotheses on the age of diversification of Fulgoromorpha
170 (Fig. A). Song and Liang (2013) placed the divergence of Delphacoidea+Fulgoroidea in the
171 Late Permian, contradicting Johnson *et al.* (2018) who propose a younger diversification of the
172 two lineages, dated from the Late Triassic. Both studies nevertheless propose a relatively
173 congruent age of origination, placing the divergence Fulgoromorpha from other Hemiptera
174 during the Carboniferous (mid-Carboniferous for Song *et al.* (2013), Late Carboniferous for
175 Johnson *et al.* (2018)), which is in line with the recent addition of Aviorrhynchidae to
176 Fulgoromorpha (Bourgoin & Szwedko, 2022). With a difference that can reach more than 50
177 millions of years, the large time gap in the dating analyses underlines the need for a better
178 understanding of planthopper evolutionary history, with more constrained divergence times
179 associated with the great periods of diversification of the different lineages.

180

181 Addressing these questions, this study proposes a new investigation of the evolutionary history
182 of extant Fulgoromorpha, through a phylogenetic analysis based on a more substantial
183 molecular dataset, combining from previously published molecular works with newly published
184 data. Second, a dating analysis was conducted to estimate divergence times of the different
185 planthopper lineages. Using duly identified and classified fossils, a new estimate of their
186 diversification timeframe is therefore proposed, aiming to refine the temporal dimension of the
187 evolutionary framework of planthoppers. Accordingly, particular attention has been paid to the
188 taxonomic sampling to better represent the diversity of the Fulgoromorpha, allowing to test the
189 monophyly of the families and some subfamilies. This is the largest phylogenetic analysis
190 integrating a comprehensive number of planthopper taxa. We take the opportunity to discuss

191 the importance of sampling and data quality, and the theoretical and methodological biases
192 responsible for the instability and lack of consensus on the evolutionary history of the
193 Fulgoromorpha.

194

195

196 **2. Material and methods**

197

198 *2.1 Taxonomic sampling*

199

200 With the objective of providing a dataset that is as representative as possible of the diversity of
201 Fulgoromorpha, the selection of terminal taxa was done with maximizing the coverage of the
202 299 taxonomic suprageneric taxa currently recognized in the planthopper classification
203 available on FLOW (Bourgoin, 2023). A preliminary taxonomic sampling was achieved with
204 the selection of at least one to several species (with their molecular data sequences already
205 available and published in previous studies) to represent each of these suprageneric taxonomic
206 rank. From this first sampling of our ingroup taxa (572 sequenced specimens), a subsequent
207 selection was made to discard doubtful molecular data yet previously used in published
208 phylogenies, reducing the taxon sampling to 531. The process of verifying molecular data and
209 excluding doubtful taxa from the sampling are detailed in the following section. In addition, 20
210 outgroup species were selected to represent the diversity of lineages within hemipteran
211 suborders: Cicadomorpha Evans, 1946, whose taxonomic diversity was covered by 11 families
212 distributed in 3 super-families with Cercopoidea Leach, 1815 (5 taxa), Cicadoidea Westwood,
213 1840 (2 taxa), Membracoidea Rafinesque, 1815 (4 taxa); Coleorrhyncha Myers & China, 1929
214 (2 taxa); Sternorrhyncha Duméril, 1806 (3 taxa); Heteroptera Latreille, 1810 (3 taxa), plus one
215 species of Thysanoptera Haliday, 1836, sister-group to Hemiptera (Johnson *et al.*, 2018).

216

217 *2.2 Terminology and compatibility of molecular sequences*

218

219 All DNA sequences were retrieved from data available on GenBank. Genes were selected to
220 constitute a heterogeneous and varied dataset, including coding and non-coding fragments. Six
221 molecular markers were included in our analysis with three non-coding nuclear genes (*18S*, *28S*
222 *D3-D5*, *28S D6-D10*), the nuclear coding Wingless (*Wg*), and two coding mitochondrial genes:
223 Cytochrome Oxidase I (*COI*) and Cytochrome b (*Cytb*). Wherever possible, sequences with
224 the same voucher code were privileged to limit the use of chimeric taxa and get rid of potential

225 misidentification. As these sequences came from different studies, a nomenclature work and
226 delineation of molecular sequences had to be carried out to verify that they were comparable
227 and could be considered as homologous markers. We used Geneious 2022.1.1 (Kearse *et al.*,
228 2012) to define the domains to which the sequences corresponded. For this purpose, all
229 sequences for each RNA marker were mapped to a reference sequence of the complete gene of
230 *Brachyplatys subaeneus* Westwood, 1837 for *18S* (accession number: KY495690) and of
231 *Geisha distinctissima* (Walker, 1858) for *COI* sequences (accession number: NC_012617.1).
232 Delineation of *28S* domains was performed by the same mapping process, following the
233 secondary structure established by the annotated *28S* guide of *Eurydema maracandica* Oshanin,
234 1871 (Yu *et al.*, 2013) and by comparing primers used in the phylogenetic studies, which target
235 specific domains for sequencing. The nomenclatural definition of the markers used in our study
236 is summarized in Table S1. When genes were sequenced in multiple fragments (*e.g.* *18S*; *28S*
237 *D6-D10*), we assembled the different regions to obtain continuous sequences with Geneious
238 2022.1.1. All assembled sequences from separate fragments are reported in Table S2.
239 Conversely, for continuously sequenced RNA genes, only fragments corresponding to the
240 interest domains were then extracted. Size and location of extracted fragments from complete
241 sequences are indicated in Table S2. For some taxa, *COI* and *Cytb* sequences were extracted
242 from complete mitochondrial genomes. The mapping procedure revealed that the sequenced
243 *COI* of several studies does not correspond to the true *COI* 5P barcode as usually recognized,
244 but to the 3P terminal region of this gene. Two data blocks were thus identified for the gene
245 *COI*. Complete *COI* sequences were also present in our dataset. Therefore, all *COI* sequences
246 (3P, 5P and complete) were considered as a single marker with '?' for the corresponding missing
247 parts in the concerned taxa.

248

249 *2.3 Detection of erroneous data for the final dataset*

250

251 Several erroneous data extracted from GenBank were identified during preliminary analyses.
252 All sequences selected in our preliminary sampling have therefore been rechecked by: (1)
253 BLAST; (2) Detection of sequence divergence within the same family during alignment; (3)
254 comparison of sequences divergence from same taxa with different specimens when it was
255 possible; and (4) Phylogenetic inference to detect artefact and to double-check contaminations
256 and reconstruction artefacts. Details on sequences that are contaminated or qualified as doubtful
257 - and therefore that should be avoided in future molecular analyses - is appended in
258 Supplementary Table S3 and will be reported in FLOW in the 'molecular data' section

259 (Bourgoin 2023, in preparation). Our final taxonomic sampling contains 551 taxa including
260 ingroup and outgroup (Supplementary Table S2). Eleven *COI* sequences are not published on
261 GenBank but attached as supplementary data (Dataset S1), whose specimens are indicated in
262 Table S2. New sequences produced are newly published in this study with 181 newly generated
263 sequences for five families (Achilidae, Cixiidae, Derbidae, Issidae, Nogodinidae)
264 corresponding to five genes. All references to these new sequences are specified in Table S2.
265 The suprageneric taxonomic diversity covered by the final dataset is illustrated in Table A.

266

267 *2.4 Alignment and phylogenetic inferences*

268

269 Multiple sequence alignment was carried out in MAFFT 7.450 as implemented in Geneious.
270 For the full *18S*, *28S D3D5* and *28S D6D10* the following parameters were used: algorithm: E-
271 INS-I; Scoring-matrix: 200 PAM / k=2; Gap open penalty: 1.5; *COI*, *Cytb* and *Wg* sequences
272 were aligned as follows: Algorithm: G-INS-I; Scoring-matrix: 200 PAM / k=2; Gap open
273 penalty: 1.5. Because of their length polymorphism, initial and terminal regions of the non-
274 coding sequences (generated with a various set of primers in the different studies), could appear
275 highly fragmented and not always congruent in coverage in the outer regions. We corrected
276 these problems by slightly refining the alignment manually. Secondary structure for 18S and
277 28S genes was not considered in the alignment process and highly variables internal regions
278 have been kept with the automatic alignment to limit eye-driven homology hypotheses. We
279 checked that alignments for protein-coding genes were congruent with codon reading frame
280 using Geneious. In our study, the supermatrix approach (de Queiroz & Gatesy, 2007) was
281 preferred to the supertree method (Gordon, 1986). We used the software SequenceMatrix 1.7.7
282 (Vaidya *et al.*, 2011) to concatenate the dataset.

283

284 We performed maximum likelihood analyses using IQ-TREE 2.1.2 (Nguyen *et al.*, 2015) with
285 a dataset partitioned by genes and codon positions. For each partition, best-fitting substitution
286 models were selected by PartitionFinder 2.2.1 (Lanfear *et al.*, 2017) under the Akaike
287 Information Criterion (Akaike, 1973). Details on optimizing partition schemes and substitution
288 models are shown in Table S4. Phylogenetic analyses were carried out with the more thorough
289 and slower nearest neighbor interchange (NNI) search. The perturbation strength was defined
290 to 0.2 as recommended by IQ-TREE with datasets containing short sequences and the number
291 of unsuccessful iterations to stop was set to 10,000. The final analysis was repeat 10 times to
292 test the robustness and stability of the results and to avoid the tree search getting stuck in a local

293 optimum. Support for nodes was evaluated with 1,000 ultrafast bootstrap (UFBS)
294 approximations (considering UFBS values ≥ 95 as strong node support). All phylogenetic
295 analyses were performed on the computer cluster CIPRES Science Gateway 3.3 (Miller *et al.*,
296 2015).

297

298 *2.5 Fossil calibrations*

299

300 To calibrate the tree, we selected 10 fossils (Table B) according to the best practices suggested
301 by Parham *et al.* (2012) for justifying fossil calibrations. As none of the present fossils were
302 previously included in a phylogenetic analysis, attribution to a phylogenetic lineage was carried
303 out according to the apomorphy-based method. Fossils that did not fulfill these specific
304 conditions were not included in the dating analysis. As a result, the selected fossils are not
305 necessarily the oldest known for a given group but are those whose attribution to a systematic
306 position and stratigraphic age have been verified and justified. All fossils were used as
307 minimum age constraints for their specific nodes: minimum ages of fossils correspond to the
308 youngest limit of the stratigraphic interval in which the fossil was found or to the precise age
309 revealed by isotopic studies. We considered here that the oldest boundary of node constraints
310 by Fulgoromorpha fossils (related to extant lineage) in our analysis corresponds to the minimum
311 age of †*Aviorrhyncha magnifica* Nel *et al.*, 2013 (310 Mya). Due to the limited taxonomic
312 sampling and computational time, outgroup taxa were not included in the dataset for dating
313 analyses (Drummond & Bouckaert, 2015). We choose to constrain the age of the root as an
314 additional calibration. In our study, tree root height corresponds to the diversification of
315 Fulgoromorpha with the divergence of Delphacoidea and Fulgoroidea. To calibrate this node,
316 we used the age provided by the fossil †*Fulgoridiella raetica* Becker-Migdisova, 1962 dated
317 from the Early Jurassic (199.6 Mya) as the minimum age, and the maximum age was set with
318 the age of Insecta (406 Mya) according to Misof *et al.* (2014) (with a 95% confidence interval
319 of 451-373 Mya).

320

321 *2.6 Bayesian relaxed-clock analyses*

322

323 Molecular dating analyses were carried out with BEAST 1.10.4 (Suchard *et al.*, 2018). BEAUti
324 1.10.4 was used to create the input for BEAST. We used a reduced partitioned dataset without
325 partitions by coding positions to limit the number of estimated parameters for improving
326 convergence of the analyses. Best-fitting substitution models (Supplementary Table S4) were

327 selected by PartitionFinder 2.2.1 with a constrained partition as an input parameter and all the
328 parameters were estimated in BEAST. We implemented 3 partitioned clock models with *18S* +
329 *28S D3-D5* + *Wg*; *28S D6-D10*; *COI* + *Cytb* under an uncorrelated lognormal distribution
330 (UCLD). We defined a uniform prior distribution between 0 and 1, with a starting value of 0.1
331 on the mean of the UCLD model. We set the tree prior to the birth-death process with the
332 following priors: a uniform prior between 0 and 10 with a starting value of 0.1 for the mean
333 growth rate, and a uniform prior between 0 and 2 with a starting value of 0.5 for the relative
334 death rate. We used the most conservative approach of node-dating, in which fossil constraints
335 were applied on the stem-node as proposed by Parham *et al.* (2012). Here, morphological
336 support for assigning a fossil to an extant lineage within a clade was limited to avoid
337 overestimating divergence times, the parent node was therefore chosen to define the minimum
338 appearance age of a group. Table S5 summarizes fossil clade assignment and priors used in the
339 analysis with distribution and shape. We generated a starting tree with the topology resulting
340 from the phylogenetic inference: the topology was ultrametricized to fit our calibration scheme
341 in BEAST using the *chronos* function of the R package *ape* (Paradis & Schliep, 2019). The tree
342 model operators were turned off to keep the topology fixed so that only branch lengths were
343 estimated in the dating analysis. All others parameters were kept to their default prior
344 distribution. BEAST analysis was run for 300 million generations and sampled every 30,000
345 generations. All analyses were performed on the computer cluster CIPRES Science Gateway
346 3.3. We used Tracer 1.7.1 to assess the convergence of the run by examining the log files to
347 check the ESS values for all parameters. Maximum clade credibility tree was reconstructed with
348 TreeAnnotator 1.10.4 after removing a burn-in of 20%.

349

350

351 **3. Results**

352

353 *3.1 Dataset characterization and phylogenetic analyses*

354

355 Taxonomic sampling covers 80% of the suprageneric taxonomic rank within the extant
356 Fulgoromorpha. Even when combining all data, there was still great heterogeneity in the
357 representation of intra-familial taxonomic diversity for some families included in our study,
358 particularly for Flatidae, Tropiduchidae and Nogodinidae. The combined dataset of 6 genes
359 contains 8,159 characters for 551 taxa (including outgroups) with lengths per locus of: 2,145
360 pb (*18S*); 786 pb (*28S D3D5*); 3,169 pb (*28S D6D10*); 1,250 pb (*COI*); 491 pb (*Cytb*); 318 pb

361 (*Wg*). The alignment contains 3,729 parsimony informative sites with 53.9% of missing data
362 (?) according to the nucleotide statistics estimated in Geneious. Same topology was recovered
363 in the 10 independent phylogenetic analyses. The most likely tree (ln L= -258,102.81) is fully
364 resolved and most of the nodes are supported with high UFBS: 25.7% of nodes have UFBS=100
365 and 40.4% of nodes supported with UFBS \geq 95 with a median of node support of 87. The least
366 supported nodes generally involve nodes reflecting infra-family relationships.

367

368 3.2 *Planthopper phylogeny*

369

370 The simplified phylogeny with major lineages collapsed is presented in Fig. B. The complete
371 phylogeny (Fig. C) is presented here in 4 parts (1-4) in which main clades are numbered from
372 1 to 26. Our study recovers extant Fulgoromorpha (UFBS=100) as monophyletic and strong
373 UFBS is found across deep nodes (*i.e.* inter-familial relationships).

374

375 Clade 1 (Fig. C.1, UFBS=100) supports families Cixiidae and Delphacidae as a clade
376 sister to the remaining planthopper families, corresponding to the recently recognized
377 superfamily Delphacoidea. Our wider taxonomic sampling for both families (122 and 126 taxa
378 for Delphacidae and Cixiidae, respectively), suggests here that Delphacidae is paraphyletic, and
379 splits into two separated groups: Eudelphacida *sec.* Asche, 1990 (= Delphacinae Leach, 1815
380 *sec.* Emeljanov, 1996) on one side (Clade 2, UFBS=100), and clade 3 (UFBS=68) including
381 Protodelphacida *sec.* Emeljanov, 1996 (= Asiracinae *sec.* Asche 1985, 1990), as a single
382 monophyletic lineage (*versus* Asche, 1985, 1990; Emeljanov, 1996), sister-group to Cixiidae
383 on the other side. In our preliminary analyses, computed with a reduced taxonomic sampling,
384 Delphacidae was found monophyletic only once, with low support (no stability of topologies in
385 10 independent analyses). Other phylogenetic units among Eudelphacida are congruent with
386 the hypotheses proposed by Asche (1985, 1990), Emeljanov (1996), Urban *et al.* (2010) and
387 Huang *et al.* (2017), as all of the previously recognized lineages either as subfamilies or tribes
388 (Kelisiini/ae Wagner, 1963, Stenocranini/ae Wagner, 1963, Delphacinae Leach, 1815) are
389 monophyletic (BS \geq 99), as well as Saccharosydniini, Tropidocephalini, Delphacini with UFBS
390 \geq 94). However, a strong support for a sister relationship between Kelisiini/ae and
391 Stenocranini/ae is observed (*versus* Emeljanov, 1996).

392

393 Clade 4 (Fig. C.2, UFBS=71) represents Cixiidae and comprises three previously
394 identified monophyletic lineages (Luo *et al.*, 2021): the oeclian lineage (Fig. C.2, Clade 5,

395 UFBS=92) with Oeclini including Bothriocerini, sister to the pentastrinian lineage including
396 Borysthenini sister to Pentastrini with low support (Fig. C.2, Clade 6, UFBS=22), and the
397 cixiian lineage (Fig. C.2, Clade 7, UFBS=93) with all other sampled tribes of our study
398 according to the following sequence: (Gelastocephalini + ((Pintalini + Australian Cixiini) +
399 (Andini + (Eucarpini + (Bennini + other Cixiini including Semonini)))). Mnemosysini,
400 previously placed in the pentastrinian lineage (Luo *et al.*, 2021), is here moved at the basal node
401 of the oeclinian lineage.

402

403 Clade 9 (UFBS=99), corresponding to all Fulgoroidea families (*sec.* Bourgoin &
404 Szwedo, 2022), separates basally into clade 8 (Fig. C.3, UFBS=100) Meenoplidae included in
405 Kinnaridae sister to all other extant Fulgoroidea families in clade 10 (UFBS=100). This strong
406 clade 10 separates the Tettigometridae (Fig. C.3, Clade 10, UFBS=100) sister to the remaining
407 planthopper families.

408

409 Clade 11 (Fig. C.3, UFBS=63) is weakly supported, although it suggests a sister
410 relationship between the strongly supported monophyletic units of Derbidae (Clade 12) and
411 Achilidae including Achilixidae (Clade 13) (UFBS=100 and 95, respectively). In Derbidae,
412 taxa show longer internal branches suggesting a higher rate of divergence within this family.

413

414 Following Clade 11, the strongly supported Clade 14 (Fig. C.3, UFBS=100) separates
415 sister families Dictyopharidae and Fulgoridae from the remaining planthoppers. If
416 Dictyopharidae monophyly is well supported (Fig. C.3, Clade 15, UFBS=93), monophyly of
417 Fulgoridae is not (Clade 16, UFBS = 50). This weakness is potentially due to the *Zanna* sp.
418 clade showing an instable basal branching with any of the two families according to our
419 preliminary analyses, always introducing a low UFBS at the corresponding node. In
420 Dictyopharidae, all tribes included in our sampling are retrieved as monophyletic, with the
421 exception of Orthopagini Emeljanov, 1983. In Fulgoridae, intra-familial relationships within
422 the family are not congruent with the current classification - based on the suggestions of
423 Lallemand (1956, 1959, 1960, 1963), Emeljanov (1979, 2004) - and the phylogenetic results of
424 Urban & Cryan (2009).

425

426 The strongly supported Tropicuchidae family (Clade 18, UFBS=100) was retrieved as
427 sister lineage to remaining Fulgoroidea families (Fig. C.4, Clade 17, UFBS=59). However, this
428 placement remains questionable due to its low support at node. In preliminary analyses the

429 placement of this family was not stable, moving within the topology with always a low support,
430 especially as sister lineage to (Dictyopharidae + Fulgoridae).

431

432 Within clade 19 (Fig. C.4, UFBS = 98), monophyly of most families is recovered with
433 strong support value for Acanaloniidae (Clade 22, UFBS=100), Caliscelidae (Clade 23,
434 UFBS=100), Flatidae (Clade 24, UFBS=99), Ricaniidae (Clade 25, UFBS=100). Surprisingly,
435 monophyly of Lophopidae was not recovered due to the genus *Serida* Walker, 1857 moved
436 within Eurybrachidae, while these families and their sister relationships (Clade 20, UFBS=98)
437 remain strongly supported monophyletic units. Issidae (Clade 26, UFBS=74) is recovered as
438 monophyletic, but with a low basal bootstrap support. Within this family, all tribal units
439 reviewed by Wang *et al.* (2016) also recovered as monophyletic (Hysteropterini, Kodaiianellini,
440 Issini, Sarimini, Parahiraciini, Hemisphaeriini), with the exception of Thioniini and
441 Mongolianina. As expected, Nogodinidae appear as a polyphyletic grouping, split according to
442 the genera in various place within the ‘higher’ planthoppers.

443

444 3.3 Dating analysis

445

446 Convergence of dating analysis was ensured by ESS values and plots indicated in Tracer (The
447 .log file resulting from the analysis is appended in supplementary data). Results of analysis are
448 presented as a simplified chronogram in Fig. D where only major clades are presented. The
449 complete tree, with node age and 95% CI, is presented in Supplementary Data as a tree file.
450 The dating analysis suggests that the diversification of extant Fulgoromorpha occurred in the
451 Early Triassic with a median age of 238.06 Mya (95% CI: 199.6–352.9 Mya). Divergence of
452 Fulgoromorpha with the rest of Hemiptera was not estimated because outgroups were excluded
453 from the analysis to solve convergence issues in dating analyses. The age of the early lineages
454 of Delphacoidea, with the Cixiidae and Delphacidae, is estimated in the Late Triassic at 213.28
455 Mya (95% CI: 131.16–262.25 Mya), while all other families in Fulgoroidea *sec.* Bourgoin &
456 Szwedo, 2022 would date back to the Middle Triassic at 227.15 Mya (95% CI: 180.21–344.97
457 Mya). Our dating results indicate that all major lineages of extant Fulgoromorpha were already
458 present by the Late Jurassic. Nevertheless, ‘higher’ planthopper families diverged during the
459 Early Cretaceous with rapid diversification during middle to Late Cretaceous. Because of our
460 conservative strategy of uniform distributions for node calibrations, the 95% CIs of our analysis
461 were relatively wide (Fig. S1). All divergence time estimates for each family are reported in
462 Table C.

463

464

465 **4. Discussion**

466

467 Our study revealed unsurprisingly that Fulgoromorpha is composed of a monophyletic
468 superfamily Delphacoidea sister to a monophyletic superfamily Fulgoroidea. This hypothesis
469 is now considered as consensual, being both supported by morphological analyses (Asche,
470 1987; Emeljanov, 1990, Bourgoïn, 1993) including from a fossil perspective (Bourgoïn &
471 Szwedo, 2022, 2023), and most molecular phylogenies (Cryan & Urban, 2012; Kim *et al.*, 2021;
472 Song & Liang, 2013; Urban & Cryan, 2007, 2012; Yu & Liang, 2018; Michalik *et al.*, 2023).

473

474 *4.1 Paraphyly of Delphacidae*

475

476 In most phylogenetic studies, Cixiidae and Delphacidae were considered as sister monophyletic
477 families. However, this result was challenged by Urban and Cryan (2007), which depicted a
478 paraphyletic Cixiidae including the Delphacidae (a scenario already suggested by Asche, 1985)
479 with a maximum parsimony analysis based on four selected species in both Cixiidae and
480 Delphacidae, although a Bayesian analysis of the same sampling recovered two monophyletic
481 sister taxa. Ceotto *et al.* (2008) recovered a similar paraphyletic Cixiidae during an analysis
482 based on four delphacid species for 55 cixiid ones. Yet, Kim *et al.* (2021), in a strongly
483 disequibrated sampling (11 and 1 species for Delphacidae and Cixiidae, respectively)
484 produced either two monophyletic sister families, or refuted the Delphacoidea clade with
485 Cixiidae sister clade to all planthoppers, or a paraphyletic Delphacidae: their unique cixiid taxon
486 *Pentastiridius* grouping with their single protodelphacid taxon *Ugyops*, both sister to the rest of
487 delphacids. This last unconventional pattern was already proposed by Bucher & Bourgoïn
488 (2019) based on a wider sampling of respectively 16 and 19 delphacid and cixiid species. Our
489 study based on a much wider taxonomic sampling for both families (122 and 126 taxa for
490 Delphacidae and Cixiidae, respectively) seems to confirm paraphyly of Delphacidae, splitting
491 into Eudelphacida *sec.* Asche 1990 and monophyletic Protodelphacida *sec.* Emeljanov, 1996,
492 sister group to Cixiidae on the other side (Fig. C.1, Clade 2, UFBS=80). Delphacidae was found
493 monophyletic only once in preliminary analyses under conditions of taxonomic under-sampling
494 within these two families and with low support (no stability of topologies in 10 independent
495 analyses). These successive results reveal that increasing the molecular sampling of delphacid

496 taxa with a better sampling at the tribal level, even confronted to a large cixiid sampling,
497 disclose the paraphyly of the family as a stable characteristic.

498

499 From a morphological perspective this result is counter intuitive, rejecting the most significant
500 and unique apomorphic character of Delphacidae with the presence of a movable and apical
501 metatibial spur exposing a gradual transformation series of the spur conformation (Markevich
502 *et al.*, 2021). It suggests two possible scenarios: (1) the spur appeared twice, independently in
503 Protodelphacida in which it remained quite simple, more or less conical, never denticulated,
504 versus flattened and always dentated in Eudelphacida (Asche, 1990; Markevich *et al.*, 2021);
505 or (2) the spur appeared once in Delphacoidea much probably unarmed, secondly disappearing
506 in Cixiidae therefore miming the plesiomorphic pattern of other planthoppers, leading to
507 consider them as 'cryptic' delphacids. While this second scenario would apparently be more
508 parsimonious (one apomorphic acquisition secondarily absent in Cixiidae), we would favor the
509 first one (two independent acquisitions) because up to now, all Cretaceous fossils observed
510 exhibit a cixioid pattern, without any metatibial spur, which should have been observed in their
511 common ancestor (Luo *et al.*, 2021). Testing further this paraphyly of Delphacidae is now
512 necessary and an even more representative sampling of Protodelphacida is strongly needed:
513 only Asiracini Motschulsky, 1863, Idiosystatini Emeljanov, 1995, Ugyopini Fennah, 1979 were
514 involved in our analysis, but Eodelphacini Emeljanov, 1995, Platysystatini Emeljanov, 1995,
515 Tetrasteirini Emeljanov, 1995 should be included in future analyses. Very unfortunately we had
516 to discard Neopunanini Emeljanov, 1995, the only available sequences (Urban *et al.*, 2011)
517 appearing to be corrupted. According to our results, relationships between Ugyopinae Fennah,
518 1969 and Asiracinae Motschulsky, 1863 suggested by Emeljanov (1996) is not supported, the
519 former being included in the later. Paraphyletic Asiracinae, as suggested by Emeljanov (1996)
520 including all other Delphacidae or as sister clade to all other Delphacidae by Asche, 1985, 1990
521 is also not supported.

522

523 *4.2 Systematics of Cixiidae*

524

525 The three recently identified monophyletic lineages (Luo *et al.*, 2021) are recovered particularly
526 with the oeclinian lineage including Bothriocerini Muir, 1923, as recently published (Le Cesne
527 *et al.*, 2021). Based on only one sequenced taxon, Mnemosysini Emeljanov, 1992 is retrieved
528 as sister to the oeclinian clade, although it was previously placed in the pentastrinian lineage
529 (Luo *et al.*, 2022). Nevertheless, we suggest that it might be an artefact in our study and it needs

530 to be consolidated with additional sequenced taxa of the tribe. Branching of Borysthenini
531 Emeljanov, 1989 as a sister clade to the pentastirini lineage (already evocated in Luo *et al.*
532 (2021)) needs confirmation with a more consistent sampling of the tribe. In the cixiini
533 lineage, the split of Cixiini Spinola, 1839 into two different independent lineages, separating
534 'Australian cixiini' (related to Pintaliini Metcalf, 1938) as sister clade Andini Emeljanov, 2002
535 to the other Cixiini taxa is strongly supported and a tribal recognition of this group should be
536 proposed, although morphological-based evidences are yet to be found. The exact placement of
537 Gelastocephalini Emeljanov, 2000 and Eucarpiini Emeljanov, 2000 needs to be confirmed with
538 a larger sampling as well as the placement of the genus *Achaemenes* Stål, 1866.

539

540 4.3 *Tettigometridae* within the *Fulgoroidea*

541

542 Another interesting result of the study is the relatively early branching of Tettigometridae as
543 sister clade to all Fulgoroidea families (except Kinnaridae-Meenoplidae having already
544 diverged). Tettigometridae were traditionally placed at the first branching lineage of
545 planthoppers according to morphological characters (Muir, 1923, 1930; Asche 1987;
546 Emeljanov, 1990; Chen & Yang, 1995). Challenged by Bourgoïn (summarized and reviewed
547 in Bourgoïn *et al.*, 1997), Tettigometridae were later constantly placed in the 'higher' families
548 group, often closely related to Tropiduchidae and Flatidae (Bourgoïn *et al.*, 1997, Yeh *et al.*,
549 2005, Urban & Cryan, 2007; Cryan & Urban, 2012; Song & Liang, 2013; Huang & Qin, 2018;
550 Yu & Liang, 2018; Kim *et al.*, 2021). The new position of Tettigometridae within Fulgoroidea
551 might be due to our larger sampling, more representative of the diversity of the group than in
552 previous studies in which the family was often summarized to just one or two strongly related
553 species. However, the Tettigometridae initial long branch also suggests a possible long branch
554 attraction effect. According to the recent revision of the higher classification of the family
555 (Mozzafarian *et al.*, 2019), still some key tettigometrid lineages are missing for an optimal
556 representation in a molecular analysis (particularly Asian Egropinae Baker, 1924 and
557 Afrotropical Plesiometrini Bourgoïn 2018) to confirm this new placement. While Meenoplidae-
558 Kinnaridae and Tettigometridae are undoubtedly monophyletic groups with their own strong
559 morphological apomorphies, it is interesting to note that both share fully reduced female
560 genitalia, although in strongly different abdominal terminalia conformations.

561

562 4.4 *The clade Derbidae-Achilidae*

563

564 Already proposed (Bourgoin, 1993, Urban & Cryan, 2007), the Achilidae+Derbidae clade
565 (Clade 11; Fig. C.3, UFBS=63) remains relatively weak in our analysis, despite strong support
566 for the two families. It likely reflects the breadth of other phylogenetic results, which often find
567 them successively placed separately (Asche, 1987; Emeljanov, 1990; Chen & Yang, 1995; Yeh
568 *et al.*, 2005; Kim *et al.*, 2021), often with Derbidae (sometimes including some achilid taxa, the
569 latter appearing paraphyletic (Urban & Cryan, 2007) as sister clade to Achilidae (Emeljanov,
570 1990; Huang & Qin, 2018). The already mentioned issue of a too short sampling probably
571 explain that, also for these two families. Unfortunately, Derbidae remain difficult to place,
572 probably due to their higher rate of divergence within this family as shown by its particular long
573 branches. While wider than in any other molecular analysis, our own sampling remains far from
574 optimal for these families and their precise relationships as well as their internal ordering of
575 tribes still need to be investigated more carefully. The genus *Bebaiotes* Muir, 1924 is strongly
576 nested within Achilidae, definitively excluding its placement within Cixiidae (Liang 1999,
577 2001). Achilixiidae currently contain two subfamilies: Achilixiinae Muir, 1923 and Bebaiotinae
578 Emeljanov, 1991 both classified within Achilidae (Emeljanov, 1991) or in a separate family
579 Achilixiidae (Urban & Cryan 2007, Bartlett *et al.*, 2018). Exact positioning of these subfamilies
580 related to Achilidae as a monophyletic group or not, still need to be solved with a wider
581 sampling analysis of the clade (Achilidae+Derbidae) including representatives of genus
582 *Achilixius* Muir, 1923.

583

584 4.5 Phylogeny and classification of Dictyopharidae + Fulgoridae

585

586 Clade 14 (Fig. C.3, UFBS=100) fully supports the monophyly of this taxonomic unit, as all
587 previously published results. However, the division between the two families remains uncertain
588 due to the uncertain placement of Zanninae Metcalf, 1938 (either retrieved within Fulgoridae
589 sister group of the remaining taxa or included in the Dictyopharidae as sister clade to the other
590 taxa). This makes the monophyly of the two families weakly supported with UFBS= 93 and 50
591 for the Dictyopharidae and the Fulgoridae, respectively. Although originating mainly from
592 Urban & Cryan (2009) data, our resulting topology for this clade differs markedly from those
593 proposed by these authors not only in suggesting paraphyletic Fulgoridae in two modalities:
594 (Zanninae + (Dictyopharidae + other Fulgoridae)) under ML analysis or ((Zanninae +
595 Dictyopharidae) + Fulgoridae) under Bayesian analysis, but also in the distribution of genera
596 within the Fulgoridae. Despite this, we confirm that the current classification of Fulgoridae in
597 subfamilies and tribes largely recognizes non-monophyletic taxa (Urban & Cryan, 2009), and

598 that a revised classification is strongly needed for this emblematic family. Of course, alleviating
599 the geographical bias in the sampling of data concerning the almost exclusively Neotropical
600 Fulgoridae is obvious, and Afrotropical, Australian and especially Asian taxa would have to be
601 added to the dataset.

602

603 For Dictyopharidae, our dataset resulted in a more structured result consistent with the tribal
604 units already recognized, but differently arranged compared to the topology obtained in the
605 morphological analysis by Song *et al.* (2018). In our analysis, Orgeriinae represent an early
606 branching position (considered as sister-clade to all other Dictyopharidae) in line with their
607 recognition as a distinct subfamily, *versus* in the study by Song *et al.* (2018) in a group of taxa
608 which was probably artificial, bringing together genera with reduced and leathery wings
609 (Scoloptini, *Fernandea* sp., Phylloscelini, Ranconini, Capenini, Orgeriini). To resolve both this
610 uncertainty in the delineation of the respective families and their inner classification, a larger
611 sampling is again necessary. It needs focusing on the hinge taxa between the two families
612 distinguished by Emeljanov (1979) with representatives of Dichopterinae Melichar, 1912,
613 Lyncidinae Schmidt, 1915, but also on the early branching groups recognized by Song *et al.*
614 (2018) in their morphological phylogeny (e.g. Aluntiini Emeljanov, 1979; Cleotychini
615 Emeljanov, 1997, Arjunini Song & Szwed, 2016).

616

617 *4.6 Tropicuchidae*

618

619 With our available sampling, the family Tropicuchidae appears as a moderately supported clade
620 sister to the rest of the ‘higher’ Fulgoroidea families (Fig. C.4, Clade 19, UFBS=98). However,
621 their sister relationship remains questionable (Fig. C.4, Clade 17, UFBS=59). Currently 25
622 tribes (four of them fossils) are described within Tropicuchidae (Stroiński *et al.*, 2022), which
623 are represented by only 10 taxa in the present dataset: how relevant is the current Tropicuchidae
624 (Fennah, 1982, Gnezdilov, 2013) classification remains to be assessed. Approaching the family
625 with only one species and mitogenomic data only probably explains its unusual branching just
626 after Meenoplidae in Michalik *et al.* (2023). This should be regarded as artefactual.

627

628 *4.7 ‘Higher’ planthopper families*

629

630 This well-supported node and generally well found in previous studies (Urban & Cryan, 2007;
631 Yeh *et al.*, 2005; Huang & Qin, 2018; Kim *et al.*, 2021) includes eight families including nearly

632 4,100 species for nearly 30% of planthopper diversity. However, all the groupings between
633 families found below this node appear weakly supported and cannot be reasonably discussed
634 further. Having already shown the significant impact of sampling throughout this work, we
635 consider it very likely that a sample that is more representative of the diversity of these families
636 in the future will have significant effects on the grouping of taxonomic units observed. A good
637 example of this instability is the Nogodinidae issue, regularly found polyphyletic and in
638 different ways, in molecular analyses (Yeh *et al.*, 2005, Urban & Cryan, 2007; Song & Liang,
639 2013, Bucher & Bourgoïn, 2019; this work). It is clear that the Nogodinidae do not form a
640 monophyletic group and that the family cannot be maintained: its non-related subunits belong
641 to several of these related families whose diagnoses will have to be reviewed in order to
642 accommodate these taxonomic subunits of the Nogodinidae.

643 What will be the impact of the huge family Flatidae on the taxonomic arrangement of all these
644 families when it will be better sampled? Except for polyphyletic Nogodinidae, all these families
645 seem to be good monophyletic groups, although the monophyly of Issidae remains
646 questionable. The "issidoid group" of families proposed by Gnezdilov, 2013 (grouping Issidae,
647 Caliscelidae, Acanaloniidae, Tropiduchidae and Nogodinidae) is not supported. Here also it is
648 too early to discuss further how these families should be classify because of the reduced
649 sampling of our dataset regarding the diversity of these taxa.

650

651 *4.8 Issidae phylogeny and classification*

652

653 Issidae molecular phylogeny was first addressed by Wang *et al.* (2016), dividing the family into
654 Thioninae, Issinae - including Issini and Hysteropterini which upgraded later to subfamily
655 (Bourgoïn *et al.*, 2020) - and Hemisphaerinae. Gneznilov *et al.* (2020) downgraded Thioninae
656 to subtribe Thionina sister to Issina, both upgraded to tribe later (Gnezdilov, 2022). In
657 Gnezdilov *et al.* (2022), Hemisphaerinae *sec.* Wang *et al.*, 2016 remains a valid taxon in a new
658 trichotomic node Issinae *sec.* Gnezdilov *et al.*, 2022 with Issini and Thioniini, both sister to
659 Hysteropterinae (*op. cit.* Fig. 3, 50% majority-rule consensus tree). A result rather similar is
660 depicted in our new analysis but Kodaianellini moved as sister clade to a paraphyletic Thioniini
661 group, sister to Issini. 2 Thioniini taxa are found as sister clade to all other Issidae (Fig. C.4,
662 Clade 26). These results address the origin of Nearctic Issidae as paraphyletic group, which
663 draw totally different diversification events: an older vicariance event splitting the family into
664 two major lineages, and one to several more recent New World dispersals. As for the other
665 planthopper families, enrichment of the Issidae dataset with new sequenced taxa since Wang *et*

666 *al.* (2016) has progressively modified the topology the tree for this family. However, as several
667 Neotropical taxa from early branching lineages of the Issidae are still missing from all these
668 analyses (which also suffer from the same bias as Gnezdilov *et al.* (2022)'s study of insufficient
669 representation of neighboring taxa with Flatidae, Nogodinidae in particular), all this generates
670 taxonomic instability at the major node of the family, and we should expect further changes in
671 the classification of Issidae in the future. Genus *Picumna* Stål, 1864 was not included in our
672 analysis because of the absence of gene in common for both taxa available on GenBank and on
673 the too short sequences. In Gnezdilov *et al.* (2022), this Nearctic genus was also basal to all
674 Issidae and he even suggested that it might represent a tribal rank. Although not discussed in
675 Gnezdilov *et al.* (2022), all recent results based on a wider Nearctic sampling agree with an
676 early split of a Nearctic lineage at this stage, fully compatible with a Gondwanan origin of the
677 family as suggested in Bourgoïn *et al.* (2018), an age of the lineage also recovered here.

678

679 4.9 Timing of diversification in extant Fulgoromorpha

680

681 Our dating analysis suggests that the diversification of extant Fulgoromorpha occurred in the
682 Early Triassic (median age = 238.06 Mya) and that their origin within Hemiptera likely
683 occurred in the Permian (Misof *et al.*, 2014). We found that the diversification of Delphacoidea
684 and Fulgoroidea *sec.* Bourgoïn & Szwedo, 2022 took place in the Middle Triassic, 213.28 Mya
685 and 227.15 Mya, respectively. All major lineages of extant Fulgoromorpha emerged and were
686 already present by the end of the Jurassic. Nevertheless, the 'higher' families clade diverged
687 during the Early Cretaceous with a rapid diversification during the middle to Late Cretaceous,
688 a period that witnessed the Angiosperm Radiation (Benton *et al.*, 2022). According to our
689 results, all planthopper families were already present around 125 Mya. Without excluding
690 dispersal events, it is therefore likely that all families have been driven in their distribution and
691 evolution in subsequent subfamilial lineages by the geographical constraints of the
692 Gondwanan break-up. Evolutionary history of all extant planthopper families might have
693 therefore been shaped by early vicariance events during the middle to Late Cretaceous period.
694 Such a scenario was already suggested in a first molecular dating analysis for the Issidae that
695 was reported from the Cretaceous between 116.67 and 131.58 Mya according to different
696 probability densities of priors on node ages (Bourgoïn *et al.*, 2018). These previous results are
697 confirmed here, *versus* Gnezdilov (2022)'s statement considering Issidae as a younger lineage
698 of Oriental origin (Eocene, Gnezdilov, 2013b), already challenged in this 2022 analysis by the
699 sister position of the Nearctic genus *Picumna* to all other Issidae.

700

701 Interestingly, all internal branches of Fulgoridae are very short, suggesting a rapid
702 diversification processes. It appears that an explosive evolutionary radiation took place for the
703 family around 135-125 Mya (Supplementary Fig. S1). Such a rapid radiation can probably
704 explain the difficulties in establishing a reliable classification of the family and in reaching a
705 clear delimitation between Dictyopharidae and Fulgoridae.

706 A similar rapid evolutionary radiation event seems to have occurred concurrently in their sister
707 group of the 'higher' planthopper families. For instance, it is clear in the sister group of the
708 Tropiduchidae, where the successive short-branched basal nodes gave rise to nearly a third of
709 the current diversity of the Fulgoromorpha, albeit with various evolutionary successes
710 according to these higher families. At this stage, Gondwana was already separated from
711 Laurasia, which is congruent with the current distribution of all these families still mainly
712 located in the tropical belt. Diversification through early vicariance events, linked with the
713 break-up of Gondwana into smaller continents and leading to the emergence of subsequent
714 lineages during the Late Cretaceous, is a hypothesis that should be tested in the future once
715 phylogenies of these families will be better advanced.

716

717 *4.10 Limitations of the study*

718

719 Using all relevant molecular data combined into a single phylogenetic analysis for the first time,
720 our study highlights the fundamental impact of sampling on the resulting tree topologies. If the
721 question "More characters or more taxa for a robust phylogeny?" has been addressed many
722 times (reviewed in Nabhan & Sarkar, 2012), our study provides another example of the impact
723 of adding many taxa, all carrying their evolutionary history, on the resolution and robustness of
724 the nodes, especially at the backbone level of the tree. Increasing the taxon sampling (here
725 defined *a priori* based on the taxonomic diversity currently recognized in the group) likely
726 increases the opportunity of including key taxa that diverged early, which makes it possible to
727 reconstruct a more consistent evolutionary history at deep nodes. This issue of homogeneous
728 representation of diversity was nevertheless a limitation for outgroup sampling. If we tried to
729 represent the maximum number of lineages within Hemiptera for the phylogenetic analyses, the
730 under sampling of taxa within these lineages led us to very high divergence rates between our
731 ingroup and outgroup taxa, which did not allow us to reach convergence for the divergence time
732 estimates. Having identified contaminated, corrupted molecular sequences used in previous
733 phylogenetic studies, we also underline the crucial importance of their good quality

734 systematically rechecked by a blast and ideally confirmed with good congruence of molecular
735 sequences for related species.

736

737 The importance of the quality of a fossil dataset for the calibration of internal nodes has also
738 been highlighted. In this study, a revision of the morphological characters justifying the
739 relatedness of a fossil taxon to an extant lineage led us to modify the sampling of the taxa
740 commonly used in the dating analyses of Fulgoromorpha, as well as their stratigraphic age that
741 are updated. Nonetheless, it is important to note that none of the fossils used here have been
742 included in a phylogenetic analysis and therefore the character sets are not stated to be taken as
743 phylogenetically justified. It is thus quite likely that the phylogenetic placement of these fossils
744 will be rearranged because of a future analysis grouping together extant and fossil taxa. We
745 have no doubt that the subsequent results that would bring together the paleontological and
746 neontological data will challenge their use as calibration points for node-dating analyses, which
747 would also have a consequent impact on divergence times and diversification for
748 Fulgoromorpha.

749

750 **5. Conclusions**

751

752 This study proposes a new phylogenetic framework and timeline for Fulgoromorpha. Although
753 challenged by studies biased by too small sampling to infer the planthopper phylogeny, we
754 generally confirm the results of Urban & Cryan (2007), with Delphacoidea including Cixiidae
755 and Delphacidae being sister to Fulgoroidea (*sec.* Bourgoin & Szwedo, 2022). However, some
756 unexpected results also emerge: (1) the possible paraphyly of Delphacidae whose
757 Protodelphacida seems more related to Cixiidae than to other delphacids; (2) the
758 Tettigometridae moving out from the group of the 'higher' families to be considered as sister
759 clade to all others Fulgoroidea families (except for Meenoplidae-Kinnaridae); and (3) the
760 Tropiduchidae placed in a sister group of the other 'higher' families including the Lophopidae-
761 Eurybrachidae. Addressing more precisely the other issues listed in the introduction, the couples
762 of previously paired families are well recovered with: (1) the Meenoplidae-Kinnaridae with the
763 paraphyletic Kinnaridae; (2) the Achilidae-Derbidae clade with the Achilidae Plectoderini
764 including the Achilixiidae (represented by the genus *Bebaiotes*); (3) the Fulgoridae-
765 Dictyopharidae clades, with Zanninae retrieved as the early branching lineage of the Fulgoridae
766 in a weakly supported node; and (4) the Lophopidae-Eurybrachidae. Four families are now
767 documented enough to start looking to their main internal phylogenetical structuration. In

768 Delphacidae Eudelphacida, all major subfamilies/tribes are fully recovered with a sister
769 relationship between Kelisiinae/i and Stenocraninae/i. Protodelphacida is a separate sister to
770 Cixiidae in a monophyetic clade including Ugyopini, Asiracini and Idiosystatini grouped in a
771 sister taxon. In Cixiidae, three main clades are recovered corresponding to the oeclian, oeclian,
772 pentastirian and cixiian lineages suggested by Luo *et al.* (2021) but with Mnemosynini
773 placed sister to the oeclian. In Fulgoridae, the current classification of subfamilies and tribes
774 does not recover at all the phylogeny. All tribal groups are recovered for Issidae excepted
775 Thioniini splitting into a group sister to all other issids and another sister to Issini, both sister
776 to Kodaianellini.

777 Fossil-calibrated molecular dating of current families estimates the first diversification of
778 planthoppers in Early Triassic around 240 Mya and those of the superfamilies Delphacoidea
779 and Fulgoroidea around 220 Mya. By the end of the Jurassic, all major planthoppers lineages
780 were originated and all families diversified around 125 Mya. In some parts of the tree topology,
781 the dating analyses point to rapid evolutionary radiations, which occurred particularly in
782 Fulgoridae around 125-130 Mya. However, both our taxon and character samplings remain
783 under-represented to draw more definitive conclusions. The Tropiduchidae and the Flatidae,
784 rich and disparate groups, seem to be the most critical clades from this point of view, and the
785 addition of new sequences for these families is a priority for testing the present results. The
786 paraphyly found in Delphacidae represents a very interesting point to study if we can complete
787 the dataset with new sequences of Protodelphacida; the same applies to the Tettigometridae and
788 the Achilixiidae whose new phylogenetic position must be confirmed. In other words, more
789 reliable molecular sequences are critically needed since many nodes remain unstable at the
790 mercy of adding a new taxon in the analysis.

791

792 **Acknowledgements**

793

794 For providing additional sequences, data and discussions, the authors are strongly indebted to
795 Birgit Loecker, Roslyn Mirrington, Maxime Le Cesne, Adeline Soulier-Perkins and Jacek
796 Szwedo. All photographs included in this publication were taken by Gernot Kunz and we thank
797 him for their use. This research was partly funded by National Natural Science Foundation of
798 China (32100369).

799

800

801 **References**

802
803 Akaike, H. (1973). *2nd International Symposium on Information Theory*. Akadémiai Kiadó.
804 Asche, M. (1985). Zur Phylogenie der Delphacidae Leach, 1815 (Homoptera Cicadina
805 Fulgoromorpha). *Marburger Entomol*, 2(1-2), 1-910.
806 Asche, M. (1987). Preliminary thoughts on the phylogeny of Fulgoromorpha (Homoptera:
807 Auchenorrhyncha). In: *Proceedings of the 6th Auchenorrhyncha Meeting*, Turin, Italy,
808 7th–11th September, 47–53.
809 Asche, M. (1990). Vizcayinae, a new subfamily of Delphacidae with revision of Vizcaya Muir
810 (Homoptera: Fulgoroidea), a significant phylogenetic link. *Bishop Mus. Occas. Papie* 30,
811 154-187.
812 Bartlett, C., Deitz, L., Dmitriev, D., Sanborn, A., Soulier-Perkins, A., & Wallace, M. (2018).
813 *The Diversity of the True Hoppers (Hemiptera: Auchenorrhyncha)*.
814 <https://doi.org/10.1002/9781118945582.ch19>
815 Benton, M. J., Wilf, P., & Sauquet, H. (2022). The Angiosperm Terrestrial Revolution and the
816 origins of modern biodiversity. *New Phytologist*, 233(5), 2017-2035.
817 <https://doi.org/10.1111/nph.17822>
818 Bourgoïn, T. (1993). Female genitalia in Hemiptera Fulgoromorpha, morphological and
819 phylogenetic data. *Annales de la Société Entomologique France*, 29(3), 225-244.
820 Bourgoïn, T. (2023). FLOW (Fulgoromorpha Lists on The Web): a world knowledge base
821 dedicated to Fulgoromorpha. Version 8, updated [23-02-2022]. [https://flow.hemiptera-](https://flow.hemiptera-databases.org/flow/)
822 [databases.org/flow/](https://flow.hemiptera-databases.org/flow/)
823 Bourgoïn, T., & Szwedo, J. (2022). Toward a New Classification of Planthoppers Hemiptera
824 Fulgoromorpha: 1. What do Fulgoridiidae really cover? *Annales Zoologici*, 72(4),
825 951-962. <https://doi.org/10.3161/00034541ANZ2022.72.4.011>
826 Bourgoïn, T., & Szwedo, J. (2023). Toward a New Classification of Planthoppers Hemiptera
827 Fulgoromorpha: 2. Higher taxa, their names and their composition. *Zootaxa* (in press).
828 Bourgoïn, T., Guilbert, E., & Wang, M. L. (2018). Issidae molecular K-libration. In: *8th*
829 *European Hemiptera Congress*, Katowice-Zawiercie, Poland, 24th-29th June.
830 Bourgoïn, T., Steffen-Campbell, J. D., & Campbell, B. C. (1997). Molecular Phylogeny of
831 Fulgoromorpha (Insecta, Hemiptera, Archaeorrhyncha). The Enigmatic Tettigometridae:
832 Evolutionary Affiliations and Historical Biogeography. *Cladistics*, 13(3), 207-224.
833 <https://doi.org/10.1111/j.1096-0031.1997.tb00316.x>
834 Bourgoïn T., Wang Rong-Rong & Gnezdilov V. M. (2015). First fossil record of Caliscelidae
835 (Hemiptera: Fulgoroidea): a new Early Miocene Dominican amber genus extends the

836 distribution of Augilini to the Neotropics. *Journal of Systematic Palaeontology* 14(3):
837 211-218.

838 Bourgoïn, T., Wang, M. L., & Nel, A. (2020). The oldest fossil of the family Issidae (Hemiptera,
839 Fulgoromorpha) from the Paleocene of Menat (France). *European Journal of Taxonomy*,
840 596, 1-8. <https://doi.org/10.5852/ejt.2020.596>

841 Brysz, A., & Szwedo, J. (2019). Jeweled Achilidae – A new look at their systematics and relation
842 to other Fulgoroidea (Hemiptera). *Monographs of the Upper Silesian Museum*, 10, 93-
843 130. <https://doi.org/10.93-130.10.5281/zenodo.3600279>

844 Bucher, M., & Bourgoïn, T. (2019). Which biases still hamper a solid planthopper phylogeny?.
845 In: *16th International Auchenorrhyncha Congress, 12th International Workshop on*
846 *Leafhoppers and Planthoppers of Economic Significance*, Cuc Phuong NP, Vietnam, 2nd-
847 8th July.

848 Ceotto, P., Kergoat, G. J., Rasplus, J. Y., & Bourgoïn, T. (2008). Molecular phylogenetics of
849 cixiid planthoppers (Hemiptera : Fulgoromorpha): New insights from combined analyses
850 of mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, 48(2),
851 667-678. <https://doi.org/10.1016/j.ympev.2008.04.026>

852 Chen, S., & Yang, C. T. (1995). The metatarsi of the Fulgoroidea (Homoptera:
853 Auchenorrhyncha). *Chinese Journal of Entomology*, 15(3), 257-269.

854 Cryan, J. R., & Urban, J. M. (2012). Higher-level phylogeny of the insect order Hemiptera: is
855 Auchenorrhyncha really paraphyletic?. *Systematic Entomology*, 37(1), 7-21.
856 <https://doi.org/10.1111/j.1365-3113.2011.00611.x>

857 de Queiroz, A., & Gatesy, J. (2007). The supermatrix approach to systematics. *Trends in*
858 *ecology & evolution*, 22(1), 34-41. <https://doi.org/10.1016/j.tree.2006.10.002>

859 Drummond, A. J., & Bouckaert, R. R. (2015). *Bayesian evolutionary analysis with BEAST*.
860 Cambridge University Press.

861 Emeljanov, A. F. (1979) Problema razgranicheniya semeïstv Fulgoridae i Dictyopharidae
862 (Homoptera, Auchenorrhyncha). *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR*,
863 82, 3–22.

864 Emeljanov, A. F. (1990). An attempt of construction of the phylogenetic tree of the
865 planthoppers (Homoptera, Cicadina). *Entomological Review*, 69(2), 353-356.

866 Emeljanov, A. F. (1991). K voprosu ob obeme i podrazdeleniyakh sem. Achilidae (Homoptera,
867 Cicadina). *Entomologicheskoe Obozrenie*, 70(2), 373-393.

- 868 Emeljanov, A. F. (1996). On the question of the classification and phylogeny of the Delphacidae
869 (Homoptera, Cicadina), with reference to larval characters. *Entomological Review*, 75(9),
870 134-150.
- 871 Emeljanov, A.F., 2004. A new genus and tribe of Strongyloematinae (Homoptera:
872 Fulgoridae). *Zoosystematica Rossica*, 3(1), 52.
- 873 Fennah, R. G. (1982). A tribal classification of the Tropiduchidae (Homoptera: Fulgoroidea),
874 with the description of a new species on tea in Malaysia. *Bulletin of Entomological*
875 *Research*, 72(4), 631-643.
- 876 Gnezdilov V.M. (2013c). Issidisation of fulgoroid planthoppers (Homoptera, Fulgoroidea) as
877 an evidence of parallel adaptive radiation. *Entomologicheskoe obozrenie*, 92(1): 62–69.
878 [In Russian]. (English translation published in *Entomological Review*, 93(7): 825–830.
879 <https://doi.org/10.1134/S001387381307004X>
- 880 Gnezdilov, V. M. (2013). Contribution to the taxonomy of the family Tropiduchidae Stål
881 (Hemiptera, Fulgoroidea) with description of two new tribes from Afrotropical Region.
882 *Deutsche Entomologische Zeitschrift*, 60(2), 179-191.
883 <https://doi.org/10.1002/mmnd.201300024>
- 884 Gnezdilov, V. M., & Bourgoïn T., (2016). [On the taxonomic position of *Issus reticulatus*](#)
885 [Bervoets, 1910 \(Hemiptera: Fulgoroidea: Issidae\) from Baltic amber. *Entomological*](#)
886 [Review 96\(5\): 631-633](#)
- 887 Gnezdilov, V. M., Konstantinov, F. V., & Bodrov, S. Y. (2020). New insights into the molecular
888 phylogeny and taxonomy of the family Issidae (Hemiptera: Auchenorrhyncha:
889 Fulgoroidea). *Труды Зоологического института РАН*, 324(1), 146-161.
890 <https://doi.org/10.31610/trudyzin/2020.324.1.146>
- 891 Gnezdilov, V. M., Konstantinov, F. V., & Namyatova, A. A. (2022). From modern to classic:
892 Classification of the planthopper family Issidae (Hemiptera, Auchenorrhyncha,
893 Fulgoroidea) derived from a total-evidence phylogeny. *Systematic Entomology*, 47(4),
894 551-568. <https://doi.org/10.1111/syen.12546>
- 895 Gnezdilov, V.M. (2013b). A modern classification of the family Caliscelidae Amyot et Serville
896 (Homoptera, Fulgoroidea). *Zoologicheskii Zhurnal* 92, 1309–1311. [English translation
897 in *Entomological Review*, 94, 211–214.] <https://doi.org/10.1134/S0013873814020092>

- 898 Gordon, A. D. (1986). Consensus supertrees: the synthesis of rooted trees containing
899 overlapping sets of labeled leaves. *Journal of classification*, 3, 335-348.
- 900 Huang, Y. X., & Qin, D. Z. (2018). Sequencing and analysis of the complete mitochondrial
901 genome of *Changeondelphax velitchkovskyi* (Hemiptera: Fulgoroidea). *Mitochondrial*
902 *DNA Part B*, 3(1), 90-91. <https://doi.org/10.1080/23802359.2017.1422407>
- 903 Huang, Y. X., Zheng, L. F., Bartlett, C. R., & Qin, D. Z. (2017). Resolving phylogenetic
904 relationships of Delphacini and Tropidocephalini (Hemiptera: Delphacidae: Delphacinae)
905 as inferred from four genetic loci. *Scientific Reports*, 7(1), 1-10.
906 <https://doi.org/10.1038/s41598-017-03624-w>
- 907 Johnson, K. P., Dietrich, C. H., Friedrich, F., Beutel, R. G., Wipfler, B., Peters, R. S., ... &
908 Yoshizawa, K. (2018). Phylogenomics and the evolution of hemipteroid insects.
909 *Proceedings of the National Academy of Sciences*, 115(50), 12775-12780.
910 <https://doi.org/10.1073/pnas.1815820115>
- 911 Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., ... & Drummond,
912 A. (2012). Geneious Basic: an integrated and extendable desktop software platform for
913 the organization and analysis of sequence data. *Bioinformatics*, 28(12), 1647-1649.
914 <https://doi.org/10.1093/bioinformatics/bts199>
- 915 Kim, M. J., Lee, K. H., Park, J. S., Jeong, J. S., Jeong, N. R., Lee, W., & Kim, I. (2021).
916 Complete Mitochondrial Genomes of *Metcalfa pruinosa* and *Salurnis marginella*
917 (Hemiptera: Flatidae) : Genomic Comparison and Phylogenetic Inference in Fulgoroidea.
918 *Current Issues in Molecular Biology*, 43(3), 1391-1418.
919 <https://doi.org/10.3390/cimb43030099>
- 920 Lallemand, V. (1956). Contribution à l'étude des Fulgoridae (Hemiptera) (1re note). *Bulletin*
921 *de l'Institut royal des sciences naturelles de Belgique*, 32(39), 1-7.
- 922 Lallemand, V. (1959). Description de nouvelles espèces de Fulgorides d'Asie et d'Afrique.
923 *Zoologische Mededelingen*, 36(16), 267-272.
- 924 Lallemand, V. (1960). De quibusdam Fulgoris. *Entomologische Mitteilungen aus dem*
925 *Zoologischen Staatsinstitut u. Zoologischen Museum Hamburg*, 24, 101-107.
- 926 Lallemand, V. (1963). Nouvelles espèces d'Homoptères. *Bulletin de l'Institut royal des sciences*
927 *naturelles de Belgique*, 32(3), 1-5.
- 928 Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., & Calcott, B. (2017). PartitionFinder
929 2: new methods for selecting partitioned models of evolution for molecular and
930 morphological phylogenetic analyses. *Molecular biology and evolution*, 34(3), 772-773.
931 <https://doi.org/10.1093/molbev/msw260>

- 932 Le Cesne, M., Bourgoïn, T., Hoch, H., Luo, Y., & Zhang, Y. (2022). *Coframalaxius bletteryi*
933 gen. et sp. nov. from subterranean habitat in Southern France (Hemiptera,
934 Fulgoromorpha, Cixiidae, Oecleini). *Subterranean Biology*, 43, 145-168.
935 <https://doi.org/10.3897/subtbiol.43.85804>
- 936 Liang, A. P. (1999). Do the Achilixiidae belong to the Cixiidae?-evidence from antennal
937 sensilla (Hemiptera: Fulgoromorpha: Fulgoroidea). In: *Talks and Posters of 10th Int.*
938 *Auchen. Meeting*, Cardiff, Wales, 6th-10th September.
- 939 Liang, A. P. (2001). Morphology of antennal sensilla in *Achilixius sandakanensis* Muir
940 (Hemiptera: Fulgoromorpha: Achilixiidae) with comments on the phylogenetic position
941 of the Achilixiidae. *Raffles Bulletin of Zoology*, 49(2), 221-226.
- 942 Luo, Y., Bourgoïn, T., Szwedo, J., & Feng, J. N. (2021). Acrotiarini trib. nov., in the Cixiidae
943 (Insecta, Hemiptera, Fulgoromorpha) from mid-Cretaceous amber of northern Myanmar,
944 with new insights in the classification of the family. *Cretaceous Research*, 128, 104959.
945 <https://doi.org/10.1016/j.cretres.2021.104959>
- 946 Markevich, D., Walczak, M., Borodin, O., Szwedo, J., & Brożek, J. (2021). Morphological
947 reassessment of the movable calcar of delphacid planthoppers (Hemiptera:
948 Fulgoromorpha: Delphacidae). *Scientific Reports*, 11(1), 22294.
949 <https://doi.org/10.1016/j.ympcv.2006.08.009>
- 950 Miller, M. A., Schwartz, T., Pickett, B. E., He, S., Klem, E. B., Scheuermann, R. H., Passarotti,
951 M., Kaufman, S., & O'Leary, M. A. (2015). A RESTful API for Access to Phylogenetic
952 Tools via the CIPRES Science Gateway. *Evolutionary Bioinformatics*, 11, EBO.S21501.
953 <https://doi.org/10.4137/EBO.S21501>
- 954 Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, A., Mayer, C., Frandsen, P. B., Ware,
955 J., Flouri, T., Beutel, R. G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler,
956 T., Rust, J., Aberer, A. J., Aspöck, U., Aspöck, H., Bartel, D., ... Zhou, X. (2014).
957 Phylogenomics resolves the timing and pattern of insect evolution. *Science*, 346(6210),
958 763-767. <https://doi.org/10.1126/science.1257570>
- 959 Michalik A., Franco D. C., Deng J., Szklarzewicz T., Stroiński A., Kobińska M. and Łukasik
960 P. (2023). Variable organization of symbiont-containing tissue across planthoppers
961 hosting different heritable endosymbionts. *Frontiers in Physiology*, 14:1135346. doi:
962 10.3389/fphys.2023.1135346
- 963 Mozaffarian, F., Bourgoïn, T., & Wilson, M. R. (2018). Nomenclatural changes in the higher
964 classification of the family Tettigometridae (Hemiptera: Fulgoroidea) with description of
965 a new tribe and new species and a review of the Iranian tettigometrid fauna. *Zootaxa*,

966 4392(3), 469-490. <https://doi.org/10.11646/zootaxa.4392.3.3>

967 Muir, F. (1923). On the classification of the Fulgoroidea (Homoptera). *Proceedings of the*
968 *Hawaiian Entomological Society*, 5, 205–247.

969 Muir, F. (1930). On the classification of the Fulgoroidea (Homoptera). 1930. On the
970 classification of the Fulgoroidea. *Annals and Magazine of Natural History*, 6(34), 461-
971 478.

972 Nabhan, A. R., & Sarkar, I. N. (2012). The impact of taxon sampling on phylogenetic inference:
973 a review of two decades of controversy. *Briefings in bioinformatics*, 13(1), 122-134.
974 <https://doi.org/10.1093/bib/bbr014>

975 Nguyen, L. T., Schmidt, H. A., Von Haeseler, A., & Minh, B. Q. (2015). IQ-TREE: a fast and
976 effective stochastic algorithm for estimating maximum-likelihood phylogenies.
977 *Molecular biology and evolution*, 32(1), 268-274.
978 <https://doi.org/10.1093/molbev/msu300>

979 Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and
980 evolutionary analyses in R. *Bioinformatics*, 35(3), 526-528.
981 <https://doi.org/10.1093/bioinformatics/bty633>

982 Parham, J. F., Donoghue, P. C. J., Bell, C. J., Calway, T. D., Head, J. J., Holroyd, P. A., Inoue,
983 J. G., Irmis, R. B., Joyce, W. G., Ksepka, D. T., Patané, J. S. L., Smith, N. D., Tarver, J.
984 E., van Tuinen, M., Yang, Z., Angielczyk, K. D., Greenwood, J. M., Hipsley, C. A.,
985 Jacobs, L., ... Benton, M. J. (2012). Best Practices for Justifying Fossil Calibrations.
986 *Systematic Biology*, 61(2), 346-359. <https://doi.org/10.1093/sysbio/syr107>

987 R Core Team (2021). R: A language and environment for statistical computing. R Foundation
988 for Statistical Computing, Vienna, Austria. Available online at [https://www.R-](https://www.R-project.org/)
989 [project.org/](https://www.R-project.org/).

990 Shcherbakov D. E. (2006). The earliest find of Tropicuchidae (Homoptera: Auchenorrhyncha),
991 representing a new tribe, from the Eocene of Green River, USA, with notes on the fossil
992 record of higher Fulgoroidea. *Russian Entomological Journal* 15(3): 315-322

993 Song, N., & Liang, A. P. (2013). A preliminary molecular phylogeny of planthoppers
994 (Hemiptera: Fulgoroidea) based on nuclear and mitochondrial DNA sequences. *PloS one*,
995 8(3), e58400. <https://doi.org/10.1371/journal.pone.0058400>

996 Song, Z. S., Bartlett, C. R., O'Brien, L. B., Liang, A. P., & Bourgoin, T. (2018). Morphological
997 phylogeny of Dictyopharidae (Hemiptera: Fulgoromorpha). *Systematic Entomology*,
998 43(4), 637-658. <https://doi.org/10.1111/syen.12293>

- 999 Stroiński, A., Bourgoïn T., & Szwedo J. (2022). Laberiini, a new tribe of Tropicuchidae
1000 planthoppers from Madagascar (Hemiptera: Fulgoroidea). *European Journal of*
1001 *Taxonomy* 836(1), 23-54. <https://doi.org/10.5852/ejt.2022.836.1913>
- 1002 Suchard, M. A., Lemey, P., Baele, G., Ayres, D. L., Drummond, A. J., & Rambaut, A. (2018).
1003 Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus*
1004 *evolution*, 4(1), vey016. <https://doi.org/doi:10.1093/ve/vey016>
- 1005 Urban, J. M., & Cryan, J. R. (2007). Evolution of the planthoppers (Insecta: hemiptera:
1006 Fulgoroidea). *Molecular Phylogenetics and Evolution*, 42(2), 556-572.
1007 <https://doi.org/10.1016/j.ympev.2006.08.009>
- 1008 Urban, J. M., & Cryan, J. R. (2009). Entomologically famous, evolutionarily unexplored : The
1009 first phylogeny of the lanternfly family Fulgoridae (Insecta: Hemiptera: Fulgoroidea).
1010 *Molecular Phylogenetics and Evolution*, 50(3), 471-484.
1011 <https://doi.org/10.1016/j.ympev.2008.12.004>
- 1012 Urban, J. M., & Cryan, J. R. (2012). Two ancient bacterial endosymbionts have coevolved with
1013 the planthoppers (Insecta: Hemiptera: Fulgoroidea). *BMC Evolutionary Biology*, 12(1):
1014 1-19. <https://doi.org/10.1186/1471-2148-12-87>
- 1015 Urban, J. M., Bartlett, C. R., & Cryan, J. R. (2010). Evolution of Delphacidae (Hemiptera :
1016 Fulgoroidea): combined-evidence phylogenetics reveals importance of grass host shifts.
1017 *Systematic Entomology*, 35(4), 678-691. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-3113.2010.00539.x)
1018 [3113.2010.00539.x](https://doi.org/10.1111/j.1365-3113.2010.00539.x)
- 1019 Vaidya, G., Lohman, D. J., & Meier, R. (2011). SequenceMatrix: concatenation software for
1020 the fast assembly of multi-gene datasets with character set and codon information.
1021 *Cladistics*, 27(2), 171-180. <https://doi.org/10.1111/j.1096-0031.2010.00329.x>
- 1022 Wang, M., Zhang, Y., & Bourgoïn, T. (2016). Planthopper family Issidae (Insecta: Hemiptera:
1023 Fulgoromorpha): linking molecular phylogeny with classification. *Molecular*
1024 *Phylogenetics and Evolution*, 105, 224-234.
1025 <https://doi.org/10.1016/j.ympev.2016.08.012>
- 1026 Wang, W., Huang, Y., Bartlett, C. R., Zhou, F., Meng, R., & Qin, D. (2019). Characterization
1027 of the complete mitochondrial genomes of two species of the genus Aphaena Guérin-
1028 Méneville (Hemiptera : Fulgoridae) and its phylogenetic implications. *International*
1029 *journal of biological macromolecules*, 141, 29-40.
1030 <https://doi.org/10.1016/j.ijbiomac.2019.08.222>
- 1031 Xu, S. Y., Long, J. K., & Chen, X. S. (2019). Comparative analysis of the complete
1032 mitochondrial genomes of five Achilidae species (Hemiptera: Fulgoroidea) and other

1033 Fulgoroidea reveals conserved mitochondrial genome organization. *PeerJ*, 7, e6659.
1034 <https://doi.org/10.7717/peerj.6659>

1035 Yang, C. T., & Fang, S. J. (1993). Phylogeny of Fulgoromorpha nymphs, first results. In:
1036 *Proceedings. 8th Auchenorrhyncha Congress*, Delphi, Greece, 9th-13th August, 25-26.

1037 Yeh, W. B., & Yang, C. T. (1999). Fulgoromorpha phylogeny based on 28S rDNA nucleotide
1038 sequence. *Chinese Journal of Entomology*, 11, 87-111.

1039 Yeh, W. B., Yang, C. T., & Hui, C. F. (1998). Phylogenetic Relationships of the Tropiduchidae-
1040 group (Homoptera: Fulgoroidea) of Planthoppers Inferred through Nucleotide Sequences.
1041 *Zoological Studies*, 37, 45-65.

1042 Yeh, W. B., Yang, C. T., & Hui, C. F. (2005). A Molecular Phylogeny of Planthoppers
1043 (Hemiptera: Fulgoroidea) Inferred from Mitochondrial 16S rDNA Sequences.
1044 *Zoological Studies*, 44(4), 519-535.

1045 Yu, F., & Liang, A. P. (2018). The complete mitochondrial genome of Ugyops sp. (Hemiptera:
1046 Delphacidae). *Journal of Insect Science*, 18(3), 25.

1047 Yu, S., Wang, Y., Rédei, D., Xie, Q., & Bu, W. (2013). Secondary structure models of 18S and
1048 28S rRNAs of the true bugs based on complete rDNA sequences of Eurydema
1049 maracandica Oshanin, 1871 (Heteroptera, Pentatomidae). *ZooKeys*, (319), 363.
1050 <https://doi.org/10.3897/zookeys.319.4178>

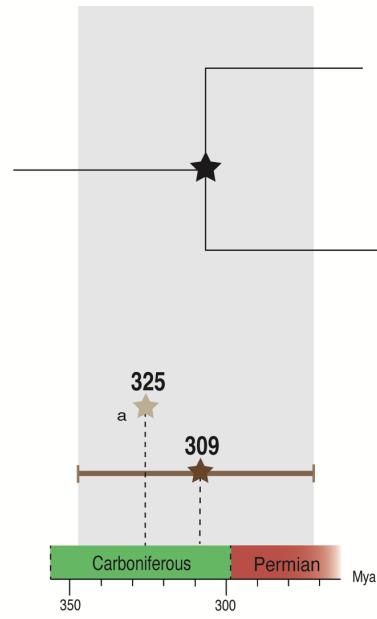
1051 Zhao, Z., Bourgoin, T., Szwedo, J., Song, Z., Chen, L., & Luo, C. (2023). The oldest genus and
1052 species of the fulgoroidian lineage in hemipteran Fulgoroidea from the Lower Cretaceous
1053 Laiyang Formation of China. *Cretaceous Research*, 143, 105423.
1054 <https://doi.org/10.1016/j.cretres.2022.105423>

1055

Fig. 1: A. Hypotheses on the origin, diversification dating and phylogenetic relationship of extant Fulgoromorpha lineages. Phylogeny is based on synthesis of few molecular studies and is summarized in Bartlett et al. (2018). Branch lengths are not to scale. B. Live representatives of Fulgoromorpha a. *Megadelphax sordidula* (Stål, 1853) (Delphacidae) b. *Reptalus quinquecostatus* (Dufour, 1833) (Cixiidae) c. *Nisia* sp. (Meenoplidae) d. *Anotia* sp. (Derbidae) e. *Plectoderes scapularis* Metcalf, 1938 (Achilidae) f. *Dictyophara europaea* (Linné, 1767) (Dictyopharidae) g. *Phrictus quinquepartitus* Distant, 1883 (Fulgoridae) h. *Paracorethrura iocnemis* (Jacobi, 1905) (Lophopidae) i. *Trienopa typica* (Distant, 1911) (Tropiduchidae) j. *Tettigometra laeta* Herrich-Schäffer, 1835 (Tettigometridae) k. *Acanalonia conica* (Say, 1900) (Acanaloniidae) l. *Ommatidiotus dissimilis* (Fallén, 1806) (Caliscelidae) m. *Nephesini* sp. (Flatidae) n. *Biolleyana costalis* (Fowler, 1900) (Nogodinidae) o. *Ricania speculum* (Walker, 1851) (Ricaniidae) p. *Hemisphaerius stali* Banks, 1910 (Issidae). All photographs belong to © Gernot Kunz.

A

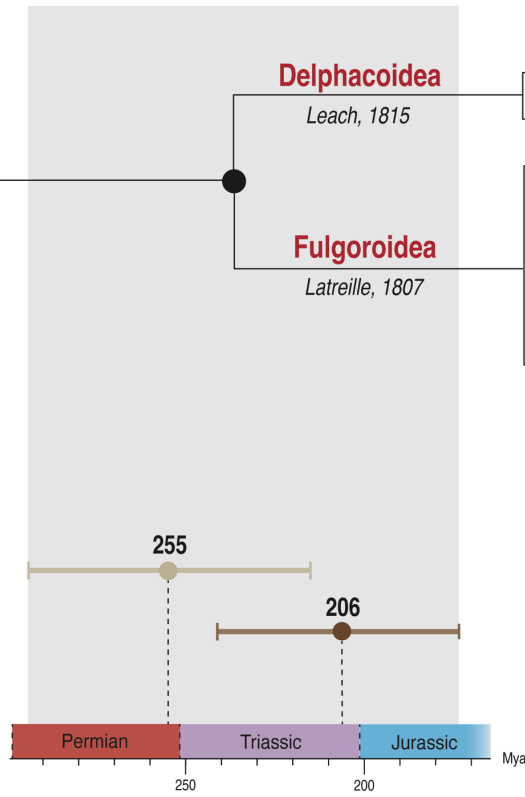
Hypotheses on the origination age of Fulgoromorpha



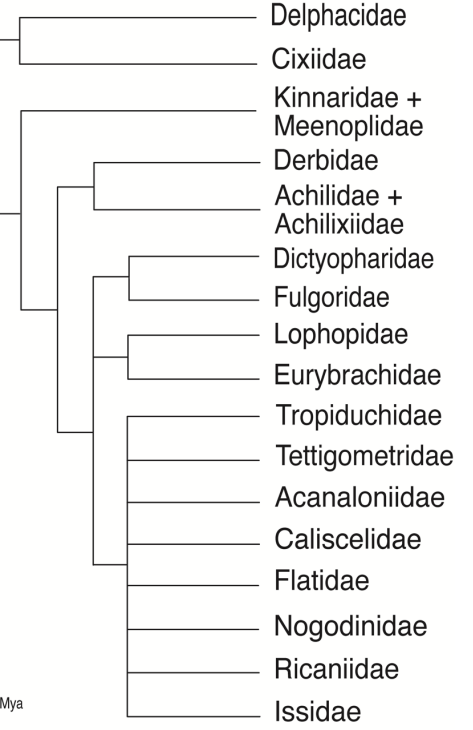
a No confidence interval is given in the corresponding studies

- ★ ● Song et al., 2013
- ★ ● Johnson et al., 2018

Hypotheses on the age of extant Fulgoromorpha diversification



Synthesis of phylogenetic hypotheses for extant Fulgoromorpha



B

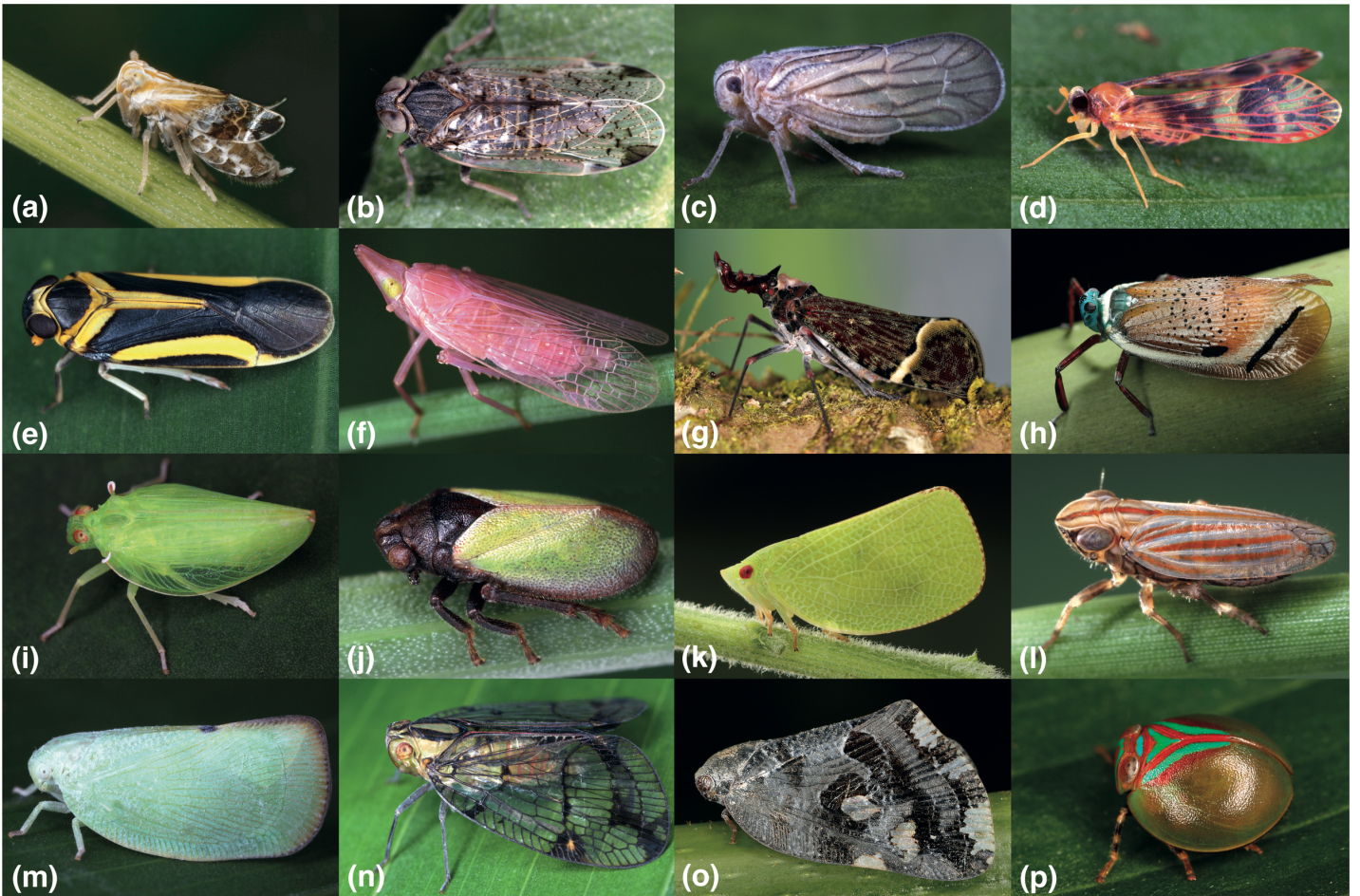


Fig. 2: Summary phylogeny of extant Fulgoromorpha with major clades (families) collapsed. Reconstructed families are color coded (Delphacidae: blue, Cixiidae: green, Issidae: purple, others families: brown shading). This color code is reused in the complete tree (Fig. 3) and the dated phylogeny (Fig. 4).

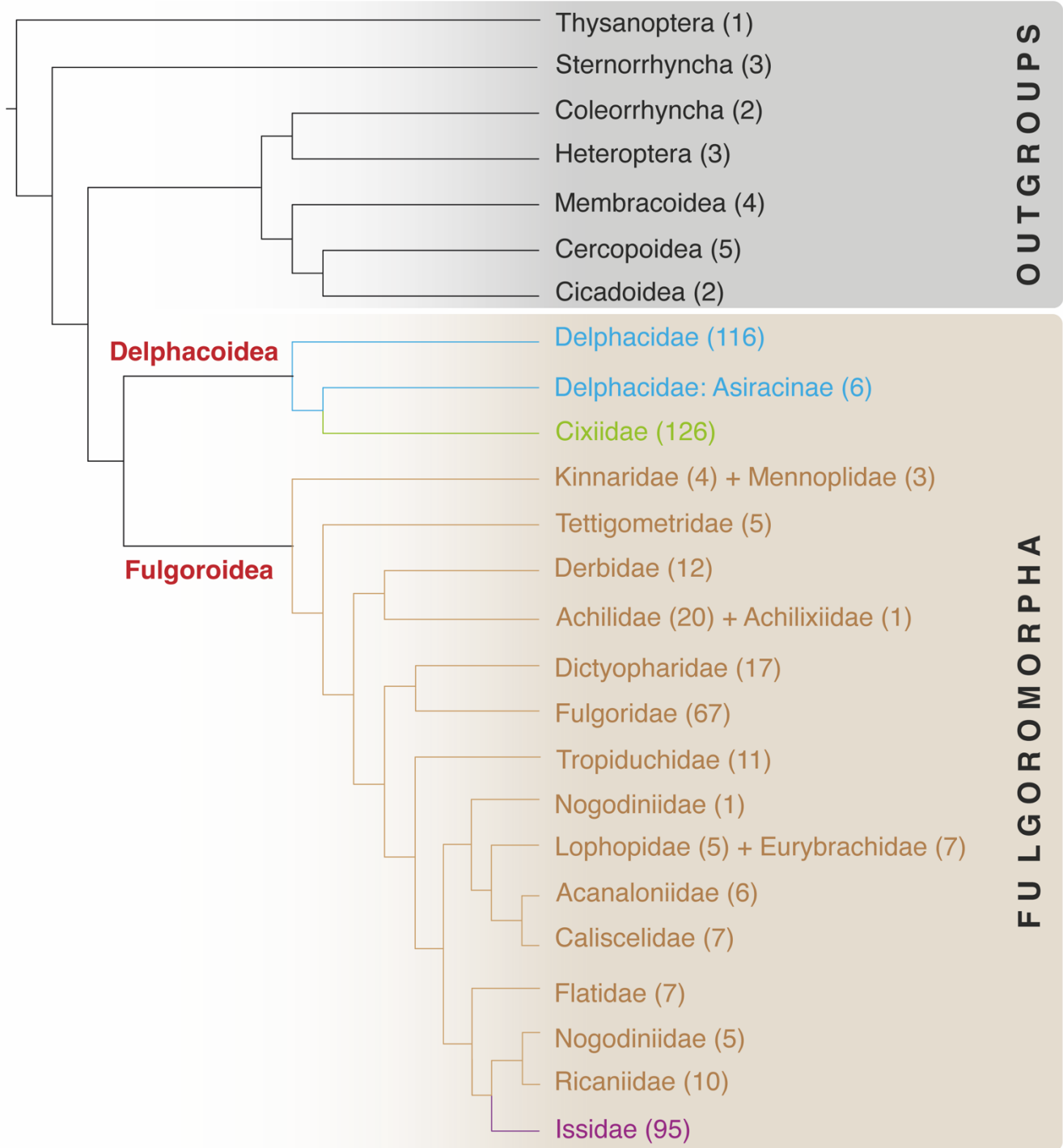


Fig. 3: Complete phylogeny of extant Fulgoromorpha reconstructed with Maximum Likelihood inference. Branch support is indicated by ML ultrafast bootstraps (1000 iterations). The tree is presented in four parts (A-D): arrows correspond to the location where the branches have been cut. Reconstructed families are color coded (Delphacidae: blue, Cixiidae: green, Issidae: purple, others families: brown shading) with subfamilies and other lineages indicated. A. Phylogeny of Delphacidae. B. Phylogeny of Cixiidae. C-D. Phylogeny of Fulgoroidea families

Outgroups

Eudelphacida

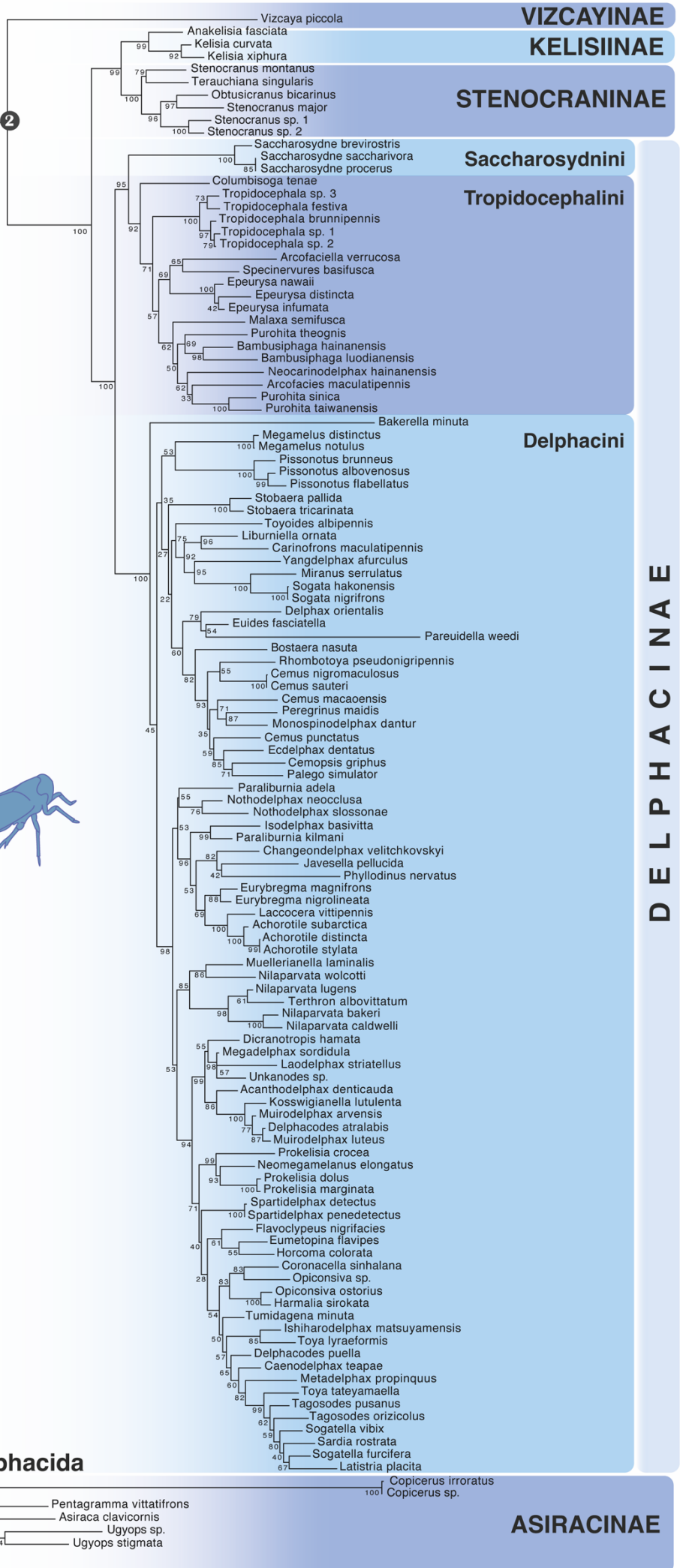
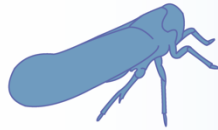
Delphacoidea

Fulgoroidea

(Fig. 3c,d)

Protodelphacida

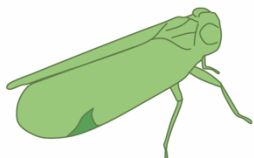
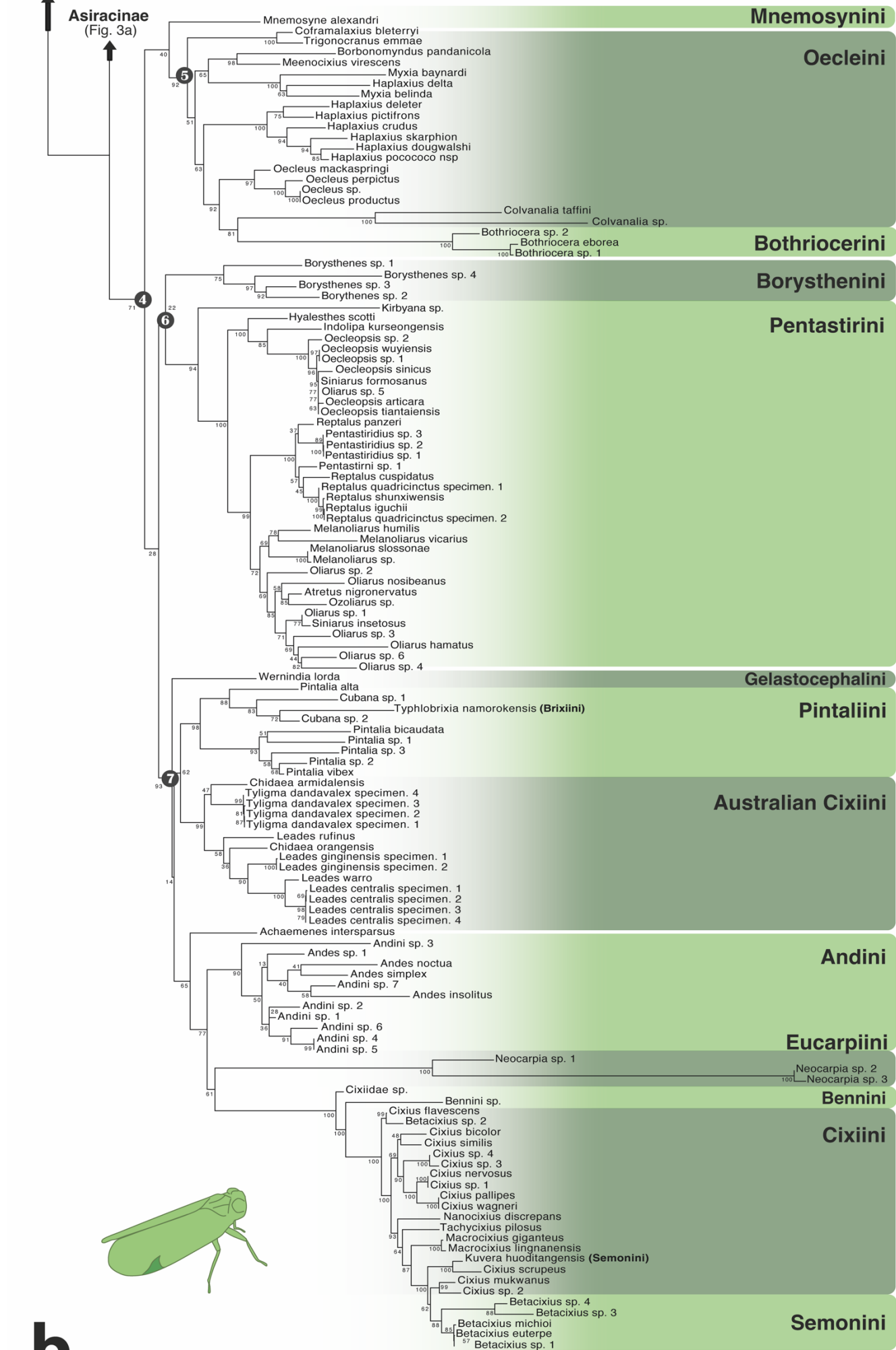
Cixiidae (Fig. 3b)



DELPHACINAE
DELPHACIDAE

a

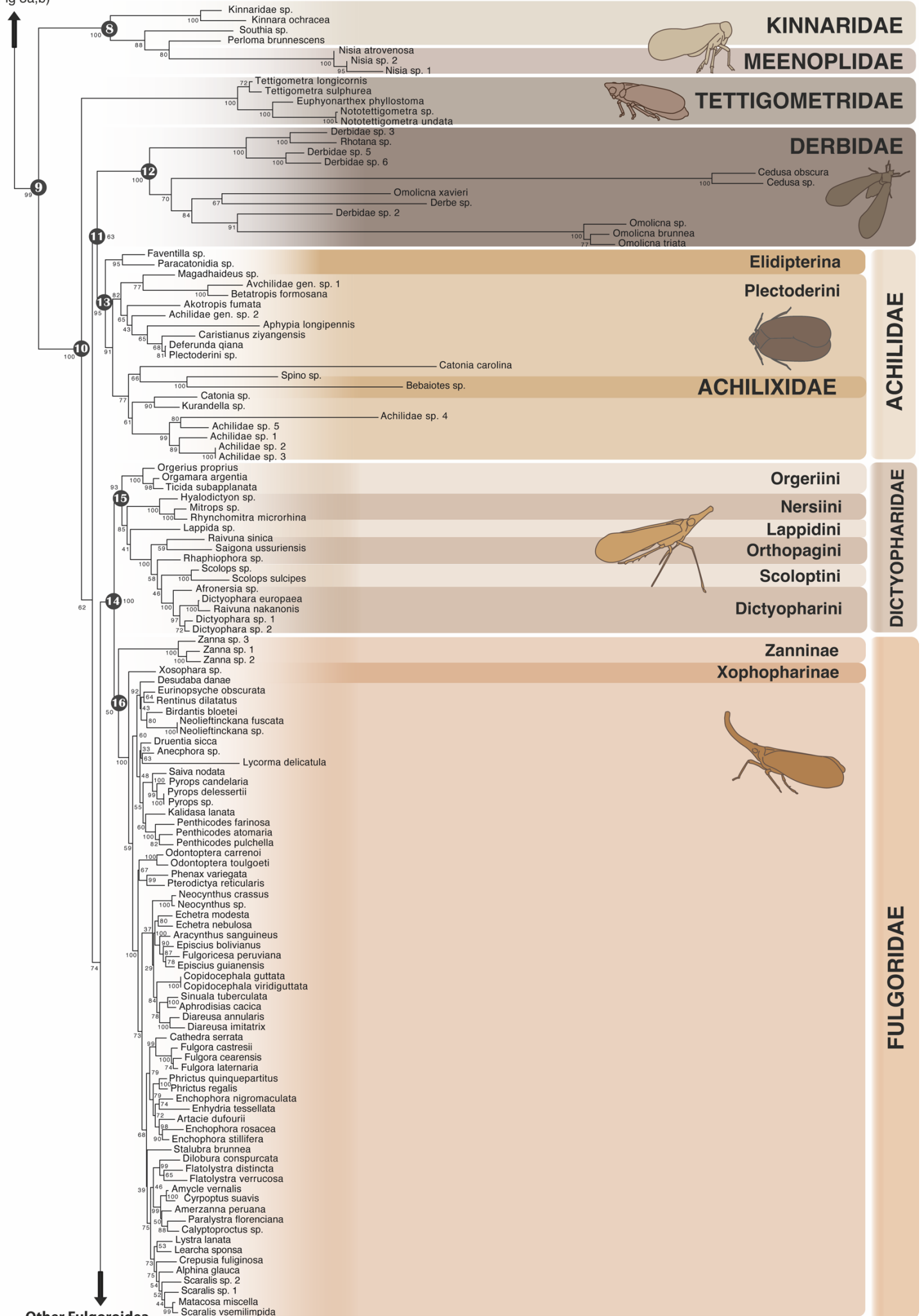
Delphacidae
(Fig. 3a)



b

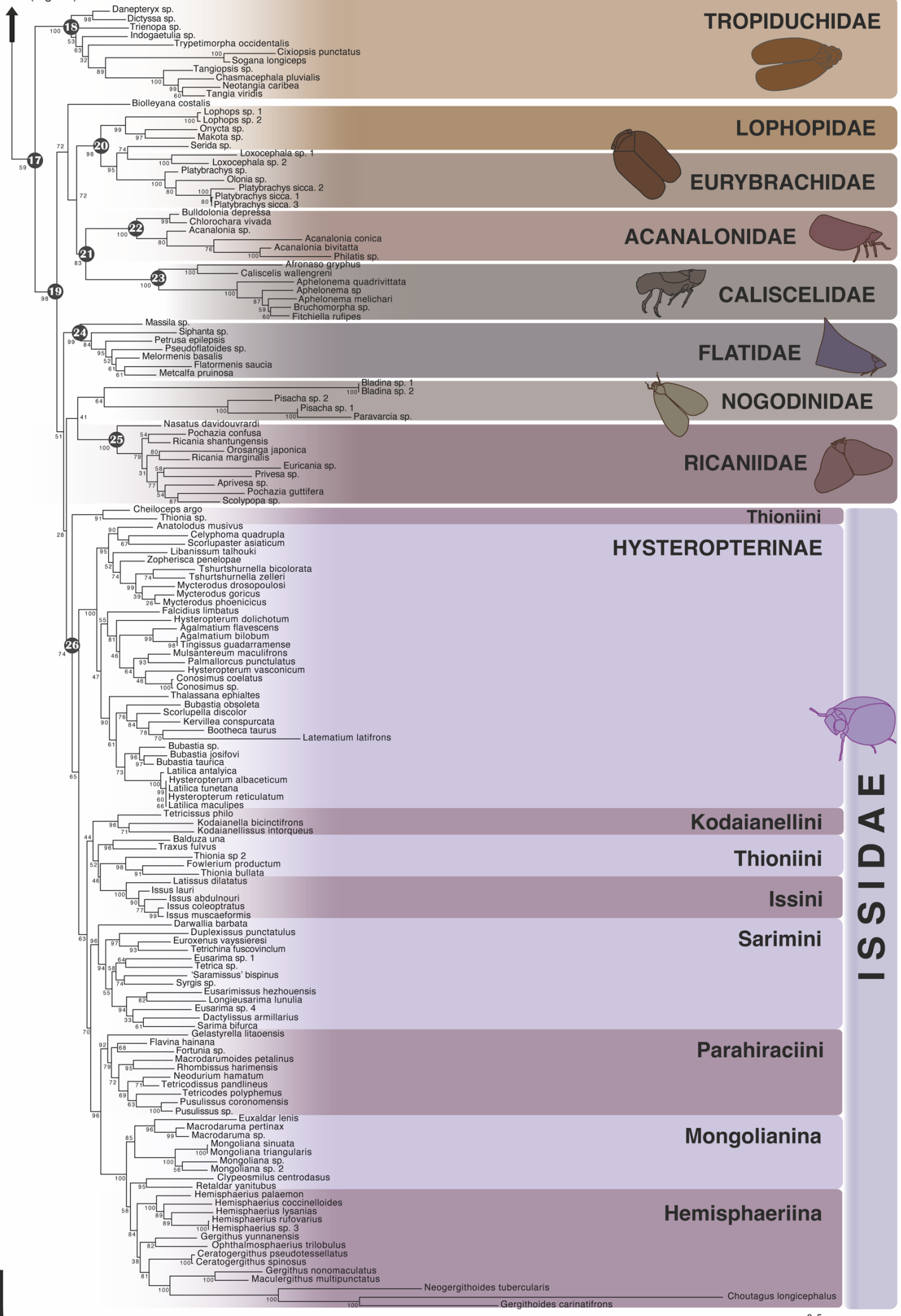
Delphacoidea

(Fig 3a,b)



Other Fulgoroidea families (Fig. 3d)

Other Fulgoroidea families (Fig. 3c)



d

Figure 4: Simplified chronogram obtained with Beast v1.10.4. Outgroup were removed from analysis. Color code is reused in the simplified phylogeny (Fig. 2) and complete tree (Fig. 3). The red circles correspond to the fossil calibration of the tree. The complete tree with confidence intervals associated with each node age is presented in supplementary data.

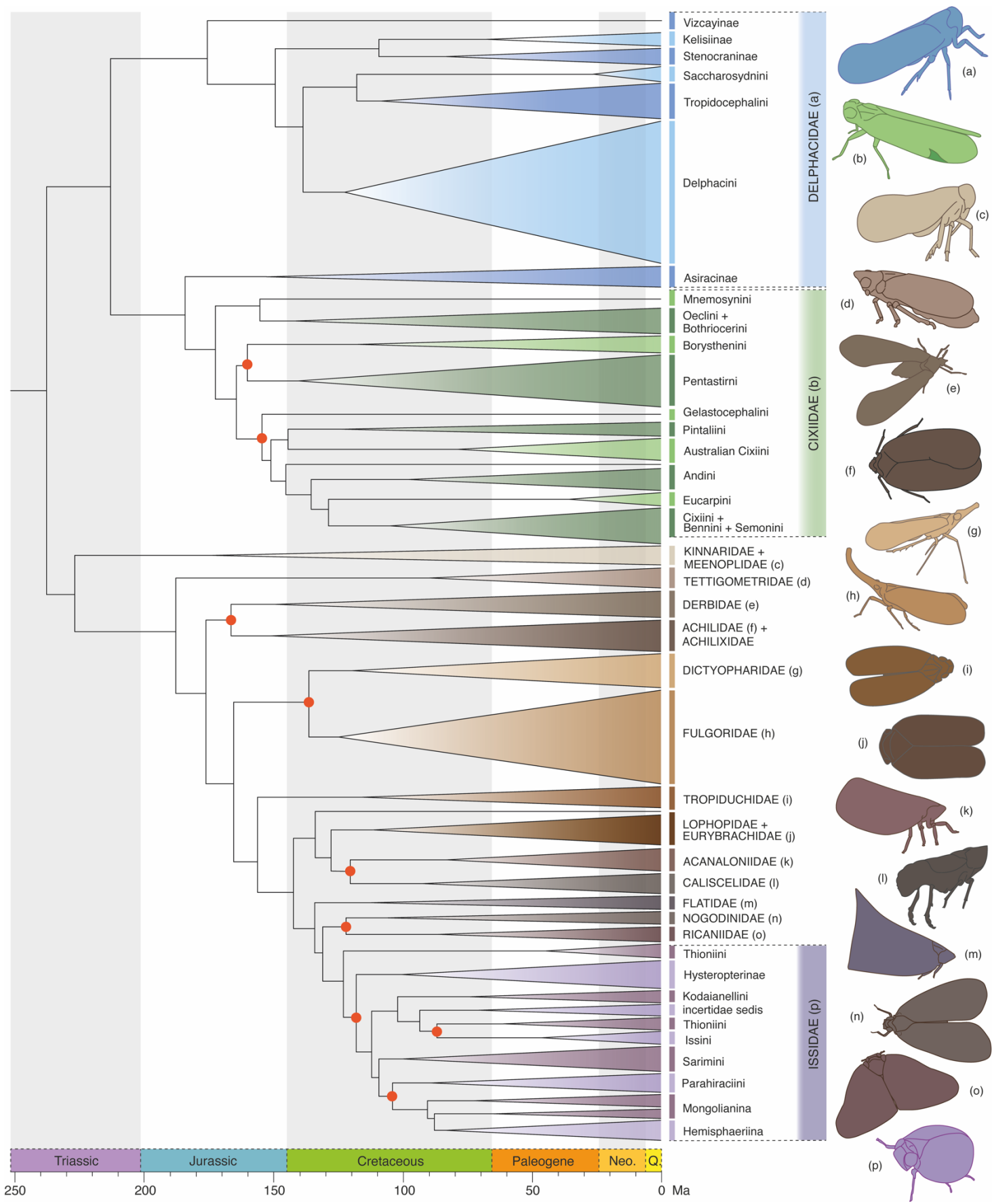


Table A: Taxonomic diversity represented by taxa included in the final analysis (in-group). Taxonomic classification follows FLOW (Bourgoin, 2023), which is based on the Metcalf (1958) catalog and recent taxonomic revisions. "." denotes a lack of classificatory rank.

Families	Subfamillies sampled	Tribes sampled	Sub-tribe sampled	Total number of terminal taxa ^a
Acanaloniidae	.	.	.	6
Achilidae	2/3	2/11	2/3	20
Achilixiidae	1/2	.	.	1
Caliscelidae	1/2	2/5	0/4	7
Cixiidae	1/1	11/16	2/3	126
Delphacidae	5/6	6/10	.	122
Derbidae	3/3	4/20	2/9	12
Dictyopharidae	2/2	5/17	1/2	17
Eurybrachidae	2/2	2/6	.	7
Flatidae	2/2	3/8	2/9	7
Fulgoridae	8/11	9/19	4/4	67
Issidae	4/4	6/9	4/9	95
Kinnaridae	2/2	3/5	.	4
Lophopidae	2/2	3/6	.	5
Meenoplidae	1/2	.	.	3
Nogodinidae	2/4	3/10	2/4	6
Ricaniidae	.	.	.	10
Tettigometridae	2/4	1/4	.	5
Tropiduchidae	2/2	7/20	2/7	11

^a Not all terminal taxa are identified to genus and specie level. Several specimens may represent the same taxonomic rank.

Table B: Fossils used in the analyses for estimating divergence dates and calibration point prior settings. Fossil selection followed the best practices suggested by Parham *et al.* (2012) to justify fossil calibrations. As none of the present fossils were included in a phylogenetic analysis, attribution to a phylogenetic lineage was carried out according to the apomorphy-based method. All dates based on stratigraphic intervals have been updated following the latest version of the International Commission on Stratigraphy 2022/10 and the latest information published. Here we use calibration points in the sense of most representatives of early-branching lineages (stem group) which only give minimum ages.

Fossil identity				Systematic assignment		Geological age (Ma)	
Fossil taxon	Museum specimen number	Mode of preservation	Locality	Taxonomic group	References	Age (Mya)	References
<i>Abraracourcix curvivenatus</i> Stroinski & Szwedo, 2012	MNHN PA5155	Amber impression	Le Quesnoy, Oise, France	Stem Ricaniidae	According to Stroński & Szwedo (2012), the specimen possesses all combinations of characters forming the venation pattern of Ricaniidae as follows: costal area narrower than costal cell, costal cell with numerous transverse veinlets, basal cell strongly rounded, longitudinal venation wavy, absence of nodal line. <i>A. curvivenatus</i> is not supposed to be related to an extant lineage within our Ricaniidae sampling.	56.8 - 55.4	Ambers from deposit of Le Quesnoy, Oise River area of the Paris basin, France were aged Lowermost Eocene, Sparnacien 55-53 Ma (Nel <i>et al.</i> , 1999). Date of this deposit was re-evaluated as equivalent to Clarkforkian by Smith <i>et al.</i> (2014).
<i>Acixiites immodesta</i> Hamilton, 1990	AMNH 43679	Compression	Crato Fm, Ceará, Brazil	Stem Achilidae	For Hamilton (1990) the flattened body of the described specimen, the overlapping tegmina and the "spurious" claval suture allow us to assign this fossil to the Achilidae without the possibility of assignment to a modern lineage. This specimen doesn't possess the veinlet connecting the posterior branch of Cua with the tegmen margin, which is very characteristic to Achilidae representents (Martill <i>et al.</i> , 2007). Nevertheless, the vertex, the pronotum and the lack of subapical setae on the hind tarsomere could related this species to more basal Derbidae. Nevertheless, the long rostrum extended beyond the apex of the hind femora excludes this species from this group.	125 - 113	The age of the Nova Olinda Member of the Crato Formation (Araipe Group) has been interpreted as Aptian (Maisey, 1990; Martill, 2007; Staniczek <i>et al.</i> , 2022, paleobiodb.org, 2022).
<i>Acrotiara multigranulata</i> Luo & Bourgoïn, 2021	HO221990	Amber inclusion	Hukawng Valley, Kachin State, Manmar	Cixiidae Stem Pentastirinian lineage	This fossil was recently described and all assigned to the new tribe Acrotiarini (Luo <i>et al.</i> , 2021). This taxon is excluded from the Oecleian lineage by the absence of a metatibial diastema and share with the Cixiian + Pentasterinian (Pentastirini + Mnemosynini) lineages the distal displacement of the icu vein distal to the apex of clavus. The presence of a pentacarinated mesonotum in the Acrotiarini species allows to place them within the pentastirinian lineage based on this only apomorphic character but as a separate lineage by the unique presence of the paired sublateral frontal carinae and the arched RA venation on tegmen.	99.41 - 98.17	The Hukawng Valleyamber deposit has been radiometrically dated using zircons to 98.79 ± 0.62 Ma, in earliest Cenomanian (Shi <i>et al.</i> , 2012). 98.17 Ma should be taken as a conservative minimum age of the deposit (Kania <i>et al.</i> , 2015; Mao <i>et al.</i> , 2018).
<i>Barremixius petrinus</i> (Fennah, 1961)	BMNH In. 59335	Compression	Lamb's Brickworks, locality 170/348485,	Cixiidae Stem Cixiian lineage	Fennah first assigned <i>B. petrinus</i> 'with confidence' to the Cixiina subtribe and uncertainly to the genus <i>Cixius</i> Latreille, 1804. In fact, the fossil lacks all apomorphic characters of both oecleidian and pentastiridian lineages.	129.4 - 125	Deposits from Lamb's Brickworks, Weald Clay Formation (Upper Members) are dated from Barremian (paleobiodb.org, 2022).

			South Godstone, Tandridge, Surrey, England, UK		Luo <i>et al.</i> (2021) erected a new genus for this fossil and provisionally maintained it into Cixiini but in the cixiini lineage with which it share the usual plesiomorphic set of characters of the lineage.		
<i>Bolbossus bervoetsi</i> (Gnezdilov & Bourgoin, 2016)	According to J. Szwedó (pers. comm.), the location of the type material is unknown.	Amber inclusion	Baltic amber of Kaliningrad Peninsula, based on the material of Pr. R. Klebs' collection	Issidae Stem Parahiraciini	<i>B. bervoetsi</i> (<i>Issus bervoetsi</i> Gnezdilov et Bourgoin, nom. n. pro) was originally described as the first fossil representative of the tribe Issini Spinola, 1939 (Bervoets, 1910). Nevertheless, Gnezdilov & Bourgoin (2016), erected it in the tribe Parahiraciini based on the venation pattern with the very embossed longitudinal veins as well as the particular shape of metope very convex. <i>B. bervoetsi</i> is not assigned to a modern lineage within the tribe.	37.8 - 33.9	Initially the material from the Pr. R. Klebs' collection was dated from Oligocene by Bervoets (1910). Material was re-examined by Szwedó <i>et al.</i> , 2004 and date was reevaluated from Eocene and later from Priabonian according to Gnezdilov & Bourgoin (2016, Szwedó comm.).
<i>Cubicostissus palaeocaeni</i> (Bourgoin & Wang, 2020)	NEL 3485	Compression	Menat Fm, Puy de Dome, France	Issidae Stem Hysteropterini	Bourgoin <i>et al.</i> (2020) described this specimen within Hysteropterini based on tegmen venation pattern with the following characters: issidized tegmen (Gnezdilov, 2013) with a brachipterous form, CuA single, forking only at the extremity of the clavus, CuA1 running parallel to the wing margin. <i>C. palaeocaeni</i> is not assigned to a modern lineage within the tribe.	61.6 - 59.2	Menat beds was previously reported as Thanetian <i>ie.</i> 58.7 – 55.8 Ma (Kedves & Russel 1982; paleobiodb.org, 2021) based on basalts associated with the Menat maar. Since then, it has been re-evaluated as being Selandian based on magnetostratigraphy (Wappler <i>et al.</i> , 2009; Mayr <i>et al.</i> , 2019).
<i>Issites glaber</i> Haupt, 1956	No. G 55/8, GPIUH collection	Compression	Geiseltal, Saxe-Anhalt, Germany	Issidae Stem Issini	Haupt (1956) described this specimen based on an impression of tegmen and assigned it within the tribe Issini based on the following characters: issidized tegmen (Gnezdilov, 2013) with a brachipterous form, R M and CuA two-branched all three. He suggested that this species is closely related to the genus <i>Issus</i> Brullé, 1832 but we consider here that this taxa is part of the stem group because we cannot assign it with certainty to a modern lineage within the tribe.	47.5 - 42.5	Haupt (1956) described this fossil from Lutetian. Fossils from the Geiseltal deposit are now more precisely dated from the middle Eocene late Geiseltalian according to Steinheimer & Hastings (2018).
<i>Netutela annunciator</i> Emeljanov, 1983	PIN 3130/168	Amber inclusion	Eastern part of Taimyr Peninsula, Yantardakh Hill, Kheta Fm, Russia	Stem Dictyopharidae	<i>N. annunciator</i> was originally assigned within Cixiidae based on the presence of a pterostigmal area (Rodendorf <i>et al.</i> , 1974). Nevertheless, Emeljanov (1983) described the specimen as a fossil representative of Dictyopharidae by justifying that the pterostigma is formed apically by the ScP vein that extends fully to the costal margin and costally by the continuation of the costa. Veins are also lacking of ciliated granules which is characteristic of Cixiidae.	86.8 - 83.4	Taimyr amber from Yantardakh Hill, Kheta formation, Russian Fed. are dated from Santonian (paleobiodb.org, 2022).
<i>Quizqueiplana alexbrowni</i> Bourgoin & Gnezdilov, 2015	MNHN.F.A51125	Amber inclusion	La Bucara mine, La Toca Fm, Cordillera Septentrional, Dominican Republic	Stem Caliscelidae	According to Bourgoin <i>et al.</i> (2015), the specimen possesses all combinations of characters forming the venation pattern of Augilini, Baker, 1915 with: strongly elongated tegmen, presence of a nodal line, arched vein after nodal ligne, Scp+R and M with a short common stem after the basal cell. Hind tibia possesses one lateral spur. As our taxonomic sampling doesn't include any Augilini representatives, we consider here that this taxa could not be included in crown Caliscelidae.	20.44 - 15.97	Ambers from La Bucara mine belongs to the La Toca Formation group of mines. It is currently dated from the Burdigalian (paleobiodb.org, 2022).
<i>Serafinana perperunae</i> Gebicki & Szwedó, 2000	AUF 05JS	Amber inclusion	Gulf of Gdańsk, Poland (secondary)	Delphacidae Stem Ugyopini	The presence of a calcar spur on hindtibia of the specimen places it without doubt within Delphacidae. Gebicki & Szwedó (2000) proposed its placement within	47.8 - 43.9	Baltic amber is a secondary deposit found mainly in glauconitic marine sediments of middle Eocene age (Lutetian Stage: 41.3-47.8 Mya), deposited along

deposit: “blue
earth”
formation)

Ugyopini Fennah, 1979 based on the general shape of the head and the position of carinae on the vertex which suggests that this specimen is closely related to some Pacific genera (*Ugyopana*, *Melanesia*, *Melanugyops*, *Livatiella*). The absence of characters for justifying its inclusion within the genus *Ugyops* Guérin-Méneville, 1834 makes us exclude this fossil from the Crown Ugyopini of our sampling.

the paleo-North Sea margin. Problems to date a precise for Baltic amber come from amber deposits being reworked and deposited in sediments that are millions of years younger than the original time of production (Weitschat and Wichard, 2002). Therefore, several ages for of Baltic amber were proposed (Mertz *et al.*, 2000; Drohojowska *et al.*, 2015; Szadziwski, 2018; Sadowski *et al.*, 2022). We retain here the age proposed by Mertz *et al.*, (2000) who consider a middle Eocene age of Baltic amber which comes from correlations with limnic sediments within Eckfeld Maar. They defined 44.3 ± 0.4 Ma as the age of Baltic amber. Accordingly, minimum age of *S. perperunae* has been choose to 43.9 Ma.

Table C: Estimated divergence times and 95% credibility intervals. Only families considered as monophyletic lineage are presented below.

Families	Estimated divergence times	95% credibility intervals	Geological periods
Acanaloniidae	83.21 Mya	[51.11, 132.07]	Late Cretaceous
Achilidae	151.14 Mya	[113.35, 231.29]	Late Jurassic
Caliscelidae	92.62 Mya	[60.77, 140.80]	Late Cretaceous
Cixiidae	172.75 Mya	[129.21, 257.14]	Middle Jurassic
Delphacidae: Eudelphacida	175.84 Mya	[131.16, 262.25]	Early Jurassic
Delphacidae: Protodelphacida	152.90 Mya	[92.48, 240.35]	Late Jurassic
Derbidae	148.96 Mya	[111.46, 224.47]	Late Jurassic
Dictyopharidae	119.71 Mya	[85.28, 182.30]	Early Cretaceous
Lophopidae + Eurybrachidae	111.80 Mya	[79.83, 167.24]	Early Cretaceous
Flatidae	112.43 Mya	[70.13, 173.50]	Early Cretaceous
Fulgoridae	124.99 Mya	[91.15, 189.83]	Early Cretaceous
Issidae	123.16 Mya	[93.64, 185.93]	Early Cretaceous
Kinnaridae + Meenoplidae	174.44 Mya	[126.55, 267.53]	Early Jurassic
Ricaniidae	86.49 Mya	[54.20, 134.17]	Late Cretaceous
Tettigometridae	89.77 Mya	[45.99, 150.39]	Late Cretaceous
Tropiduchidae	115.87 Mya	[78.88, 178.97]	Early Cretaceous