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Clarifying the phylogeny and systematics of the recalcitrant tribe Leptocircini (Lepidoptera: Papilionidae) with whole-genome data

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1 **Clarifying the phylogeny and systematics of the**
2 **recalcitrant tribe Leptocircini (Lepidoptera:**
3 **Papilionidae) with whole-genome data**
4

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19

20 *Running head*

21 Phylogenomic of Leptocircini (Papilionidae)

22 **Abstract**

23 Leptocircini is a dazzling tribe of Papilionidae, including dragontails, kite swallowtails, and
24 swordtails. This tribe is widely distributed, notably throughout the tropics of Africa, Southeast
25 Asia, and the Americas, making it a fascinating model in evolutionary biology. However,
26 despite accounting for 25% of the global swallowtail butterfly diversity, Leptocircini have been
27 surprisingly neglected in phylogenetic analyses. This has left unanswered questions about their
28 taxonomy and systematics. Here, we present a new taxonomic working list for Leptocircini,
29 featuring 162 valid species. Using a combination of long and short reads data, we produced
30 five new reference genomes, and we generated highly covered and scaffolded whole genomes
31 for 148 individuals to infer densely sampled phylogenetic hypotheses. Based on mitochondrial
32 or thousands of nuclear genes and multiple phylogenetic approaches, a robust phylogenomic
33 tree is recovered, representing ~90% of the known species, which allowed examination of
34 several key phylogenetic hypotheses. We found the monotypic genus *Protographium* Munroe
35 to be sister of genus *Graphium* Scopoli. Additionally, we found that subgenus *Paranticopsis*
36 Wood-Mason and de Nicéville is nested within subgenus *Pathysa* Reakirt, which we found is
37 likely attributed to an ancient gene flow. We therefore synonymize *Paranticopsis*, **syn.rest.** To
38 keep a consistent approach to subgeneric classification across the tribe and family, we divided
39 genus *Eurytides* Hübner into three subgenera: *Mimoides* Brown, *Eurytides sensu stricto*, and
40 *Protesilaus* Swainson. This led to several taxonomic implications: *Asiographium* Möhn,
41 **syn.rest.**, *Boreographium* Grishin, **syn.n.**, *Hyalaus* Grishin, **syn.n.**, and *Neographium* Möhn,
42 **syn.n.** are synonymized with *Eurytides (Mimoides)*; and *Eurygraphium* Möhn, **syn.rest.** is
43 synonymized with *Eurytides (Eurytides)*. Our analyses finally raised concerns about potential
44 taxonomic inflation in two species-groups within *Graphium* and *Eurytides (Protesilaus)*. This
45 study illuminates the clade's evolutionary history and paves the way for further research on
46 this diverse group of charismatic butterflies.

47

48 **Keywords:** *Eurytides*, gene flow, *Graphium*, incomplete lineage sorting, phylogenomics,

49 reference genome, scaffolding.

50

51 Introduction

52 The swallowtail butterflies (Papilionidae) of the tribe Leptocircini Kirby include species with
53 a high diversity of wing shapes, sizes and colors, such as dragontails, kite swallowtails and
54 swordtails. They comprise about 160 species distributed worldwide, which represent about a
55 quarter of all Papilionidae (*ca.* 600 recognized species; Zakharov et al., 2004; Häuser et al.,
56 2005; Condamine et al., 2012; Nakae, 2021). The phylogenetic relationships within tribe
57 Leptocircini remain highly uncertain and have never been the subject of comprehensive and
58 thorough phylogenetic studies, contrary to some well-studied swallowtail tribes (Papilionini:
59 Ae, 1979; Hancock, 1983; Igarashi, 1984; Aubert et al., 1999; Caterino and Sperling 1999;
60 Reed and Sperling 1999; Yagi et al., 1999; Zakharov et al., 2004; Condamine et al., 2013a,
61 2013b; Lewis et al., 2015; Wu et al., 2015; Owens et al., 2017; Condamine et al., 2023;
62 Troidini: Silva-Brandão et al., 2005; Condamine et al., 2012, 2013a, 2015; Parnassiini: Nazari
63 et al., 2007; Michel et al., 2008; Condamine et al., 2018; He et al., 2023; Tian et al., 2023).

64 Nevertheless, Leptocircini has been the subject of several morphological studies and
65 revisions based mainly on genitalia and wing venation in the 1960s-2000s (e.g. Munroe, 1961;
66 Hancock, 1983; Miller, 1987; Smith and Van-Wright, 2001; Makita et al., 2003; Hancock
67 2006). Recently, the genus *Graphium* Scopoli has been the focus of molecular work in localized
68 parts of the phylogeny to describe new species, often based on the mitochondrial COI gene or
69 a few genes (e.g. *Graphium (Pazala)* Moore: Hu et al., 2018, 2019; Zhang et al., 2020;
70 *Graphium (Graphium)*: Page and Treadaway, 2014; Cotton et al., 2022). Leptocircini has also
71 appeared in several attempts to reconstruct the global phylogeny of Papilionidae, but usually
72 with a low sampling fraction (e.g. Makita et al., 2003 [25%]; Simonsen et al., 2011 [6.8%];
73 Page and Treadaway 2014 [24%]; Zhang et al., 2019 [29%]; Zhang et al., 2021 [6.8%]) and
74 none of these phylogenies are sufficiently robust to to enable a firm classification to be
75 constructed. The most comprehensive phylogenetic work dealing with family Papilionidae and

76 including Leptocircini was conducted by Allio et al. (2021a) and used seven mitochondrial and
77 nuclear genes. However, the sampling of Leptocircini only included 42% of the tribe and the
78 phylogenetic relationships were not robust enough to discuss the topology and its consistency
79 with the existing literature. This apparent neglect is quite surprising for a group as studied and
80 popular as Papilionidae, but probably stems from multiple explanations. Indeed, Leptocircini
81 are known to be particularly difficult to collect in the field due to their still largely unknown
82 behaviour and traits, seasonality, the speed and height of their flight (Collins and Morris, 1985;
83 Smith and Vane-Wright, 2001; Nakae, 2021).

84 *Leptocircini are distributed worldwide*

85 Most of the species richness of Leptocircini is contained in genus *Graphium*, which alone
86 includes ~110 of the 160 species of Leptocircini. As a typical component of the Old-World
87 tropics, *Graphium* is composed of five subgenera including a species-rich African subgenus
88 (*Arisbe* Hübner) and four Indomalayan-Australasian subgenera (*Graphium*, *Paranticopsis*
89 Wood-Mason and de Nicéville, *Pathysa* Reakirt and *Pazala*) (**Fig. 1**). The Australian
90 monotypic genus *Protographium* Munroe is thought to be sister to *Graphium* based on its
91 morphology (Munroe, 1961; Munroe and Erlich 1960; Nakae 2021). Genus *Eurytides* Hübner
92 is the second richest genus in Leptocircini with >40 species, and is exclusively found in the
93 Americas. The systematics and taxonomy of both *Graphium* and *Eurytides* have undergone
94 many changes and uncertainties, with numerous subgenera or genera having been proposed
95 (see taxonomic details in the following paragraph). Here, we test all existing or unresolved
96 subgeneric names, including latest clade-level studies (e.g. Smith and Vane-Wright, 2001;
97 Mohn, 2002; Zhang et al., 2024) and global family-level assessments (Tyler et al., 1994; Nakae,
98 2021). It corresponds to five subgenera for *Graphium*: *Arisbe*, *Graphium*, *Paranticopsis*,
99 *Pathysa* and *Pazala* (see details hereafter) and nine subgenera for *Eurytides*: *Asiographium*

100 Möhn, *Bellerographium* Möhn, *Boreographium* Grishin, *Eurygraphium* Möhn, *Eurytides*
101 Hübner, *Hyalaus* Grishin, *Mimoides* Brown, *Neographium* Möhn and *Protesilaus* Swainson.

102 External to *Protographium* and these two diverse genera are two smaller genera
103 containing three species each: (1) *Iphiclides* Hübner is the only Leptocircini genus with an
104 Eurasian distribution; and (2) *Lamproptera* Gray, commonly called dragontail butterflies, is a
105 South-east Asian clade with a divergent and peculiar morphology (**Fig. 1**).

106

107 *Leptocircini have a complex and still unstable taxonomic history.*

108 *Graphium* has been the subject of several morphological and molecular studies, attempting to
109 understand its classification and evolutionary relationships. To our knowledge, all studies have
110 shown genus *Graphium* to be monophyletic (e.g. Makita et al., 2003; Allio et al., 2021a).
111 Despite several studies that upgraded some subgenera to genera (e.g. Niculescu, 1977; Igarashi,
112 1984; D'Abrera, 1982; Page and Treadaway, 2014), the subgeneric classification of genus
113 *Graphium* is now commonly accepted (e.g. Munroe 1961; Collins and Morris 1985; Miller
114 1987; Parsons 1998; Racheli and Cotton 2009; Hardy and Lawrence 2017; Nakae 2021).
115 However, the classification and validity of subgenera within *Graphium* remain highly
116 controversial, despite multiple morphological and molecular analyses. *Graphium* (*Pazala*) is
117 usually considered as monophyletic and valid and placed as the sister group to the other
118 *Graphium* subgenera (Hancock, 1983; Miller 1987), but sometimes not (Makita et al., 2003;
119 Allio et al., 2021a). However, *Graphium* (*Arisbe*), *Graphium* (*Graphium*), *Graphium*
120 (*Paranticopsis*) and *Graphium* (*Pathysa*) have a more complex taxonomic history.

121 Saigusa et al. (1982) considered Asian *Graphium* (*Graphium*) as monophyletic with
122 three species-groups: *sarpedon*, *agamemnon*, and *eurypylus*. However, no species of *Graphium*
123 (*Arisbe*) were included in their analysis, which was later considered as a limitation, as Hancock

124 (1993) found that tailed *Arisbe* species were more closely related to *Graphium* (*Graphium*).
125 Hancock (1993) therefore divided *Graphium* (*Arisbe*) into non-tailed species (*Arisbe*) and
126 tailed species (*antheus*-like) and included these latter in *Graphium* (*Graphium*). Smith and
127 Vane-Wright (2001) tested this morphological hypothesis in a cladistic framework, but were
128 ‘unable to resolve African and Oriental species-groups’. On the other hand, several studies,
129 instead of questioning the monophyly *Graphium* (*Arisbe*), have rather considered the
130 monophyly of *Graphium* (*Graphium*) as doubtful, and particularly the placement of the
131 *eurypylus* species-group. Indeed, the monophyly of *Graphium* (*Graphium*) was not supported
132 in Makita et al. (2003), the *eurypylus* species-group being sister to *Graphium* (*Arisbe*). Page
133 and Treadaway (2003a) suggested a narrower definition of *Graphium* (*Graphium*), including
134 only certain species-groups (*sarpedon*, *codrus*, *macleayanus*, *wallacei* and *agamemnon*
135 groups) and established a generic status for *Arisbe* and subgeneric status for *eurypylus*, *Pazala*,
136 and *Pathysa* (all included in this broader genus *Arisbe*). Recently, Allio et al. (2021a) found a
137 polyphyletic *Graphium* (*Graphium*), but the *eurypylus* species-group was found to be sister to
138 *Graphium* (*Pazala*) and the other *Graphium* (*Graphium*) species-groups, and not sister to
139 *Graphium* (*Arisbe*). Recent studies based on molecular data have been unable to resolve the
140 issue, perhaps due to limited species representation.

141 Several studies considered *Graphium* (*Paranticopsis*) to be included in *Graphium*
142 (*Pathysa*) (Munroe and Erlich, 1960; Hancock, 1983; Miller, 1987). Smith and Vane-Wright
143 (2001) used *Graphium* (*Paranticopsis*) as a valid subgenus, but the study only included *G.*
144 *macareus*, which showed relatedness to the African clade *Graphium* (*Arisbe*), rather than
145 *Graphium* (*Pathysa*) and *Graphium* (*Pazala*). Later, Makita et al. (2003), Page and Treadaway
146 (2003a, 2003b, 2004, 2014), Wilson et al. (2014) and Allio et al. (2021a) observed polyphyletic
147 patterns or unresolved relationships between *Graphium* (*Paranticopsis*) and *Graphium*
148 (*Pathysa*), but their phylogenies were poorly supported.

149 A sister-group relationship between *Lamproptera* and *Graphium* was proposed by
150 Hancock (1983), Igarashi (1984) and Miller (1987) following Ehrlich (1957) on the basis of
151 larval and pupal morphological characters (Racheli and Cotton 2009). This relationship was
152 recovered based on morphological characters in Smith and Vane-Wright (2001) (but without
153 any *Eurytides* included) and based on morphological and molecular data in Page and
154 Treadaway (2014). However, the relationship between *Lamproptera* and *Graphium* was
155 described as unstable by Makita et al. (2003), as their molecular data showed that *Eurytides*
156 and *Iphiclides* were more closely related to *Graphium* than *Lamproptera*. In addition, they did
157 not formally question the ‘traditional’ *Lamproptera* + *Graphium* group that was proposed at
158 the time. Simonsen et al. (2011) found that *Graphium* instead forms a sister group to the
159 Neotropical Leptocircini (*Eurytides*, see below) and that *Iphiclides* and *Lamproptera* were
160 early-diverging clades of Leptocircini, but with a non-robust relationship. Finally, Allio et al.
161 (2020a, 2021a), found *Lamproptera* to be sister to *Iphiclides*, forming a sister clade to all other
162 Leptocircini, but again with rather weak support even with genomic data.

163 The Neotropical Leptocircini have never been the focus of any well sampled study.
164 Although they have appeared in several previously cited studies focused on *Graphium* (e.g.
165 Makita et al., 2003; Page and Treadaway 2014), they were only represented by a few species
166 and mainly included as outgroups. They also appear in several general studies of Papilionidae
167 (Simonsen et al., 2011; Allio et al., 2021a), where up to 18 species were sampled (~44%, Allio
168 et al., 2021a). Despite limited sampling, these studies suggest that Neotropical Leptocircini
169 form a monophyletic group, though their internal classification remains complex.

170 Genus *Eurytides* was first described by Hübner in 1821. It was subsequently placed
171 within genus *Papilio* (Rotschild and Jordan, 1906; Jordan, 1907-1908) or *Graphium* (Ford,
172 1944). Munroe (1961) reestablished *Eurytides* as a genus and divided it into *Eurytides*
173 (*Protesilaus*) and *Eurytides* (*Eurytides*). *Eurytides* was long thought to be closely related to the

174 Australian *Protographium leosthenes* (which Munroe [1961] also erected as a monospecific
175 genus) and some *Eurytides* species were even placed in *Protographium* by Brown (1991) and
176 Tyler et al. (1994). The two subgenera *Protesilaus* and *Eurytides* as defined by Munroe (1961),
177 were later elevated to genera by Hancock (1983), downgraded again to subgenera by Miller
178 (1987), and restored to genera by Brown (1991). Brown (1991) also described *Mimoides* as a
179 genus including the Neotropical mimetic Leptocircini species that were previously placed by
180 Munroe (1961) in *Eurytides* (*Protesilaus*). Lately, Zhang et al. (2019) proposed downgrading
181 *Mimoides* to a subgenus of *Eurytides* to account for its close relationship with *E. marcellus*.

182 Möhn (2002) removed Neotropical species from genus *Protographium* and proposed
183 two new subgenera: *Eurytides* (*Neographium*) (*philolaus* species-group) and *Eurytides*
184 (*Asiographium*) (monospecific, type-species *E. asius*). He also described two new subgenera
185 of *Eurytides*: *Eurytides* (*Bellerographium*) (monospecific, type-species *E. bellerophon*) and
186 *Eurytides* (*Eurygraphium*) (*thyastes* species-group). Lamas (2004) synonymized some of these
187 names in *Protographium* (*Asiographium*, *Eurygraphium*, *Neographium*) or *Eurytides*
188 (*Bellerographium*). However, since the type specimen of *Protographium* is the Australian *P.*
189 *leosthenes*, which appears to be unrelated to *Eurytides* (Zhang et al. 2019), this synonymy is
190 likely incorrect. Finally, Zhang et al. (2021) proposed the monospecific subgenus *Eurytides*
191 (*Boreographium*) (monospecific, type-species *E. marcellus*), and Zhang et al. (2024) proposed
192 the monospecific subgenus *Eurytides* (*Hyalaus*) (monospecific, type-species *E. epidaus*), based
193 on a limited sampling, to account for the proximity of these species with *Eurytides* (*Mimoides*)
194 rather than with the *Eurytides* (*Neographium*) species.

195 ***A well-sampled phylogenomic dataset to resolve the tree of Leptocircini***

196 To date, all phylogenetic studies of Leptocircini lack a high species sampling or are limited to
197 morphological or a few molecular markers, which have resulted in highly unstable
198 classifications and many unresolved relationships. It has long been shown that phylogenetic

199 studies based on a handful of molecular markers can result in poorly supported phylogenetic
200 relationships due to a limited number of phylogenetically informative characters (Wiens and
201 Penkrot 2002; Funk and Omland 2003; Wiens et al., 2010; Ross 2014; Mutanen et al., 2016).
202 On the other hand, genomic data can alleviate some of the phylogenetic issues by expanding
203 the number of characters from a few thousand to hundreds of thousands (Delsuc et al., 2005;
204 Philippe and Blanchette 2007; Pennisi 2008), and help to produce better resolved phylogenetic
205 trees and particularly robust backbones. For instance, using genome-scale data associated with
206 a reference genome of *Papilio xuthus* (sequenced by Li et al., 2015), Allio et al. (2020a) were
207 able to retrieve thousands of single-copy genes and inferred a robust phylogenetic backbone
208 for swallowtail butterflies. Although this study lacked the sampling to constitute a complete
209 species-level phylogeny, it represents a promising approach to combining reference genomes
210 and fragmented whole genomes. Indeed, in the era of high-quality complete genomes that is
211 flourishing (Formenti et al., 2022), the swallowtail butterflies are no exception. However,
212 genus *Papilio* remains the most studied, with >30 whole genomes published since 2015 (e.g.
213 Lu et al., 2019 and references therein), while the first high-quality genomes of Leptocircini
214 were only published recently (*Lamproptera curius*, He et al., 2022; *Iphiclides podalirius*,
215 Mackintosh et al., 2022). However, there is no reference genome for *Graphium* available yet,
216 even though this genus represents the second most speciose genus in Papilionidae.
217 Furthermore, a reference genome for *Graphium* can provide crucial data for the genomics of
218 swallowtail butterflies since the expected size of their genomes is larger than that of
219 phylogenetically related genera (Allio et al., 2020a).

220 In this study, we first establish a list of valid Leptocircini species based on previous
221 molecular and morphological studies and then infer a robust and near complete species-level
222 phylogeny for the tribe. We sequenced and assembled five new reference genomes of
223 Leptocircini, including four *Graphium* species, and 136 *de novo* shotgun whole genomes,

224 which together allow us to extract thousands of nuclear genes and mitogenomes for around
225 88% of the total specific diversity of Leptocircini. Our study aims to provide a reference
226 phylogenetic framework for assessing the monophyly of genera and subgenera as well as
227 species relationships within Leptocircini. For this objective, we include all enigmatic and long-
228 debated groups and species to be robustly placed in the swordtail tree of life, such as
229 *Protographium leosthenes*, *Graphium phidias* and other species that will be key for testing
230 diversification and biogeographic hypotheses (e.g. *Eurytides marcellus*), the evolution of
231 mimicry (e.g. *Eurytides (Mimoides)*, *Graphium (Paranticopsis)*) and host-plant associations
232 (e.g. *Graphium (Pazala)*, *Lamproptera*, *Iphiiclides*), as well as rare and understudied species
233 (e.g. *Graphium (Arisbe)*, *Eurytides*). On the basis of this dataset, we also explored the
234 hypothesis of gene flow and incomplete lineage sorting to explain topological discordances
235 between the species tree and gene trees.

236

237 **Material and Methods**

238 *Species list, taxon sampling and sequencing strategy*

239 We first established a taxonomic working list of Leptocircini species (**Table 1**). This species
240 list takes into account some recent taxonomic lists and the results of recent studies (Hu et al.,
241 2018, 2019; Zhang et al., 2020; Nakae, 2021; Cotton et al., 2022; Huang 2023; and this study).
242 Due to the limited recent general phylogenetic studies conducted on Leptocircini, it is likely
243 that they will continue to receive attention as a model clade for taxonomic studies, and we
244 expect that many species boundaries will be tested with new genomic data, or at a populational
245 level, which could ultimately revise this taxonomic working list.

246 Of the 162 species currently featured in the new taxonomic list presented here (including
247 all of ‘valid’, ‘unconfirmed’ and ‘doubtful’ status), we sampled 147 species representing 90%

248 of the total diversity as follows: 143 species from this study (150 individuals, including 148
249 whole-genomes, using a combination of fresh and museum specimens), plus 4 species
250 (mitogenomic data) from GenBank (**Table 1**). However, the total number of species might
251 evolve with further systematic studies, as the validity of some species is still debated (e.g.
252 conflicts within *Graphium (Pazala)*, Hu et al., 2018, 2019 *versus* Huang 2023). The missing
253 species were essentially concentrated in *Graphium (Pazala)* (four missing) and *Graphium*
254 (*Arisbe*) (six missing), some of them being extremely rare or of doubtful status (**Table 1**). We
255 added 11 outgroup species representing several swallowtail genera to root the Leptocircini tree
256 based on large-scale phylogenetic studies of Papilionidae (Condamine et al., 2012; Allio et al.,
257 2020a, 2021): *Baronia brevicornis*, *Papilio xuthus*, *Parnassius apollo*, *Ornithoptera*
258 *alexandrae*, *Teinopalpus imperialis*, *Meandrusa payeni*, *Bhutanitis thaidina*, *Sericinus*
259 *montela*, *Luehdorfia chinensis*, *Hypermnestra helios* and *Archon apollinus*. The complete
260 taxon sampling and accession numbers are provided in **Tables S1, S2**.

261 Sequencing was performed in ~50x short-reads Illumina sequencing based on previous
262 estimates of genome sizes (Allio et al., 2020b; He et al., 2022). Among these sampled species,
263 five reference genomes were produced with a combination of long reads and short reads data:
264 *Iphiclides podalirius* (collected in the wild), *G. antheus* for *Graphium (Arisbe)*, *G. agamemnon*
265 and *G. doson* for subgenus *Graphium (Graphium)*, and *G. antiphates* for subgenus *Graphium*
266 (*Pathysa*), all obtained from rearing.

267 ***DNA extractions and library preparations for whole genome sequencing***

268 For museum and collection specimens (taking legs, rarely abdomens), DNA extractions were
269 performed with the DNAeasy Blood and Tissue kit (QIAGEN), and library preparations
270 followed the methods of Meyer and Kirscher (2010), but with slight modifications as described
271 in Tilak et al. (2015). DNA quality and concentration and fragment length varied markedly
272 between specimens. Final DNA purity and concentrations were measured using both Nanodrop

273 (Thermo Fisher, USA) and Qubit (Thermo Fisher, USA) and resulting libraries were analysed
274 for size distribution by Agilent 2200 TapeStation. Illumina 150 bp paired-end sequencing was
275 run on a NovaSeq 6000 instrument to obtain a genome depth-of-coverage of about 50x, hence
276 varying from 20 to 60 Gb per library depending on the genus.

277 For reference genomes, DNA extractions were performed with butterflies killed and
278 stored in a freezer at -20°C without any additional preservation product. Tissues from the
279 thorax were used to extract high-molecular weight DNA. Following Reboud et al. (2023) who
280 tested two different extraction methods, we used the Qiagen genomic DNA kit to obtain a better
281 260/230 ratio as estimated with Nanodrop assays guaranteeing DNA purity for long-read
282 sequencing with Oxford Nanopore Technology (ONT). Final DNA purity and concentrations
283 were measured using both Nanodrop (Thermo Fisher, USA) and Qubit (Thermo Fisher, USA).
284 Whole-genome libraries were prepared using the resulting high-molecular-weight DNA as
285 input for the Nanopore LSK-109 ligation kit (Oxford Nanopore Technologies, UK) following
286 the manufacturer's protocol. Long-read (LR) sequencing was performed on a GridION device
287 with two to six R9.4.1 flow cells. Remaining DNA extractions were sent to Novogene Europe
288 (Cambridge, UK) for two short-read Illumina library preparations per genome. Libraries were
289 generated using NEBNext DNA Library Prep Kit following manufacturer's recommendations,
290 and indices were added to each library. Genomic DNA was randomly fragmented to a size of
291 350 bp by shearing, then DNA fragments were end-polished, A-tailed, and ligated with the
292 NEBNext adapter for Illumina sequencing, and further PCR enriched by P5 and indexed P7
293 oligos. The PCR products were purified (AMPure XP system) and the resulting libraries were
294 analysed for size distribution by Agilent 2100 BioAnalyzer and quantified using real-time PCR.
295 Since the genome sizes for *Graphium* was estimated to be about 1 Gb and *Iphiclides* about 390
296 Mb (Allio et al., 2020a), Illumina 150 bp paired-end sequencing was run on a NovaSeq 6000

297 instrument to obtain about 100 and 40 Gb, respectively, corresponding to a genome depth-of-
298 coverage of ~100x after combining the two libraries.

299

300 *Assembling reference genomes*

301 For each reference genome (*G. agamemnon*, *G. antheus*, *G. doson*, *G. antiphates*, *I. podalirius*),
302 raw LR sequence data (fast5 files) were basecalled using Guppy 5.0.15 (Oxford Nanopore
303 Technology) with the super-high accuracy mode and a quality control of 10 (min_score 10).
304 Sequencing adapters were trimmed using Porechop 0.2.3
305 (<https://github.com/rrwick/Porechop>). Draft genome assemblies were performed with the LR
306 assembler Flye 2.8.3 (Kolmogorov et al., 2019) with default options. For *Graphium* genomes,
307 duplicated haplotigs and heterozygous contig overlaps were removed from the draft assembly
308 using purge_dups 1.2.5 (Guan et al., 2020) based on the LR depth (**Fig. 2**).

309 The Illumina raw reads were cleaned, filtered, and paired using fastp 20.0 (Chen et al.,
310 2018) with default options (**Fig. 2**). To improve base accuracy and reduce assembly errors, the
311 Flye draft assemblies were polished using short-reads (SR) with POLCA (Zimin and Salzberg,
312 2020) implemented in MaSuRCA 4.0.1 (Zimin et al., 2013). Assembly statistics were then
313 assessed using the gVolante2 platform (Nishimura et al., 2017) to retrieve the number and size
314 of contigs, the presence, completeness and duplication of BUSCO genes of the Lepidoptera
315 *odb10* database (Manni et al., 2021). We checked for possible contaminations using BlobTools
316 1.1.1 (Laetsch and Blaxter, 2017) set to the *ncbi* and *diamond* databases. We found no evidence
317 of artificial contamination coming from laboratory manipulation, but some contigs were clearly
318 identified as belonging to exogenous organisms such as symbionts. We removed all contigs
319 that belonged to plants or symbionts (*Wolbachia*, Ascomyota, Acetobacteraceae, Bacteroidota,
320 and Microsporidia).

321 We compared our genome of *I. podalirius* with the one published by Mackintosh et al. (2022)
322 using the option `-cx asm5` of Minimap2 (Li, 2018). We excluded all alignments smaller than
323 10 kb and those with a mapping quality below 60 (*i.e.* the maximum) and we then calculated
324 the average gap-compressed divergence (*i.e.*, counting consecutive gaps as one) provided by
325 the program. We computed the BUSCO scores of both genomes using *compleasm* (Huang and
326 Li, 2023)

327 *Assembling shotgun whole genomes*

328 The Illumina SR were filtered and paired with fastp 19.5-21.0 (Chen et al., 2018) using the
329 default options (**Fig. 2**). The assemblies were performed by MEGAHIT 1.2.7-1.2.9 (Li et al.,
330 2015) and submitted to the gVolante platform to obtain assembly statistics as well as assessing
331 the proportion of genes found from the *odb10* database of Lepidoptera (BUSCO 5, Manni et
332 al., 2021). The gVolante platform retrieves BUSCO genes classed in ‘single copy’, ‘multicopy’
333 and ‘fragmented’ categories. To improve the contiguity and the number of BUSCO genes
334 recovered in these draft assemblies, they were scaffolded with the scaffold option of RagTag
335 (Alonge et al., 2021) when a close reference genome was available (same species-group or
336 same subgenus). Species of the genera *Eurytides* and *Protographium* did not have any close
337 reference genome. In that case, only assemblies with less than 25% BUSCO completeness were
338 scaffolded on the reference *Graphium agamemnon* to retrieve more BUSCO genes. To
339 compare draft genome assemblies with scaffolded genome assemblies, the resulting assemblies
340 were again submitted to gVolante. The BUSCO single copy genes in fasta nucleotide file of
341 each individual were retrieved using BUSCOMP 0.13 (Edwards, 2019).

342 *Assembling mitogenomes and phylogenetic reconstruction*

343 For reference genomes, each *Graphium* individual, LR were mapped with Minimap 2.17 (Li
344 2018) on the mitogenome of *G. xenocles* (MZ394042) for *G. agamemnon*, *G. antiphates*, *G.*
345 *doson*, and on the mitogenome of *G. leonidas* (FC1205, this study) for *G. antheus*. The reads
346 that mapped with the reference were filtered by quality via SAMtools (Li et al., 2009) (*view -*
347 *q 30*). For each individual, a subset of reads was created so that mitogenomes would have an
348 expected depth of coverage of 200× (3.6 Mb). We used Flye 2.8.3 to assemble the mitogenomes
349 and the resulting assemblies were given to MitoFinder 1.4 (Allio et al., 2020b) to annotate and
350 extract thirteen protein-coding genes (ATP6, ATP8, COX1-3, CYTB, ND1-4, ND4L, ND5-6)
351 and 2 non-coding genes (rrnL, rrnS). The complete mitogenome of *Iphiclides podalirius* was
352 identified as a contig of the whole-genome assembly and was also selected for annotation by
353 MitoFinder.

354 For shotgun assemblies, MEGAHIT draft-assemblies of each species were given to
355 MitoFinder to extract and annotate the mitogenome. Some assemblies only displayed
356 fragmented mitogenomes, pseudogenes, fungi contamination or cross-contamination. When
357 the identification of ‘real’ mitogenomic contigs was not possible manually, GetOrganelle (Jin
358 et al., 2020) was used with a close reference for mapping to reconstruct complete, or less
359 fragmented, mitogenomes. This method was only used on difficult individuals as the
360 computation time of GetOrganelle is longer and not necessary when MEGAHIT already
361 reconstructed the full mitogenome. For every species, we used MitoFinder to annotate and
362 extract genes. For missing species, we retrieved the COI-5P gene or complete mitochondrion
363 from GenBank (see **Table S1** for more details).

364 We selected 11 outgroup species as previously described (see *Species list and taxon*
365 *sampling* section), either using the mitogenome of the same individual as for the nuclear

366 analyses, or by taking the complete mitogenome of the same species on GenBank (see
367 **Table S1**).

368 To account for frameshifts (both artificial and biological) and stop codons, sequences
369 were aligned with MACSE 2.07 (Ranwez et al., 2018), setting an invertebrate mitochondrial
370 genetic code (*-gc_def 5*), a frame-shift penalty of 5 (*-fs 5*) and an internal stop codon penalized
371 by 10 (*-stop 10*). Maximum-likelihood (ML) phylogenetic inference was implemented with
372 IQ-TREE 2.2.0 (Minh et al., 2020a) using ModelFinder to select the best-fit partition scheme
373 and the best-fitting substitution model for each partition (*-m MFP+MERGE* option, Chernomor
374 et al., 2016, Kalyaanamoorthy et al., 2017) applied to an initial subset of 41 possible partitions
375 (the three codon-position of the 13 protein-coding genes and the 2 non-coding genes). Branch
376 support of the ML tree was evaluated with 1,000 ultrafast bootstraps (UFBS; *-B 1000* option,
377 Hoang et al., 2018).

378

379 ***Phylogenomic analyses with nuclear data***

380 Phylogenomic analyses of genome-scale data were based on BUSCO genes. For each of the
381 5,286 lepidopteran core genes, we assessed the number of represented individuals, and applied
382 two different sampling criteria on these genes to form two datasets. *Dataset 1* corresponds to
383 all genes that gather at least 145 out of 159 individuals (91.2% of sampling for each gene),
384 which corresponds to 1,402 genes. The *Dataset 2* was produced with a threshold of 50%
385 (80/159 individuals) sampling for each gene, which corresponds to 4,525 genes.

386 The nucleotide sequences of the 1,402 genes (*Dataset 1*) were aligned with MAFFT
387 7.453 (Kato and Standley, 2013). For each alignment, a gene tree was reconstructed with IQ-
388 TREE with the best-fitting substitution model for each gene (*-m TESTNEW* option) and 1,000
389 UFBS. We used PhylteR (Comte et al., 2023) to detect potential outlier genes in our dataset,

390 applying two different settings for the 'k' parameter ($k=4$ and $k=6$), which controls the strength
391 of outlier detection (**Fig. S1**). Four and three outliers were identified respectively, and two of
392 these latter were not among the four outliers detected by $k=4$. We manually checked all the
393 outlier gene trees. Finally, we decided to retain these few genes for the next stage of
394 phylogenetic analysis 1) we were uncertain about the extent of artificial versus biological
395 signals, 2) these cases represent only 0.028% ($k=4$: 4/1402) or 0.021% ($k=6$: 3/1402) of the
396 entire dataset, and 3) the outlier genes detected did not consistently overlap between different
397 k values. A supertree of the gene trees was produced with ASTRAL 5.7.7 (Zhang et al., 2018)
398 following a tree-reconciliation (or 'supertree approach').

399 A supermatrix approach was also performed on both datasets. First, the nucleotide
400 alignments of *Dataset 1* were concatenated into a single matrix. Maximum-likelihood
401 phylogenetic inference was carried out with IQ-TREE. A first analysis was performed applying
402 the GTR+I+G model to each of the 1402 partitions (*-m GTR+I+G*, one partition per gene).
403 Second, we performed an analysis using ModelFinder to select the best-fit partition scheme
404 and the best-fitting substitution model for each partition (*-m MFP+MERGE* option), on the
405 initial subset of 1,402 possible partitions. Branch support was evaluated with 1,000 ultrafast
406 bootstraps (UFBS; *-B 1000* option). We performed ten independent IQ-TREE likelihood
407 searches based on the best-fit partition scheme and substitution models to estimate the global
408 log-likelihood score of the tree. *Dataset 1* was also analysed with an amino-acid supermatrix,
409 and the phylogeny was reconstructed with IQ-TREE using the LG protein model (*-m*
410 *LG+G4+F*, Le and Gascuel, 2008) and branch support evaluated with 1,000 UFBS. These
411 same options were also used with a concatenated matrix of 4,525 amino acid genes (*Dataset*
412 2).

413 Finally, because traditional statistical measures of nodal support are prone to inflation
414 in phylogenomic data sets (Minh et al., 2020b), we performed gene concordance factor (gCF)

415 and site concordance factor (sCF) analysis implemented in IQ-TREE 2 (Minh et al., 2020a),
416 using respectively the gene trees of *Dataset 1*, and the nucleotide supermatrix of *Dataset 1*, in
417 comparison with the consensus tree of the IQTREE_1402_NT analysis (**Table 2**).

418

419 *Analysis of incomplete lineage sorting and gene flow*

420 To investigate the hypotheses that incomplete lineage sorting (ILS) or gene flow (GF) have
421 caused topological conflicts between the species tree and gene trees in *Graphium (Pathysa)*
422 and *Graphium (Paranticopsis)* (see *Results*), we used Aphid (Galtier, 2023), a maximum-
423 likelihood method that aims to quantify the sources of phylogenetic conflict via topology and
424 branch length analysis of rooted three-species gene trees. Given a triplet of species A, B, C and
425 outgroup species, and assuming a main topology ((A, B), C), Aphid classifies all gene trees
426 into five categories: no event detected (the gene tree follows the main topology ((A, B), C) and
427 its branching time), non-discordant ILS (same topology but branching times are higher than in
428 the main topology), non-discordant GF (same topology but branching times are smaller than in
429 the main topology), discordant ILS (noted ILS_c ('c' for conflict), where topologies differ from
430 the main topology, and branching times are higher), and discordant GF (GF_c, topologies differ
431 from the main topology and branching times are smaller). For the last two cases, Aphid also
432 gives the 'discordant topology imbalance' associated with the event (predominance of ((A, C),
433 B) or ((B, C), A)). The rationale is that GF events occur after population isolation and therefore
434 result in shorter branch lengths, whereas ILS events are caused by ancestral polymorphisms
435 older than population isolation. Aphid can therefore identify GF even when alternative
436 topologies occur at similar frequencies, unlike the statistics derived from the ABBA/BABA
437 test.

438 All gene trees that could be rooted with *Baronia brevicornis* were selected for the
439 analyses (1,330 gene trees). To investigate the potential ILS and GF that could lead to the

440 observed paraphyly of *Graphium* (*Pathysa*) and polyphyly of *Graphium* (*Paranticopsis*), we
441 focused our tests on five species-groups: the *aristeus* species-group (hereafter referred to as
442 “*Pathysa 1*”), the *antiphates* species-group (“*Pathysa 2*”), the clade formed by *G. agetes* and
443 *G. stratiotes* (“*Pathysa 3*”), the *macareus* species-group (“*Paranticopsis 1*”) and the
444 *deucalion* species-group (“*Paranticopsis 2*”). Four configurations of triplets were tested, each
445 requiring different A, B, C species (**Fig. 3**). In our case, A, B and C did not correspond to single
446 species but to entire clades (species-groups). To account for the impact of selecting only one
447 species as a representative of an entire species-group, the analysis of each triplet was repeated
448 with five different A, B and C species randomly selected in each species-group (**Table S3**). For
449 each series of triplets, we calculated the mean of the five replicates tested. In all analyses,
450 *Graphium* (*Arisbe*) *antheus* was selected as outgroup of the triplets. Aphid was run with default
451 options.

452

453 **Results**

454 ***Reference genomes***

455 We assembled *de novo* genomes of five Leptocircini species representing the genera *Iphiclides*
456 (*I. podalirius*), and *Graphium* with *Graphium (Arisbe)* (*Graphium antheus*), *Graphium*
457 (*Pathysa*) (*G. antiphates*) and *Graphium (Graphium)* (*G. agamemnon*, *G. doson*) using LR and
458 SR data (**Table 3**). Final depth of coverage estimates of LR assemblies ranged from 12 to 66×
459 coverage, and SR polishing of these genomes from ~66 to 110× coverage. Overall, all
460 assemblies had high BUSCO scores (between 97.3% and 98.8% complete BUSCO genes) but
461 moderate N50 (70 kb - 1.1 Mb, **Table 3**). The sizes of the assembled genomes varied from
462 Mb (*I. podalirius*) to 2,052 Mb (*G. antiphates*). Two assemblies (*G. antheus*: 1,686 Mb; *G.*
463 *antiphates*: 2,052 Mb) had higher size than expected in the literature, even after having
464 removed the detected artificial duplication in the assembly through the *purge_dup* step and
465 both assemblies still had >12% of duplicated BUSCO genes (**Table 3**). This could be due to
466 highly heterozygous genomes but could not be corrected with other genome assemblers either.
467 Our assembly of *I. posalirius* was larger than the one generated by Mackintosh et al. (2022)
468 (469 Mb vs. 430 Mb) but both genomes were very similar in the number of BUSCO single-
469 copy genes recovered (97.09% vs. 97.77%). The mapping performed with Minimap2 resulted
470 in 393 Mb of alignment with a divergence of 0.77%.

471

472 ***Shotgun whole-genome assemblies***

473 We assembled 136 *de novo* whole genomes of Leptocircini using Illumina SR data. Assembly
474 with MEGAHIT resulted in draft assemblies with an average Complete single-copy genes
475 BUSCO score of 57.9% (**Fig. 4**). The mean of Fragmented and Missing genes was 16.7% and
476 24.0%, respectively. Mean assemblage sizes vary greatly according to genus: 424 Mb for

477 *Protographium*, 489 Mb for *Iphiclides*, 839 Mb for *Lamproptera*, 839 Mb for *Eurytides*, and
478 1,093 Mb for *Graphium*. After a scaffolding step with RagTag with a phylogenetically close
479 reference genome when available, the average complete single-copy genes BUSCO of all
480 assemblies improved to 73.0% (**Fig. 4**) and that of Fragmented and Missing genes BUSCO
481 score decreased to 10.8% and 15.3%, respectively.

482

483 *Phylogenomics of Leptocircini*

484 All genome-scale phylogenetic analyses provided very similar phylogenetic trees, with
485 identical backbones, but differed in branch length estimates and relationships in some species-
486 groups (**Fig. 5, Figs. S1, S3, S4, S5**).

487 All analyses recovered high mean and median branch support (**Fig. S6**). For instance,
488 the IQ-TREE analysis of *Dataset 1* (supermatrix of 1,402 nucleotide genes for a total matrix of
489 3.5 Mb, 'IQTREE_1402_NT') showed a mean branch support of 99.5 and a median of 100,
490 with 94.2% of nodes having maximal branch support (**Fig. S6**).

491 Both IQTREE_1402_NT analyses (*GTR+I+G* and *MPF+MERGE* options) produced
492 trees identical in topology and almost identical in branch length (mean branch length $1.848e^{-2}$
493 vs. $1.832e^{-2}$, **Figs. 5, S7, S8**), but the *GTR+I+G* analysis was 11.8 times faster (38h vs. 448h).
494 The *MFP+MERGE* analysis was selected as the reference topology (**Fig. 5**). The number of
495 final partitions in this IQ-TREE analysis was reduced to 183 (compared to the initial 1402
496 possible partitions). All log-likelihood values from the 10 tree searches were consistent,
497 ranging between -54,638,088.158 and -54,638,088.200, varying only at the decimal level. The
498 resulting trees were identical in topology, and the branch length variations were infinitesimal,
499 with differences ranging between $-3e^{-6}$ and $2e^{-7}$ (**Fig S9**). For the mitochondrial analysis, the
500 number of final partitions was reduced to 14 partitions (compared to the initial 41 partitions).

501 Overall, all maximum likelihood trees of the nucleotide *Dataset 1* (IQTREE_1402_NT,
502 **Fig. 5**; ASTRAL_1402_NT, **Fig. S2**), the amino-acid *Dataset 2* (IQTREE_4525_AA, **Fig. S3**)
503 and the mitochondrial analysis (IQTREE_15_Mito, Fig. S5) recovered strong support for the
504 monophyly of all genera: *Iphiclides* (UFBS_{NT}/UFBS_{AA}/LPP = 100/100/1), *Lamproptera*
505 (100/100/1), *Eurytides* (100/100/1), and *Graphium* (100/100/1). *Protographium* was recovered
506 as sister to *Graphium* with maximal support (100/100/1), except in the mitochondrial analysis
507 (UFBS_{mito}= 95).

508 Considering the former higher-level systematics (**Fig. 5**), nine subgeneric names have
509 been proposed for genus *Eurytides* (e.g. Mohn 2002; Lamas, 2004; Nakae, 2021; Zhang et al.
510 2021, 2024). *Eurytides* (*Asiographium*) and *Eurytides* (*Bellerographium*) were strongly nested
511 within *Eurytides* (*Neographium*) (UFBS_{NT}/UFBS_{AA}/LPP = 100/100/1) and *Eurytides*
512 (*Eurytides*) (100/100/1) respectively. *Eurytides* (*Eurygraphium*) was found monophyletic and
513 sister to *Eurytides* (*Eurytides*) (100/100/1) and *Eurytides* (*Protesilaus*) was found
514 monophyletic and sister to this previous clade (100/100/1). *Eurytides* (*Hyalas*) was found
515 sister to all *Eurytides* (*Mimoides*) (100/100/1) and *Eurytides* (*Boreographium*) was found sister
516 to this previous clade (100/100/1). Finally, *Eurytides* (*Neographium*) was found sister to the
517 clade formed by *Mimoides*+*Hyalas*+*Boreographium* (100/100/1).

518 Within genus *Graphium*, *Graphium* (*Pazala*), *Graphium* (*Graphium*) and *Graphium*
519 (*Arisbe*) were recovered as monophyletic with strong support (UFBS_{NT}/UFBS_{AA}/LPP =
520 100/100/1 for the crown node of each subgenus). However, *Graphium* (*Pathysa*) as delimited
521 by Nakae (2021) was found to be paraphyletic in all analyses (100/100/1, **Fig. 5**, **Fig. S10**), and
522 *Graphium* (*Paranticopsis*) was found to be polyphyletic in all analyses (100/97/1, see **Fig. 5**).
523 Indeed, the latter was separated into two distinct clades: the *deucalion* species-group and the
524 *macareus* species-group which was sister to *G. agetes* (*Pathysa*) + *G. stratiotes* (*Pathysa*),.

525 Overall, topological conflicts between all phylogenetic analyses were mostly limited to
526 shallow nodes with short internode lengths within well-supported clades or deeper nodes with
527 low branch support, especially in *Eurytides* (*Protesilaus*) (**Fig. S11**), the species *idaeoides* and
528 *encelades* within *Graphium* (*Pathysa/Paranticopsis*) (**Fig. S10**), the *adamastor* species-group
529 (*Graphium* (*Arisbe*), **Figs. 5, S2, S3, S4, S5**), and in *Graphium* (*Graphium*) (e.g. the *doson* and
530 *sarpedon* species-groups, **Figs. 5, S2, S3, S4, S5**).

531

532 ***Concordance factors***

533 Gene and site concordance factors (gCF and sCF) had systematically lower values than UFBS
534 (see **Fig. S12** for comparison of UFBS_{NT}/gCF/sCF). The median and mean values were
535 respectively 77.42 and 68.49 for the gCF, and 55.80 and 56.48 for the sCF. Several clades had
536 overall poor gCF and sCF values (**Fig. 6, Figs. S12, S13**), such as the sister relationship
537 between *Lamproptera* and *Iphiclidides*; or deep nodes in *Graphium* (*Arisbe*), *Graphium*
538 (*Graphium*) and *Graphium* (*Pathysa/Paranticopsis*); or recent nodes within species-groups
539 such as the *Eurytides* (*Protesilaus*) clade, the *adamastor* species-group in *Graphium* (*Arisbe*),
540 and the *sarpedon* species-group in *Graphium* (*Graphium*).

541

542 ***Incomplete lineage sorting and gene flow in Pathysa-Paranticopsis***

543 *Graphium* (*Pathysa*) was found to be paraphyletic and *Graphium* (*Paranticopsis*) polyphyletic:
544 the *macareus* species-group (“*Paranticopsis 1*”) was found to be sister to *G. agetes* and
545 *G. stratiotes* (“*Pathysa 3*”) and they were separated from the *deucalion* species-group
546 (“*Paranticopsis 2*”). In addition, this topology is associated with a high rate of discordant gene
547 tree topologies that could be explained by GF or ILS. Our sampling of *Graphium* (*Pathysa*)
548 and *Graphium* (*Paranticopsis*) species is almost complete (except the very rare *Graphium*

549 *euphratoides*, assumed to be in the “*Pathysa 2*” species-group based on morphology) and all
550 species possess more than 90% of the 1,402 genes. Our data thus provides a suitable framework
551 for testing the hypotheses of GF and ILS between *Graphium* (*Paranticopsis*) and *Graphium*
552 (*Pathysa*).

553 Aphid was run on four different series of triplets. The total number of genes classified
554 by Aphid was very similar between triplets and within replicates (>1000, **Table S3**). When the
555 observed topology was set as the main topology, *i.e.* triplet nb 1 (“*Pathysa 3*”, “*Paranticopsis*
556 *1*”, “*Paranticopsis 2*”), GF was detected between “*Paranticopsis 1*” and “*Paranticopsis 2*”
557 (46.7% of GF, and 56.9% of imbalance toward (“*Paranticopsis 1*”, “*Paranticopsis 2*”) in these
558 46.7%, **Table 4**). When the tested topology was set to triplet nb 2 (“*Paranticopsis 1*”,
559 “*Paranticopsis 2*”), “*Pathysa 3*”), a high proportion of GF was detected between
560 “*Paranticopsis 1*” and “*Pathysa 3*” (which was expected as it is supported by the ‘main
561 topology’). In that case, the proportion of ILS between “*Paranticopsis 1*” and “*Pathysa 3*” was
562 not particularly higher than in the first triplet. Finally, when “*Pathysa 2*” was included in the
563 triplet (triplets nb 3 and nb 4, **Table 3**), GF was detected between “*Pathysa 2*” and the two
564 other taxa of the triplet, with a slight imbalance for GF between “*Pathysa 2*” and *Paranticopsis*
565 (55.8 and 58.4% of imbalance in triplet n°3 and n°4 respectively, **Table 4**). This GF was higher
566 when the *Paranticopsis* clade was represented by “*Paranticopsis 2*” than by “*Paranticopsis*
567 *1*” (33.4% in triplet nb 3 against 25.7% in triplet nb 4; **Table 4**).

568

569 **Discussion**

570 *Whole genome assemblies of Leptocircini*

571 Our study provides the first robust and near complete phylogenomic framework for tribe
572 Leptocircini, thanks to the *de novo* assemblies of 150 individuals (143 species) including five
573 reference genomes. The final phylogeny represents more than 90% of total Leptocircini
574 richness. Our genome of *Iphiclides podalirius* generated using Oxford Nanopore sequencing
575 (FC536) was larger compared to the PacBio-sequenced genome published by Mackintosh et
576 al. (2022) (468 Mb vs. 430 Mb), whereas both samples were coincidentally collected in the
577 same town near Montpellier (Saint-Martin-de-Londres, France). Despite the size difference,
578 both genomes show highly similar gene completeness, with comparable BUSCO scores. The
579 discrepancy in assembly size might be linked to assembly differences (*e.g.*, more haploid
580 contigs in FC536 or less efficient assembly of complex repeat-rich regions in Mackintosh et al.
581 2022) or biological factors (*e.g.*, variation in transposable element content). Interestingly,
582 Reboud et al. (2023) assembled four genomes of *Ornithoptera alexandrae* (two per population)
583 with long and short reads data using the same pipeline and found slight differences in the
584 genome size between the two populations (~321 Mb in the lowland population vs. ~326 Mb in
585 the highland population), suggesting some variation in genome size within Papilionidae species
586 can occur. Sequence divergence between the assemblies of *Iphiclides podalirius* was 0.77%,
587 which is consistent with heterozygosity levels observed in other Papilionidae populations
588 investigated so far (which range from 0.1% to over 1% (Mackintosh et al., 2019; Reboud et al.,
589 2023; Marino et al., 2023). We have produced the first reference genomes for genus *Graphium*,
590 and despite considerable sequencing efforts (*e.g.* *Graphium antiphates*, 114 Gb of long reads),
591 the assembly of highly contiguous genomes of *Graphium* species remains a challenge. Their
592 genomes appear to be highly heterozygous, and contain many repeats, further complicating the
593 assembly step. Nevertheless, these new reference genomes allowed RagTag to scaffold and

594 recover around 20% more genes than the draft assemblies of the shotgun whole genomes, even
595 recovering genes from the ‘missing’ BUSCO category. The closer the reference used was, the
596 better the scaffolding step, and in our case, we still lack a good *Eurytides*. reference genome to
597 scaffold the Neotropical Leptocircini species. With an average of 73% complete single-copy
598 BUSCO genes, the scaffolded genomes provided robust data for reconstructing the phylogeny
599 and will surely be useful for further genome studies such as molecular evolution (e.g. dN/dS
600 as in Allio et al., 2021a).

601 ***Phylogeny and global taxonomic revision of Leptocircini***

602 Overall, genus-level relationships are fairly consistent with previous studies. We recovered
603 *Protographium* as sister to all *Graphium*, in agreement with the results of Munroe (1961) and
604 Zhang et al. (2019). *Lamproptera* and *Iphiclides* are found to be sisters, although both branch
605 supports and gCF indicate it is a complicated node to resolve, which is consistent with
606 Condamine et al. (2012), Allio et al. (2020a, 2021a), but not consistent with Makita et al.
607 (2003), Simonsen et al. (2011), Page and Treadaway (2014), and Kawahara et al. (2023).

608 Our phylogeny is the first to show a robust and well-sampled phylogenetic framework
609 of *Eurytides*. Following global assessments for the family (Tyler et al. 1994; Nakae 2021) and
610 clade-based studies (Möhn 2002; Lamas, 2004; Zhang et al. 2021, 2024), nine subgenera of
611 *Eurytides* were considered in this study. *Eurytides* (*Neographium*) is not monophyletic because
612 of *Eurytides* (*Asiographium*). In addition, *Eurytides marcellus* and *E. epidaus* are more closely
613 related to *Eurytides* (*Mimoides*) than other *Eurytides* (*Neographium*) species. The case of *E.*
614 *marcellus* was previously discussed in Zhang et al. (2021) who proposed the monospecific
615 *Eurytides* (*Boreographium*) Grishin (type-species *E. marcellus*), based on a reduced species
616 sampling, to accommodate the non-monophyly of *Eurytides* (*Neographium*). Following this
617 work and notably adding *E. epidaus* in the sampling, Zhang et al. (2024) proposed the
618 monospecific subgenus *Eurytides* (*Hyalaus*) Grishin (type-species *E. epidaus*) to again address

619 the non-monophyly of *Eurytides* (*Neographium*). Here, in view of the dense global sampling
620 that this study provides, in order to maintain consistency of the subgeneric level within the
621 entire tribe (and family) and to avoid the description of too many taxonomic entities
622 (monospecific and/or paraphyletic subgenera), we propose merging all species of the clade
623 *Asiographium+Boreographium+Neographium+Hyalaus+Mimoides* into *Eurytides*
624 (*Mimoides*), thus placing *Eurytides* (*Boreographium*), *Eurytides* (*Hyalaus*), *Eurytides*
625 (*Asiographium*) and *Eurytides* (*Neographium*) as synonyms of subgenus *Eurytides* (*Mimoides*)
626 (*Boreographium* **syn. nov.**, *Asiographium* **syn. rest.**, *Hyalaus* **syn. nov** and *Neographium* **syn.**
627 **nov.**).

628 *Eurytides* (*Eurygraphium*) (the *thyastes* species-group) is found sister to *Eurytides*
629 (*Eurytides*). Lamas (2004) synonymized *Eurygraphium* within *Protographium* but instead we
630 synonymize it with *Eurytides*. (*Eurygraphium* **syn. rest.**). Lamas (2004) also synonymized
631 *Bellerographium* Möhn within *Eurytides* (*Eurytides*), which we confirm with this study.
632 Finally, in agreement with Nakae (2021) and Zhang et al. (2024), we confirm the subgeneric
633 status of *Eurytides* (*Protesilaus*). As a result, *Eurytides* is divided in three subgenera: *Eurytides*
634 (*Eurytides*), *Eurytides* (*Mimoides*) and *Eurytides* (*Protesilaus*).

635 The relationships within genus *Graphium* are very consistent with Miller (1987), but
636 differ from Smith and Vane-Wright (2001), Makita et al. (2003), Page and Treadaway (2014)
637 and Allio et al. (2021a), especially regarding the strong support for monophyly of *Graphium*
638 (*Graphium*).

639 *Graphium phidias* has had an ambiguous placement in the literature. It was long placed
640 within *Graphium* (*Paranticopsis*), due to its similar wing pattern (Munroe, 1961, and with
641 caution, e.g. Racheli and Cotton, 2009; Page and Treadaway, 2014). It was found to be sister
642 to the *eurypylus* species-group in Makita et al. (2003), and sister to *Graphium* (*Arisbe*),
643 *Graphium* (*Paranticopsis*) and *Graphium* (*Pathysa*) in Allio et al. (2021a). It was placed in

644 *Graphium* (*Graphium*) in Nakae (2021). Here, *G. phidias* is strongly supported as sister to the
645 *eurypylus* species-group, with a rather long branch, suggesting an early divergence from this
646 group.

647 *Graphium* (*Graphium*) is usually divided into three species-groups: the *eurypylus*,
648 *sarpedon* and *agamemnon* species-groups (Munroe, 1961; Saigusa et al., 1982; Makita et al.,
649 2003; Racheli and Cotton 2009; Page and Treadaway 2014). However, the *sarpedon* species-
650 group is not recovered as monophyletic, as the *agamemnon* species-group is nested within the
651 clade, dividing it into the *sarpedon* and the *macleayanus* species-groups. However, the short
652 branches separating these three clades (as well as their low gCF supports) suggest a rapid
653 evolution into different species-groups, and it would not be surprising if these relationships
654 were to change.

655 The inclusion of *Graphium* (*Paranticopsis*) within *Graphium* (*Pathysa*) has long been
656 suspected in the literature (e.g. Munroe and Ehrlich, 1960; Hancock 1983; Miller 1987; Makita
657 et al., 2003; Page and Treadaway, 2014), but has never been clearly demonstrated or strongly
658 supported. Our study provides strong support for this relationship, by placing *G. stratiotes* and
659 *G. agetes* as the sister clade of the *macareus* species-group, making *Graphium* (*Paranticopsis*)
660 polyphyletic. An ambiguous placement of *G. agetes* and *G. stratiotes* with species of the
661 *Graphium* (*Paranticopsis*) group had been found several times in previous studies (e.g. Makita
662 et al., 2003; Wilson et al., 2014), but was never strongly supported. Wilson et al. (2014) found
663 that two subspecies of *G. agetes* were either sister of *Graphium* (*Paranticopsis*) or *Graphium*
664 (*Pathysa*) species-groups, but this relied on a poorly resolved maximum parsimony tree based
665 on 28S rRNA sequences. Interestingly, Inayoshi (2023) reports the morphology of *G. agetes*
666 male genitalia supports its relationship with ‘the mimetic species of the *macareus* group’.
667 Whatever the complexity of relationships within the clade *Pathysa+Paranticopsis*, (i.e. the
668 polyphyly of *Graphium* (*Paranticopsis*) being real or not, see below), *Graphium* (*Pathysa*)

669 would always remain paraphyletic. We therefore propose to retain only *Graphium (Pathysa)*
670 Reakirt, and synonymize *Graphium (Paranticopsis)* Wood-Mason and de Nicéville (**syn.**
671 **rest.**).

672 Finally, our tree confirms the monophyly of *Graphium (Arisbe)* and strongly supports
673 the delineation of *Graphium (Arisbe)* as a subgenus of *Graphium* restricted to all the
674 Afrotropical taxa, and not present in Asia.

675 ***Ancient gene flow could explain discordant phylogenetic relationships.***

676 In our study, we found a strong phylogenetic discordance within the *Pathysa s.l.* clade,
677 with low sCF and gCF values at key nodes of the different species-groups. According to Minh
678 et al., (2020), low gCF values are difficult to interpret as they may result from weak
679 phylogenetic signals in individual loci, or from discordance between gene trees resulting from
680 GF or ILS. Here, the small branches recovered suggest rapid radiation from this clade that
681 could reinforce unresolved or erroneous genetic trees.

682 The distinctive distribution of traits within this clade (shift to mimicry being discordant
683 with the observed topology, see **Fig. 7**) led us to investigate the possibility of ILS and GF in
684 the history of this clade. Indeed, two sets of morphological traits are observed in this clade. On
685 the one hand, *Pathysa* (as circumscribed by Nakae, 2021) have tailed wings and a wing pattern
686 with dark stripes on a pale background (**Fig. 7**). On the other hand, *Paranticopsis* as
687 circumscribed by Nakae (2021) mimic various Nymphalidae in subfamily Danainae (mainly
688 *Ideopsis*, *Tirumala*, *Parantica* and *Euploea*) that are tailless with a mostly black wing pattern
689 (**Fig. 7**). The ‘*Pathysa* traits’ are common in other distant parts of the tree. For instance, the
690 striped wing pattern with tails is largely distributed across the phylogeny of Leptocircini.
691 (*Protographium leosthenes*, *Iphiclides*, *Graphium (Protesilaus)*, *Graphium (Pazala)* and some
692 *Graphium (Arisbe)* and even in other Papilionidae tribes (Papilionini, Sericinini). Therefore, it

693 is assumed that these traits are likely to be the ancestral traits, whereas mimetic *Paranticopsis*
694 would be considered as the ‘derived traits’ (Hancock, 1983). Our consensus phylogeny i.e. the
695 ‘observed’ topology (**Fig. 5, Fig. 7, Fig. S10**) indicates that *Graphium (Paranticopsis)* is nested
696 within *Graphium (Pathysa)*, causing *Graphium (Pathysa)* to be paraphyletic. Although this
697 was expected based on previous works and literature (e.g. Munroe and Ehrlich, 1960; Hancock,
698 1983; Miller, 1987; Smith and Vane-Wright, 2001), the polyphyly of *Paranticopsis* appears
699 surprising given the rather complex derived traits shared by both *Graphium (Paranticopsis)*
700 species-groups (**Fig. 7**).

701 The question is then: Is the distribution of traits we observe in the phylogeny the result
702 of 1) convergence of the derived traits (or of the ancestral traits), 2) ILS from ancient
703 polymorphism of ancestral and derived traits in the common ancestor of “*Pathysa 3*” and
704 *Paranticopsis*, or 3) GF between the different clades of *Graphium (Paranticopsis)* and/or
705 *Graphium (Pathysa)*, including the gene coding for the considered traits or not? Another way
706 of phrasing this problem is: Are the regions of the genome shared by “*Pathysa 3*” and
707 “*Paranticopsis 1*” the results of a speciation event or the result of a massive GF?

708 Although basic in appearance, these different scenarios were overall very difficult to
709 validate or even to distinguish. Yet, several hypotheses could be ruled out by our analyses.
710 First, the hypothesis that the observed topology is the ‘true’ topology and that *Graphium*
711 (*Paranticopsis*) derived traits are the results of a convergence gained twice in the phylogeny is
712 unlikely because of the large number of discordant topologies in the gene trees. Second, the
713 hypothesis that the observed distribution of traits is the result of ILS is not very likely because
714 of the rather low ILS supports found in all triplets. Finally, the pattern of GF and their direction
715 was the most predominant, but also the most complex to decipher.

716 When the ‘observed’ topology was set as the ‘main’ topology, i.e. the tree
717 (“*Pathysa 3*”, “*Paranticopsis 1*”), “*Paranticopsis 2*”), a high proportion of GF was detected

718 between “*Paranticopsis 1*” and “*Paranticopsis 2*”. This supports the scenario of a GF from
719 “*Paranticopsis 2*” to “*Paranticopsis 1*”, and that this GF include the derived traits (**Fig. 8C**).
720 In that case, the last event of speciation would have been between “*Pathysa 3*” and
721 “*Paranticopsis 1*” (as represented in the observed topology). Thereby, when the tested
722 topology is set to (“*Pathysa 3*”, (“*Paranticopsis 1*”, “*Paranticopsis 2*”)), if the last speciation
723 event was in reality between “*Pathysa 3*” and “*Paranticopsis 1*”, we should have found a large
724 number of trees supporting ILS between “*Pathysa 3*” and “*Paranticopsis 1*”. This was not
725 clearly the case, therefore we could not totally exclude the scenario in which “*Paranticopsis*
726 *1*” and “*Paranticopsis 2*” was the last event of speciation and that massive GF happened
727 between “*Pathysa 3*” and “*Paranticopsis 1*” (**Fig. 8D**). These two scenarios could probably be
728 distinguished by comparing the age (or absolute divergence) of the most recent nodes in the
729 two types of topologies (*Paranticopsis* monophyletic or not), but this would probably be very
730 difficult because of the overall very small branch length between our three clades. Finally, we
731 found some GF between “*Pathysa 2*” and “*Pathysa 3*”, meaning that ancestral traits could also
732 have been transferred to “*Pathysa 3*” (**Fig. 8E**). This could not really be excluded, but it is
733 overall less likely because the amount of GF detected is smaller than in the two first cases.

734 The case of *Graphium (Pathysa)* and *Graphium (Paranticopsis)* is an example of the
735 difficulty in classifying and interpreting the origin of discordant topologies in a genomic
736 dataset. This confirms that one of the main challenges of modern phylogenomics is to manage
737 the heterogeneity of evolutionary histories contained and revealed in the multitude of markers
738 used (Richards et al., 2018; Scornavacca et al., 2020; Dong et al., 2022). Furthermore, our case
739 is likely to be particularly difficult to decipher because we are testing discordances for
740 phylogenetic scales that are deeper than simple species pairs, which probably blurs the
741 dominant signal by the long history and possible multiplicity of evolutionary processes
742 between the different clades (Zhang et al., 2020; Dong et al., 2022) or by the potential existence

743 of ghost lineages (Tricou et al., 2022). In any case, our example includes such small branches
744 in the inferred consensus tree that it suggests a rapid radiation of this clade and thus
745 undoubtedly reinforces the proportion of unresolved or difficult-to-classify trees for Aphid
746 (Galtier, 2023). Here, gene ontology would likely help to understand how and when the genes
747 encoding the derived or ancestral trait would have been transferred.

748 ***Further work in species-groups is needed***

749 Apart from *Graphium (Pathysa)*, concordance factor analyses (gCF and sCF) revealed poor
750 support in several species-groups, such as *Eurytides (Protesilaus)*, *Graphium (Arisbe)* and
751 some *Graphium (Graphium)* (**Fig. 6, Figs. S12, S13**). These were usually more ‘recent nodes’
752 that could also reflect ongoing GF and recent ILS.

753 In the *adamastor* species-group (in *Arisbe*), most gCF values range between 7% to 39%
754 (8 nodes, gCF: mean = 36.0, median = 31.4), which means that in all these cases, the main
755 topology is at best retrieved in only a third of the gene tree topologies, whereas the last value
756 of the index, called gDFP (including all trees that are not either the main topology or the two
757 alternatives of the quartet *i.e.* paraphyly of the quartet and polytomy topologies) was usually
758 the most predominant alternative for the *adamastor* species-group (8 nodes, gDFP: mean =
759 51.3, median = 54.3). It is difficult to draw conclusions based only on this information, but it
760 shows that in this species-group, the 1,402 genes generally have insufficient information to
761 separate species clearly, or are not informative enough to distinguish or resolve well the
762 ‘species’ of the *adamastor* species-group. Yet, the same genes are informative in other parts of
763 the tree, such as the rest of *Graphium (Arisbe)* that do not have so many irresolutions (whole
764 tree gCF: mean = 68.49, median = 77.42; gDFP: mean = 18.618, median = 9.735, **Fig. S13**). It
765 could reflect an ongoing GF between these different ‘species’, and could also mean that they
766 might not all deserve a species status. Previous reviews of this particular species-group already
767 warned about potential over-splitting in this group (Smith and Vane-Wright, 2001; Hancock,

2006). Furthermore, some of their putative species are even missing such as *G. aurivilliusi*, *G. kigoma* and *G. poggianus*, *G. ucalegonides* and *G. rileyi* (now rather considered subspecies of *G. fulleri*), *G. olbrechtsi* and *G. abri* (**Table 1**).

In *Eurytides* (*Protesilaus*), the same pattern of low gCF values and strong prevalence of alternative topologies and polytomies were found (12 nodes, gCF: mean = 39.8, median = 27.9; gDFP: mean = 52.0, median = 58.9). Indeed, the observed topologies of this clade in our different analyses were very unstable (**Fig. S11**), and this clade probably needs robust population-level sampled phylogeny and taxonomic revisions (as the current species are largely sympatric cryptic species). At least one species tested here was found to be invalid: *E. exiguus* (second paratype in Winhard (2018) was sequenced) is a synonym of *E. glaucolaus leucas* (**syn. nov.**) (**Table 1**). This synonymy was also confirmed by examination of male genitalia, which are identical.

In *Graphium* (*Pazala*), our phylogenomic tree based on the nuclear genome lacks a few recently described species (*G. confucius*, *G. daiyuanae*, *G. sichuanica*, *G. wenlingae* only in COI, **Fig. S5**). In *Graphium* (*Graphium*), our sampling was conservative in the *sarpedon* species-group by only selecting *G. anthedon* for the group *anthedon/isander/choredon* group from Cotton et al. (2022). For both cases, the degree of resolution was low despite our conservative sampling (*Graphium* (*Pazala*), 8 nodes: gDFP: mean = 19.5, median = 18.5; *sarpedon*, 5 nodes, gDFP: mean = 35.1 median = 35.5).

We are concerned that further splitting in these groups will result in the same scenario, which may lead to never-resolved phylogenies. The back-and-forth between new description and synonymizing increases confusion and taxonomic instability (e.g. in subgenus *Pazala*, Hu et al., 2018; Huang, 2023), which should be avoided when taxonomic changes are not strongly supported (Christenhusz 2020). Within the *sarpedon* group, genetic structure is expected in a widely distributed clade with several subspecies described from different islands, but as Huang

793 (2020) pointed out, populations can maintain strong structuring without leading to speciation,
794 and phylogeny as measures of population structure do not appear to be good predictors of
795 speciation, even with many loci (Sukumaran and Knowles, 2017). Indeed, there may be
796 structure in the genomics of the species, but such a population structure does not necessarily
797 mean that they are different species or even that speciation is ongoing.

798 The best practice when testing taxonomic hypotheses is to be able to support a new
799 revision with several approaches, ideally combining strong genetic, morphological and
800 biological/ecological evidence (even if the latter is not the easiest to obtain or subject to marked
801 and observable differences) on a large and representative sampling of the different populations
802 and possible contact zones (Mutanen 2005; Padial et al., 2010; Schlick-Steiner et al., 2010;
803 Yeates et al., 2011; Sangster, 2014). It is important to rely on metrics that have been shown to
804 be informative for delimiting species within the group studied (Mutanen, 2005; Tóth and
805 Varga, 2011; Mikitová et al., 2021; Wingert, 2022). In the case of butterflies, variations in wing
806 size and colour pattern, or genitalia size, are expected according to environmental variations,
807 while marked differences in genitalia shape and structure may correspond to prezygotic barriers
808 and species differentiation (Mutanen, 2005; Mutanen and Pretorius, 2007, Tóth and Varga,
809 2011; Mikitová et al., 2021). For genetic evidence, it has been shown that DNA barcoding has
810 its limitations and should generally not be considered as solid and sufficient evidence (Moritz
811 and Cicero, 2004; Will et al., 2005). Nonetheless, comparative methods integrating a large
812 number of genetic and metric markers can be used (Will et al., 2005; Galtier et al., 2019; Arias-
813 Cárdenas et al., 2024; Khan et al., 2024; Wingert et al., 2024). Galtier (2019) proposed
814 comparing the genetic differentiation for pairs of species to be delimited with pairs of species
815 well recognized by the community as a basis for comparison. The genetic differentiation can
816 be estimated by pairwise calculation of indices of population polymorphism structure (such as
817 F_{ST}), indices of genetic differentiation (D_a , D_{xy} ; Nei 1987; Fraisse et al., 2021; De Jode et al.,

818 2023), as well as analyses of population structure (PCA, admixture, structure). This approach
819 can help to determine these species complexes as objectively and integratively as possible, as
820 was recently performed for mammals such as aardwolf and armadillos (Allio et al., 2021b;
821 Barthe et al., 2024).

822 *On the generic and subgeneric status within Leptocircini*

823 While the concept of genus is fundamental in biology and paleontology (Allmon, 1992), its
824 definition remains subjective and inconsistent across different taxa. Genera are generally
825 understood as groups of species that share specific characteristics, often indicating close
826 evolutionary relationships, or in the case of monotypic genera, emphasizing the uniqueness of
827 a species (Condamine et al. 2023). However, there are no universally accepted criteria for
828 determining genus boundaries, beyond the requirement for monophyly supported by
829 synapomorphies. Attempts to standardize the genus concept have proposed several guidelines,
830 including the number of species contained within the genus, group compactness, divergence
831 time, distinctness from related taxa, and degree of confidence in the assessment of its
832 phylogenetic relationships (e.g. Ashlock and Mayr, 1991; Talavera et al., 2012; Dorchin et al.,
833 2018; Sigward et al., 2018; Nakahara et al., 2020). However, one of the most arbitrary problems
834 in systematics is still striking a balance between these standards while preserving taxonomic
835 stability. In this context, practical considerations play a crucial role, as the elevation of
836 subgenera to full genera can obscure broader phylogenetic relationships and complicate
837 communication for non-specialists. The *International Code of Zoological Nomenclature*
838 (ICZN, 1999, 2012) emphasizes taxonomic stability as a guiding practice, and this should be
839 carefully considered in any potential taxonomic revision.

840 While this new phylogenomic study of Leptocircini provided an opportunity to
841 reevaluate et revised genera and subgenera delineation within the tribe, the question of
842 rehabilitating some subgenera into genera could be raised, particularly as some of them have

843 already undergone taxonomic back-and-forth in this respect. Here, we propose that the
844 elevation of subgenera to genera is not warranted at this time (for both *Graphium* and
845 *Eurytides*), for several reasons. First, although some subgenera of *Graphium* have been used
846 as generic names in certain publications, most studies retain these taxa at the subgeneric level,
847 and we advocate for this approach (e.g. Munroe 1961; Collins and Morris 1985; Miller 1987;
848 Parsons 1998; Racheli and Cotton 2009; Hardy and Lawrence 2017; Nakae 2021).
849 Classification within *Eurytides* has been more variable, but the most recent studies have used
850 subgenus levels (Nakae, 2021; Zhang et al. 2021, 2024). Second, while some authors have
851 argued for the recognition of genera based on crown ages (e.g., Avise and Johns, 1999;
852 Talavera et al., 2012), divergence times can vary widely between clades. For instance, genera
853 and subgenera in Leptocircini represent much older lineages (Allio et al., 2021a) compared to
854 other butterfly families like Nymphalidae, where younger divergence times are more common
855 (Chazot et al., 2021), thus making Papilionidae rather an exception in Papilionoidea with “old
856 genera”. As a contrary example, Talavera et al. (2012), in their work on *Polyommatus* blue
857 butterflies, designated a divergence age of 4–5 million years to define genera. Such a time
858 frame is clearly not applicable to Papilionidae or Leptocircini, as no compact, uniform groups
859 appear at this age—they are much older. The evolutionary history of Papilionidae,
860 characterized by slower diversification rates and smaller species richness compared to other
861 families, further supports a more conservative approach to genus-level recognition. In fact,
862 differences in crown ages might also likely reflect variations in species diversification of
863 Papilionoidea families. Such a disparity in evolutionary timelines between different butterfly
864 families is expected and also reflected in species diversity, with Nymphalidae comprising more
865 than 6,400 species while Papilionidae has only ~640 species, suggesting that the taxonomic
866 groups within these families have experienced different evolutionary histories and radiation
867 patterns. Therefore, it seems reasonable for the age of taxonomic groups—and the ranks of

868 subgenus and genus—to differ across families. Furthermore, the use of divergence times would
869 be delicate to apply here because our phylogeny is not dated. Attempts to apply divergence
870 times from the last recent dated phylogeny of Papilionidae (Allio et al. 2021a) would be delicate
871 too because there are significant differences in phylogenetic topologies for Leptocircini
872 between the two studies, and such differences in phylogenetic relationship could imply
873 significant differences in ages of major Leptocircini lineages. Finally, we think it is important
874 to consider this matter of genus delineation with a global approach to the taxonomy of other
875 tribes within Papilionidae, such as Papilionini, Troidini, and Parnassiini and to maintain
876 consistency within the family. For the genus *Papilio* specifically, this issue has been recently
877 addressed by Condamine et al. (2023). In addition, several genera in Troidini and Parnassiini
878 contain subgenera that, while not always well known, do not warrant genus-level recognition
879 based on molecular and morphological data. For instance, current subgenera within *Parnassius*
880 or *Ornithoptera* are not suitable as genera without clear morphological criteria, and elevating
881 them as such would create unnecessary and disputable complexity. This suggests that more
882 comprehensive analyses are necessary before any taxonomic elevation can be justified.

883 In summary, while revising the taxonomic ranks within Leptocircini could be valuable,
884 we believe it is essential to approach this within the broader framework of Papilionidae
885 taxonomy. A comprehensive, well-sampled, and robustly dated phylogeny of the entire family
886 would provide a more solid basis for such revisions. Until then, maintaining the current
887 classification system, with subgenera recognized at their existing rank, ensures consistency and
888 stability across the family.

889

890 **Data availability**

891 All genomic data related to the project have been deposit on GenBank (BioProject
892 PRJNA1131164). See Table S1 and Table S2 for accession number details of each genome
893 (BioSample and raw DNA sequenced data (SRA) numbers). All alignments, gene trees, tree
894 files and assembly scripts are available on the Figshare:
895 doi.org/10.6084/m9.figshare.27195603

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911 **Conflicts of interest statement**

912 The authors declare no conflict of interest.

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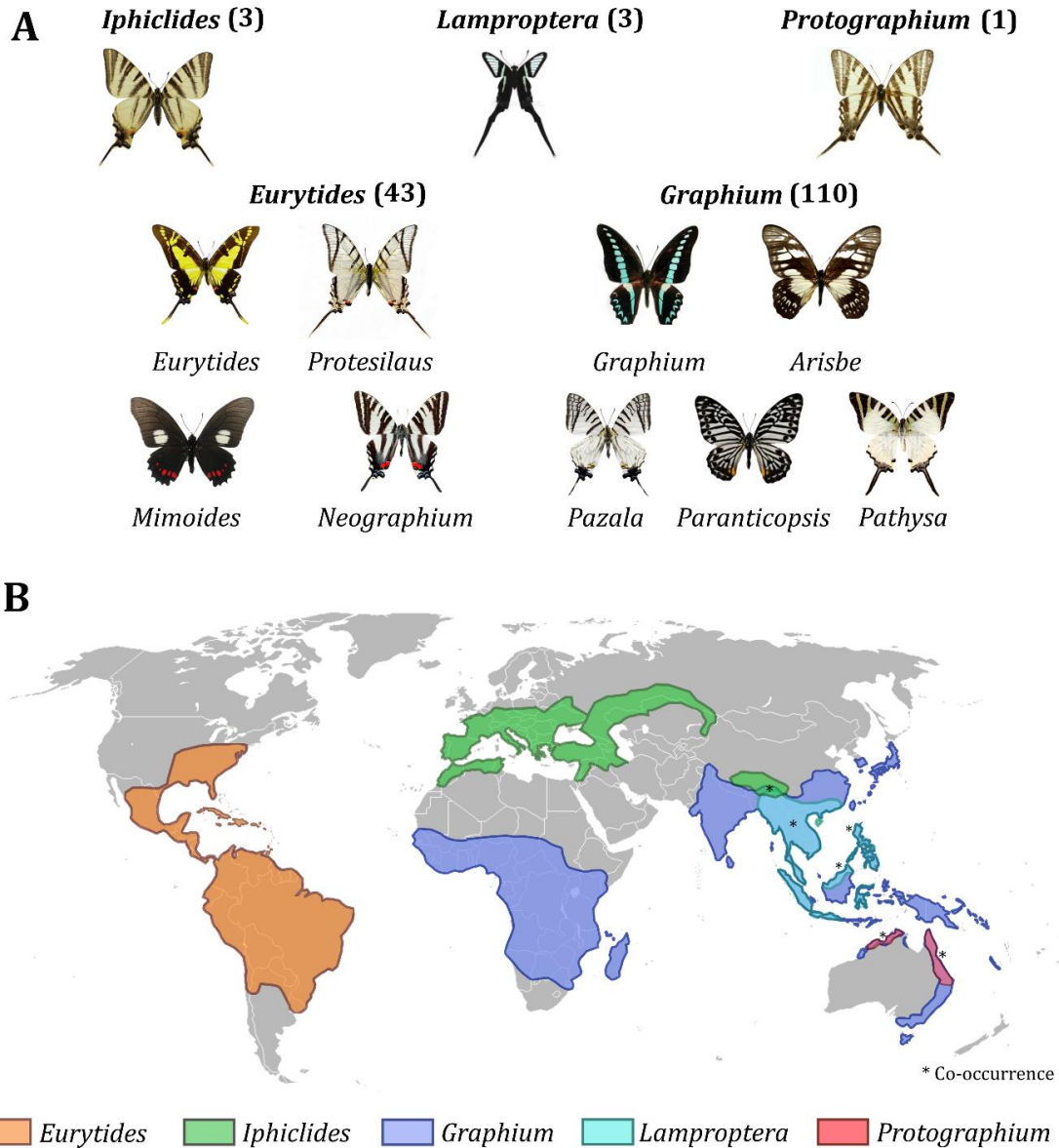
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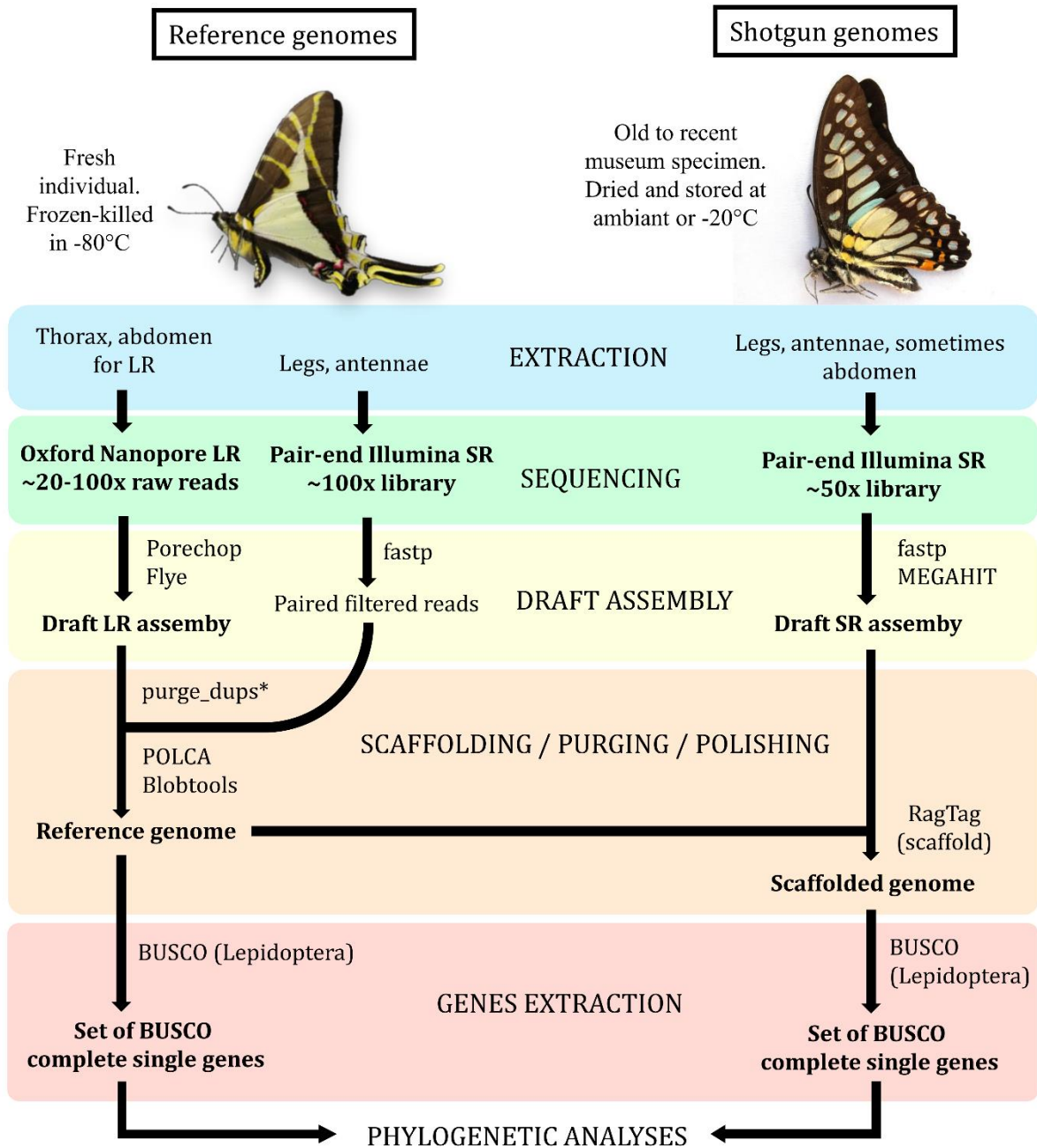
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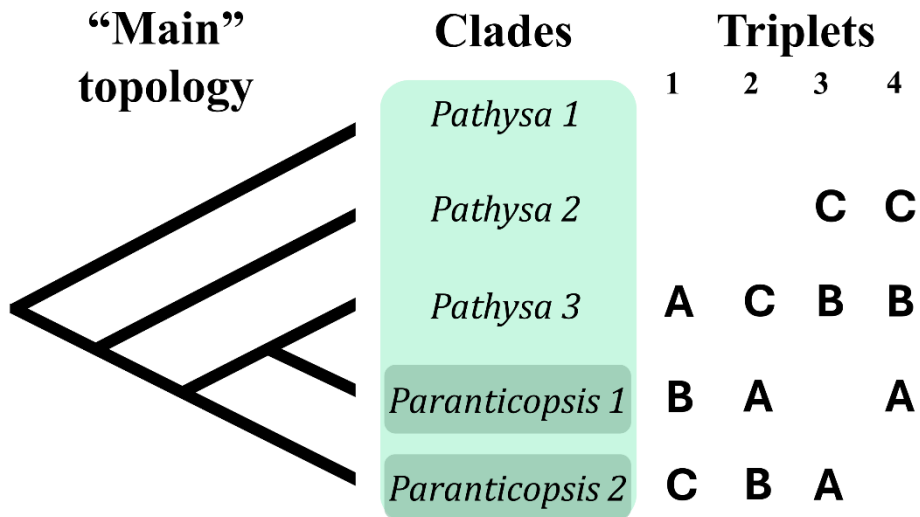
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1320 **Fig. 1:** Overview of Leptocircini and their global distribution. **A.** Habitus of Leptocircini
 1321 genera (bold font) and subgenera (regular font) following the systematic treatment of Nakae
 1322 (2021), *i.e.* monospecific subgenera of *Eurytides* are not represented (see Fig. 5 for complete
 1323 subgeneric classification). The species richness is indicated for each genus between
 1324 parentheses (refer to Table 1). **B.** Distribution pattern of Leptocircini genera. The distribution
 1325 map of each genus is drawn approximately according to the literature and *iNaturalist*
 1326 occurrences (www.inaturalist.org) and GBIF (<https://www.gbif.org/fr/>). Butterfly pictures:
 1327 *Iphiclides podalirius*, *Lamproptera curius*, *Protographium leosthenes*, *Eurytides* (*E.*) *thyastes*,
 1328 *E.* (*Protesilaus*) *telesilaus*, *E.* (*Neographium*) *marcellus*, *E.* (*Mimoides*) *ariarathes*, *Graphium*
 1329 (*Arisbe*) *adamastor*, *G.* (*G.*) *milon*, *G.* (*Paranticopsis*) *delessertii*, *G.* (*Pazala*) *mandarinus*, *G.*
 1330 (*Pathysa*) *antiphates*.



1331

1332 **Fig. 2:** Conceptualization of the sequencing and assembly pipeline for reference genomes (left)
 1333 and shotgun genomes (right) used to construct phylogenomic datasets of nuclear data, based
 1334 on long reads (LR) and short reads (SR) data.



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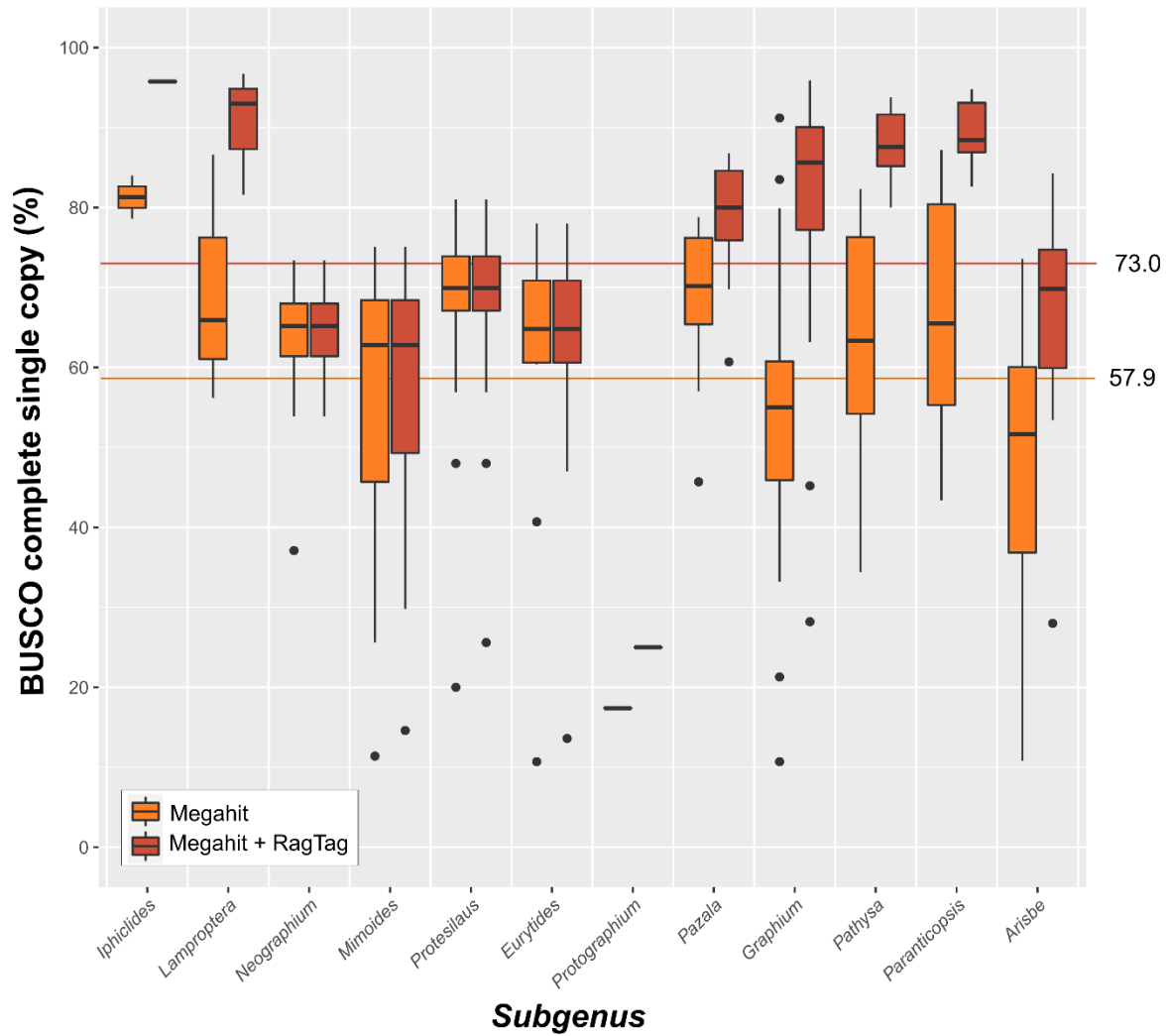
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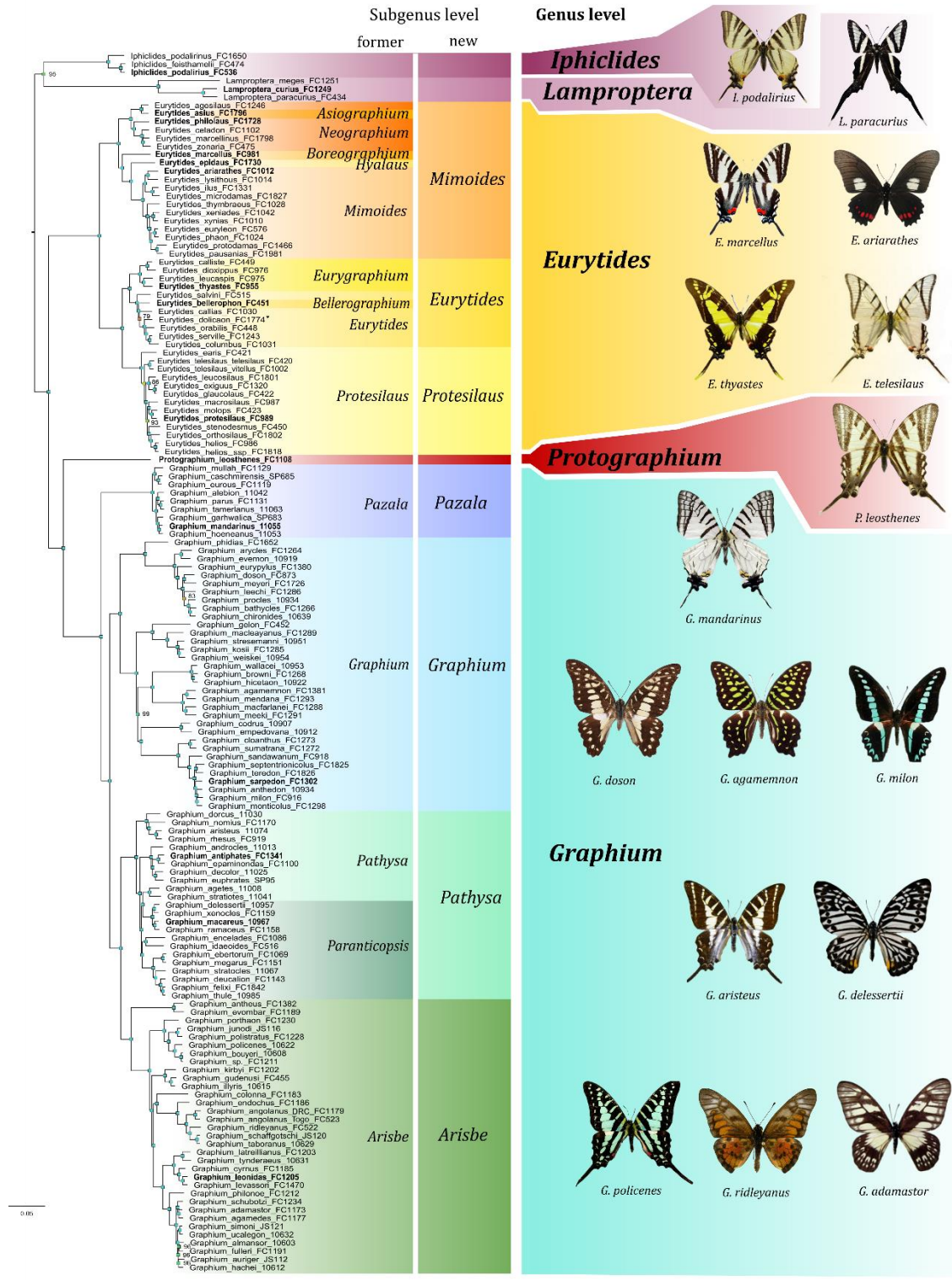
Fig. 3: Definition of the four series of triplets for the Aphid analyses. On the left is the observed phylogenetic relationships between the different clades, considered as the ‘main’ topology. On the right are the four tested series of ABC triplets for Aphid. The first conforms to the main topology, the second assumes that “*Paranticopsis 1*” and “*Paranticopsis 2*” shared parts of their genome because of a speciation event. The third and fourth allow testing hypotheses of gene flow or ILS with “*Pathysa 2*”.



1343

1344 **Fig. 4:** Effect of scaffolding fragmented shotgun whole genomes on the recovery of BUSCO genes.
 1345 Initial taxonomy followed the systematic treatment of Nakae (2021). Boxplots of BUSCO single
 1346 complete genes values of all assembly ($n=147$ specimens) within a subgenus, before (orange) and after
 1347 (red) the scaffolding. Horizontal coloured lines correspond to the mean BUSCO single complete score
 1348 of all individuals before (orange) and after (red) the scaffolding. Draft assemblies of subgenera
 1349 *Neographium*, *Mimoides*, *Protosilaus* and *Eurytides* were only scaffolded when the initial BUSCO
 1350 score was under 25%.

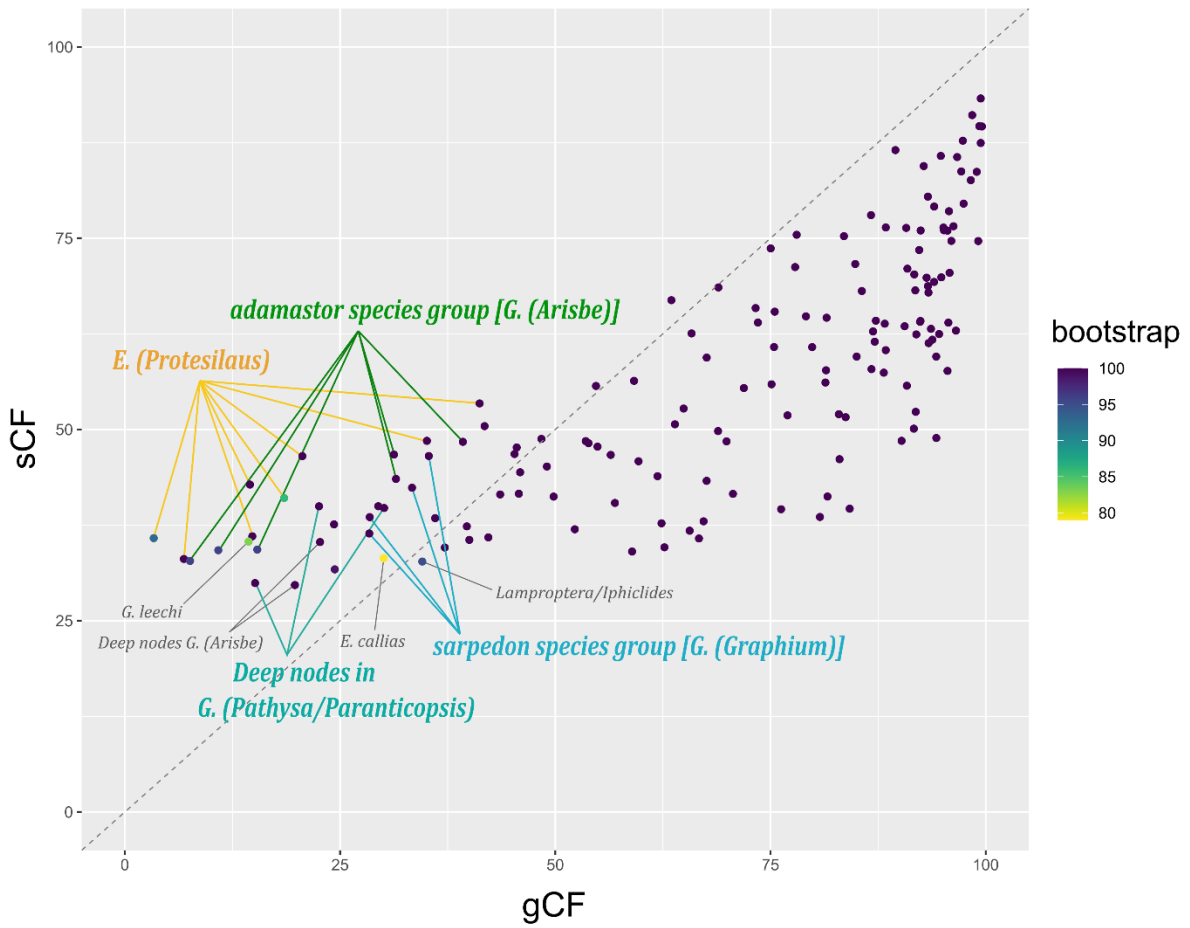
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1353 **Fig. 5:** Phylogenomic relationships of Leptocircini (*IQTREE_1402_NT*). The phylogeny has been
 1354 reconstructed with a supermatrix approach of 1,402 single-copy genes and a maximum-likelihood
 1355 inference in IQ-TREE. Light blue squares at nodes correspond to a bootstrap value equal to 100. Values
 1356 <100 are indicated. Genera are in italic bold font, and subgenera in regular italic. Species in bold front
 1357 are type species of subgenera. *The type species of *Eurytides* (*Eurytides*) is *Eurytides iphitas*, which is
 1358 closely related to *Eurytides dolicaon* (Zhang et al. 2024). Illustration credit: *L. paracurius* (Adam
 1359 Cotton), *G. mandarinus* (Hu et al., 2019), *G. milon*, *G. aristeus* (Alex Dumchus), *G. ridleyanus* (CC-
 1360 BY-NC Thomas Desloges), *G. doson* (Ariane Chotard).

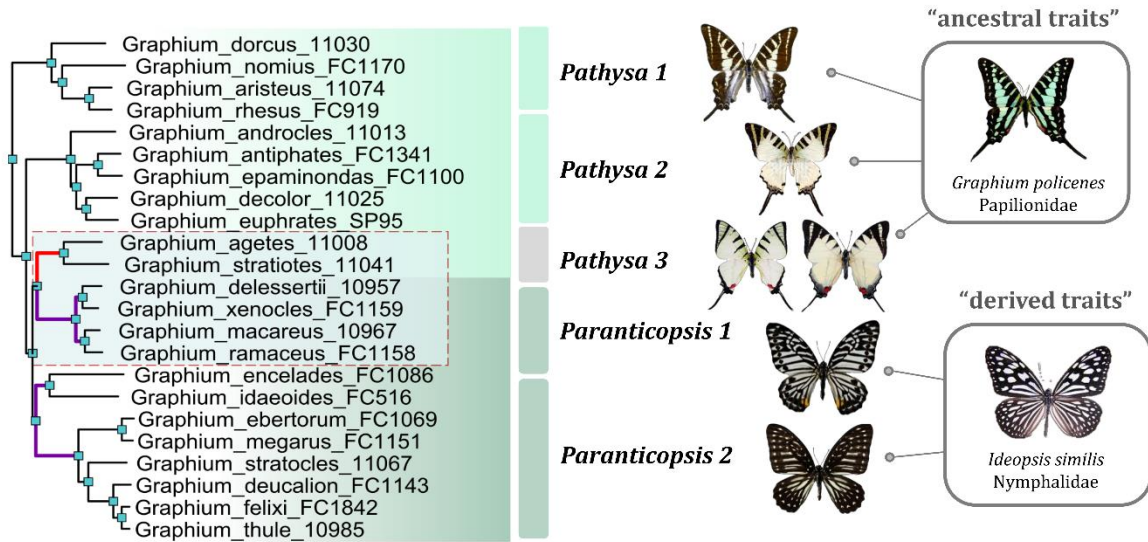
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1363 **Fig. 6:** Values of gCF and sCF values. Each point represents a node in the phylogeny and is coloured
1364 by its ultrafast bootstrap (UFBS) value. The dashed line corresponds to the identity line. Several clades
1365 or taxa with both poor gCF and sCF values are pointed by coloured or grey lines. *Eurytides* is
1366 abbreviated by *E.* and *Graphium* by *G.* in species names.

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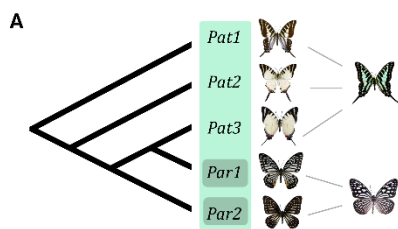


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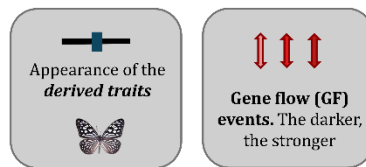
1369 **Fig. 7:** Phylogenetic relationships of the clade *Graphium* (*Pathysa*/*Paranticopsis*) (*IQTREE_1402_NT*
 1370 analysis). The different species-groups are delimited and named. Each species-group is linked to its
 1371 phenotypic traits, corresponding either to the ‘ancestral traits’ (striped wing pattern and tail), or the
 1372 ‘derived traits’ (mimetic wing pattern). Branch supports (ultrafast bootstrap) are indicated at nodes.

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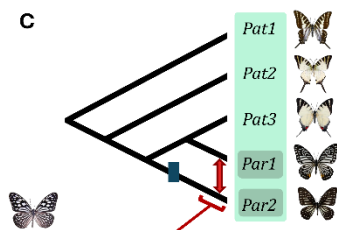
Observed topology and traits



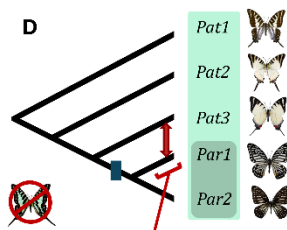
B Symbols legend



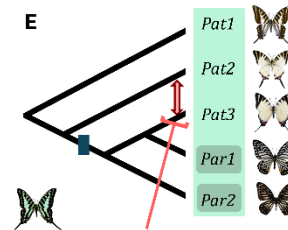
Remaining likely scenarios



GF with transfer of the genes coding for the derived traits



GF (massive) but genes coding for the ancestral traits are not transferred



GF (light) and the genes coding for the ancestral traits are transferred

1374

1375 **Fig. 8:** A. Observed topology and trait distribution between the different species-groups of *Graphium*
 1376 (*Pathysa*) and *Graphium* (*Paranticopsis*). B. Significance of the symbols used in the illustration of the
 1377 remaining likely scenarios. C, D and E. Scenarios that could explain the observed topology and trait
 1378 distribution. *Pat* = *Pathysa*, *Par* = *Paranticopsis*. Note that in C, the appearance of derived traits could
 1379 have also happened along the *Par1* branch, and be transferred to *Par2*.

1380 **Tables**

1381

Table 1: Taxonomic working list for Leptocircini species. The list includes subgenera that are currently recovered as monophyletic in molecular phylogenies, and species that belong to each subgenus. In the comment section, species in blue were sampled in our study and species in red were unsampled.

Genus <i>Eurytides</i> Hübner, [1821]	Sampling	Taxonomic status	Comment
Subgenus <i>Eurytides</i> Hübner, [1821]			
<i>Eurytides (Eurytides) bellerophon</i> (Dalman, 1823) comb. rev.	Sampled	Valid	
<i>Eurytides (Eurytides) callias</i> (Rothschild & Jordan, 1906)	Sampled	Valid	
<i>Eurytides (Eurytides) calliste</i> (Bates, 1864) comb. rev.	Sampled	Valid	
<i>Eurytides (Eurytides) columbus</i> (Kollar, 1849) stat. rev.	Sampled	Valid	We propose a stat. rev. based on morphological, nuclear and mitochondrial divergence
<i>Eurytides (Eurytides) dioxippus</i> (Hewitson, [1856]) comb. rev.	Sampled	Valid	
<i>Eurytides (Eurytides) dolicaon</i> (Cramer, 1775)	Sampled	Valid	
<i>Eurytides (Eurytides) iphitas</i> Hübner, [1821]	Unsampled	Valid	Probably extinct (Grice et al., 2019, Domagala and Gonzales 2021). Last specimen seen in 1977
<i>Eurytides (Eurytides) leucaspis</i> (Godart, 1819) comb. rev.	Sampled	Valid	
<i>Eurytides (Eurytides) orabilis</i> (Butler, 1872)	Sampled	Valid	
<i>Eurytides (Eurytides) salvini</i> (Bates, 1864)	Sampled	Valid	
<i>Eurytides (Eurytides) serville</i> (Godart, [1824])	Sampled	Valid	
<i>Eurytides (Eurytides) thyastes</i> (Drury, [1782]) comb. rev.	Sampled	Valid	<i>E. t. marchandii</i> is treated as a separate species in Möhn (2002) and Maza Elvira & Maza Elvira (2022). This remains to be genetically assessed.
Subgenus <i>Mimoides</i> Brown, 1991			
<i>Eurytides (Mimoides) agesilaus</i> (Guérin-Méneville, 1835) comb. nov.	Sampled	Valid	The species <i>E. oberthueri</i> (Rothschild & Jordan, 1906) is a supposed natural hybrid of <i>E.agesilaus</i> x <i>E.philolaus</i>
<i>Eurytides (Mimoides) anaxilaus</i> (C. Felder & R. Felder, 1865) comb. nov.	Unsampled	Valid	

<i>Eurytides (Mimoides) ariarathes</i> (Esper, 1788)	Sampled	Valid
<i>Eurytides (Mimoides) asius</i> (Fabricius, 1781) comb. nov.	Sampled	Valid
<i>Eurytides (Mimoides) celadon</i> (Lucas, 1852) comb. nov.	Sampled	Valid
<i>Eurytides (Mimoides) epidaus</i> (Doubleday, [1846]) comb. nov.	Sampled	Valid
<i>Eurytides (Mimoides) euryleon</i> (Hewitson, [1856])	Sampled	Valid
<i>Eurytides (Mimoides) ilus</i> (Fabricius, 1793)	Sampled	Valid
<i>Eurytides (Mimoides) lysithous</i> (Hübner, [1821])	Sampled	Valid
<i>Eurytides (Mimoides) marcellinus</i> (Doubleday, [1845]) comb. nov.	Sampled	Valid
<i>Eurytides (Mimoides) marcellus</i> (Cramer, 1777) comb. nov.	Sampled	Valid
<i>Eurytides (Mimoides) microdamas</i> (Burmeister, 1878)	Sampled	Valid
<i>Eurytides (Mimoides) pausanias</i> (Hewitson, 1852)	Sampled	Valid
<i>Eurytides (Mimoides) phaon</i> (Boisduval, 1836)	Sampled	Valid
<i>Eurytides (Mimoides) philolaus</i> (Boisduval, 1836) comb. nov.	Sampled	Valid
<i>Eurytides (Mimoides) protodamas</i> (Godart, 1819)	Sampled	Valid
<i>Eurytides (Mimoides) thymbraeus</i> (Boisduval, 1836)	Sampled	Valid
<i>Eurytides (Mimoides) xeniades</i> (Hewitson, 1867)	Sampled	Valid
<i>Eurytides (Mimoides) xynias</i> (Hewitson, 1875)	Sampled	Valid
<i>Eurytides (Mimoides) zonaria</i> (Butler, 1869) comb. nov.	Sampled	Valid
Subgenus <i>Protesilaus</i> Swainson, [1832]		
<i>Eurytides (Protesilaus) aguiari</i> (D'Almeida, 1937)	Unsampled	Valid
<i>Eurytides (Protesilaus) earis</i> (Rothschild & Jordan, 1906)	Sampled	Valid
<i>Eurytides (Protesilaus) exiguus</i> (Winhard, 2018)	Sampled	syn. nov.
<i>Eurytides (Protesilaus) glaucolaus</i> (Bates, 1864)	Sampled	Valid

E. epidaus was split into four species (*E. epidaus*, *E. fenochionis*, *E. tlahuica* and *E. tepicus*) by Maza Elvira & Maza Elvira (2022) based on wing pattern and genitalia. This remains to be genetically assessed.

E. p. xanticles could be a species

E. t. aconophos is treated as a separate species in Maza Elvira & Maza Elvira (2022). This remains to be genetically assessed.

We propose a **syn. nov.**, as a synonym of *E. glaucolaus leucas*, also supported by identical genitalia

<i>Eurytides (Protesilaus) helios</i> (Rothschild & Jordan, 1906)	Sampled	Valid	
<i>Eurytides (Protesilaus) leucosilaus</i> (Zikán, 1937)	Sampled	Uncertain	Sometimes considered as subspecies of <i>E. molops</i> , but monophyly not recovered in this study. Might be a synonym of <i>E. glaucolaus</i>
<i>Eurytides (Protesilaus) macrosilaus</i> (Gray, [1853])	Sampled	Valid	
<i>Eurytides (Protesilaus) molops</i> (Rothschild & Jordan, 1906)	Sampled	Valid	
<i>Eurytides (Protesilaus) orthosilaus</i> (Weymer, 1899)	Sampled	Valid	
<i>Eurytides (Protesilaus) protesilaus</i> (Linnaeus, 1758)	Sampled	Valid	
<i>Eurytides (Protesilaus) stenodesmus</i> (Rothschild & Jordan, 1906)	Sampled	Valid	
<i>Eurytides (Protesilaus) telesilaus</i> (C. Felder & R. Felder, 1864)	Sampled	Valid	

Genus <i>Graphium</i> Scopoli, 1777	Sampling	Taxonomic status	Comment
Subgenus <i>Arisbe</i> Hübner, [1819]			
<i>Graphium (Arisbe) abri</i> Smith & Vane-Wright, 2001	Unsampled	Doubtful	Described as a species from two specimens. Have never been genetically assessed. Could be a subspecies or melanic form of <i>G. adamastor</i> or <i>G. agamedes</i> , or a natural hybrid (Hancock, 2006).
<i>Graphium (Arisbe) adamastor</i> (Boisduval, 1836)	Sampled	Valid	
<i>Graphium (Arisbe) agamedes</i> (Westwood, 1842)	Sampled	Valid	
<i>Graphium (Arisbe) almansor</i> (Honrath, 1884)	Sampled	Valid	
<i>Graphium (Arisbe) angolanus</i> (Goeze, 1779)	Sampled	Valid	
<i>Graphium (Arisbe) antheus</i> (Cramer, 1779)	Sampled	Valid	
<i>Graphium (Arisbe) auriger</i> (Butler, 1876)	Sampled	Valid	
<i>Graphium (Arisbe) aurivilliusi</i> (Seeldrayers, [1897])	Unsampled	Doubtful	Uncertain type locality. Only three specimens known. Could be a natural hybrid of <i>G. adamastor</i> x <i>G. schubotzi</i> (Hancock 2006).
<i>Graphium (Arisbe) biokoensis</i> Gauthier, 1984	Unsampled	Unconfirmed	From Bioko Island. Recent revision in Cipolla (2021a, 2021b) and Bollino and Bouyer (2024). Might be a subspecies of <i>G. policensis</i>

<i>Graphium (Arisbe) bouyeri</i> Cipolla, 2021	Sampled	Valid	Recent revision in Cipolla (2021a, 2021b) and Bollino and Bouyer (2024). Relationship with <i>G. biokoensis</i> remains to be genetically tested.
<i>Graphium (Arisbe) colonna</i> (Ward, 1873)	Sampled	Valid	
<i>Graphium (Arisbe) cyrnus</i> (Boisduval, 1836)	Sampled	Valid	
<i>Graphium (Arisbe) endochus</i> (Boisduval, 1836)	Sampled	Valid	
<i>Graphium (Arisbe) evombar</i> (Boisduval, 1836)	Sampled	Valid	
<i>Graphium (Arisbe) fulleri</i> (Grose-Smith, 1883)	Sampled	Valid	
<i>Graphium (Arisbe) gudenusi</i> (Rebel, 1911)	Sampled	Valid	
<i>Graphium (Arisbe) hachei</i> (Dewitz, 1881)	Sampled	Valid	
<i>Graphium (Arisbe) illyris</i> (Hewitson, 1873)	Sampled	Valid	
<i>Graphium (Arisbe) junodi</i> (Trimen, 1893)	Sampled	Valid	
<i>Graphium (Arisbe) kigoma</i> Carcasson, 1964	Unsampled	Unconfirmed	A subspecies of <i>almansor</i> or <i>poggianus</i> (Hancock 2006)
<i>Graphium (Arisbe) kirbyi</i> (Hewitson, 1872)	Sampled	Valid	
<i>Graphium (Arisbe) latreillianus</i> (Godart, 1819)	Sampled	Valid	
<i>Graphium (Arisbe) leonidas</i> (Fabricius, 1793)	Sampled	Valid	
<i>Graphium (Arisbe) levassori</i> (Oberthür, 1890)	Sampled	Valid	
<i>Graphium (Arisbe) liponesco</i> (Suffert, 1904)	Unsampled	Valid	
<i>Graphium (Arisbe) morania</i> (Angas, 1849)	Unsampled	Valid	
<i>Graphium (Arisbe) olbrechtsi</i> Berger, 1950	Unsampled	Unconfirmed	Might be a subspecies of <i>G. schubotzi</i> . Insufficient data
<i>Graphium (Arisbe) philonoe</i> (Ward, 1873)	Sampled	Valid	
<i>Graphium (Arisbe) poggianus</i> (Honrath, 1884)	Unsampled	Valid	
<i>Graphium (Arisbe) policenes</i> (Cramer, 1775)	Sampled	Valid	
<i>Graphium (Arisbe) policenoides</i> (Holland, 1892)	partial Mito only	Valid	
<i>Graphium (Arisbe) polistratus</i> (Grose-Smith, 1889)	Sampled	Valid	

<i>Graphium (Arisbe) porthaon</i> (Hewitson, [1865])	Sampled	Valid
<i>Graphium (Arisbe) ridleyanus</i> (White, 1843)	Sampled	Valid
<i>Graphium (Arisbe) schaffgotschi</i> (Niepelt, 1927)	Sampled	Valid
<i>Graphium (Arisbe) schubotzi</i> (Schultze, 1913)	Sampled	Valid
<i>Graphium (Arisbe) simoni</i> (Aurivillius, [1899])	Sampled	Valid
<i>Graphium (Arisbe) taboranus</i> (Oberthür, 1886)	Sampled	Valid
<i>Graphium (Arisbe) tynderaeus</i> (Fabricius, 1793)	Sampled	Valid
<i>Graphium (Arisbe) ucalegon</i> (Hewitson, [1865])	Sampled	Valid

Subgenus *Graphium* Scopoli, 1777

<i>Graphium (Graphium) agamemnon</i> (Linnaeus, 1758)	Sampled	Valid
<i>Graphium (Graphium) anthedon</i> (C. Felder & R. Felder, 1864)	Sampled	Valid
<i>Graphium (Graphium) arycles</i> (Boisduval, 1836)	Sampled	Valid
<i>Graphium (Graphium) bathycles</i> (Zinken, 1831)	Sampled	Valid
<i>Graphium (Graphium) browni</i> (Godman & Salvin, 1879)	Sampled	Valid
<i>Graphium (Graphium) chironides</i> (Honrath, 1884)	Sampled	Valid
<i>Graphium (Graphium) cloanthus</i> (Westwood, [1841])	Sampled	Valid
<i>Graphium (Graphium) codrus</i> (Cramer, 1777)	Sampled	Valid
<i>Graphium (Graphium) doson</i> (C. Felder & R. Felder, 1864)	Sampled	Valid
<i>Graphium (Graphium) empedovana</i> (Corbet, 1941)	Sampled	Valid
<i>Graphium (Graphium) eurypylus</i> (Linnaeus, 1758)	Sampled	Valid
<i>Graphium (Graphium) evemon</i> (Boisduval, 1836)	Sampled	Valid
<i>Graphium (Graphium) gelon</i> (Boisduval, 1859)	Sampled	Valid
<i>Graphium (Graphium) hicetaon</i> (Mathew, 1886)	Sampled	Valid
<i>Graphium (Graphium) kosii</i> Müller & Tennent, 1999	Sampled	Valid

G. a. isander and *G. a. choredon* were considered subspecies in this study, because of the subspecies status and paraphyly of *G. a. crudus* in Cotton et al., 2022

<i>Graphium (Graphium) leechi</i> (Rothschild, 1895)	Sampled	Valid	
<i>Graphium (Graphium) macfarlanei</i> (Butler, 1877)	Sampled	Valid	
<i>Graphium (Graphium) macleayanus</i> (Leach, 1814)	Sampled	Valid	
<i>Graphium (Graphium) meeki</i> (Rothschild & Jordan, 1901)	Sampled	Valid	
<i>Graphium (Graphium) mendana</i> (Godman & Salvin, 1888)	Sampled	Valid	
<i>Graphium (Graphium) meyeri</i> (Hopffer, 1874)	Sampled	Valid	
<i>Graphium (Graphium) milon</i> (C. Felder & R. Felder, 1865)	Sampled	Valid	
<i>Graphium (Graphium) monticolus</i> (Fruhstorfer, 1896)	Sampled	Valid	
<i>Graphium (Graphium) phidias</i> (Oberthür, 1896)	Sampled	Valid	
<i>Graphium (Graphium) procles</i> (Grose-Smith, 1887)	Sampled	Valid	
<i>Graphium (Graphium) sandawanum</i> Yamamoto, 1977	Sampled	Valid	
<i>Graphium (Graphium) sarpedon</i> (Linnaeus, 1758)	Sampled	Valid	
<i>Graphium (Graphium) septentrionalis</i> Page & Treadaway, 2013	Sampled	Valid	
<i>Graphium (Graphium) stresemanni</i> (Rothschild, 1915)	Sampled	Valid	
<i>Graphium (Graphium) sumatrana</i> (Hagen, 1894)	Sampled	Valid	
<i>Graphium (Graphium) teredon</i> (C. Felder & R. Felder, 1864)	Sampled	Valid	
<i>Graphium (Graphium) wallacei</i> (Hewitson, 1858)	Sampled	Valid	
<i>Graphium (Graphium) wayabulaensis</i> Hanafusa, 1998	Unsampled	Unconfirmed	= <i>batjanensis</i> Okano, 1984 <i>nomen nudum</i> . Generally considered as a valid species close to <i>G. stresemanni</i> .
<i>Graphium (Graphium) weiskei</i> (Ribbe, 1900)	Sampled	Valid	
Subgenus <i>Pathysa</i> Reakirt, [1865]			
<i>Graphium (Pathysa) agetes</i> (Westwood, 1843)	Sampled	Valid	
<i>Graphium (Pathysa) androcles</i> (Boisduval, 1836)	Sampled	Valid	
<i>Graphium (Pathysa) antiphates</i> (Cramer, 1775)	Sampled	Valid	
<i>Graphium (Pathysa) aristeus</i> (Stoll, 1780)	Sampled	Valid	
<i>Graphium (Pathysa) decolor</i> (Staudinger, 1888)	Sampled	Valid	

<i>Graphium (Pathysa) delessertii</i> (Guérin-Méneville, 1839) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) deucalion</i> (Boisduval, 1836) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) dorcus</i> (de Haan, 1840)	Sampled	Valid	
<i>Graphium (Pathysa) ebertorum</i> Koçak, 1983 comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) encelades</i> (Boisduval, 1836) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) epaminondas</i> (Oberthür, 1879)	Sampled	Valid	
<i>Graphium (Pathysa) euphrates</i> (C. Felder & R. Felder, 1862)	Sampled	Valid	
<i>Graphium (Pathysa) euphratoides</i> (Eimer, 1889)	Unsampled	Unconfirmed	
<i>Graphium (Pathysa) felixi</i> (Joicey & Noakes, 1915) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) idaeoides</i> (Hewitson, 1855) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) macareus</i> (Godart, 1819) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) megarus</i> (Westwood, 1844) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) nomius</i> (Esper, 1799)	Sampled	Valid	
<i>Graphium (Pathysa) ornatus</i> (Rothschild, 1895)	Unsampled	Unconfirmed	
<i>Graphium (Pathysa) ramaceus</i> (Westwood, 1872) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) rhesus</i> (Boisduval, 1836)	Sampled	Valid	
<i>Graphium (Pathysa) stratiotes</i> (Grose-Smith, 1887)	Sampled	Valid	
<i>Graphium (Pathysa) stratocles</i> (C. Felder & R. Felder, 1861) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) thule</i> (Wallace, 1865) comb. rev.	Sampled	Valid	
<i>Graphium (Pathysa) xenocles</i> (Doubleday, 1842) comb. rev.	Sampled	Valid	
Subgenus Pazala Moore, 1888			
<i>Graphium (Pazala) alebion</i> (Gray, [1853])	Sampled	Valid	
<i>Graphium (Pazala) confucius</i> Hu, Duan & Cotton, 2018	Mito NCBI only	Unconfirmed	Subspecies of <i>G. mandarinus</i> in Huang (2023), reinstated as a species in Hu et al. (2023) on morphological and biological grounds.

<i>Graphium (Pazala) daiyuanae</i> Hu, Zhang & Cotton, 2018	COI-5P NCBI only	Unconfirmed	Subspecies of <i>G. mandarinus</i> in Huang (2023)
<i>Graphium (Pazala) eurous</i> (Leech, 1893)	Sampled	Valid	
<i>Graphium (Pazala) garhwalica</i> (Katayama, 1988)	Sampled	Valid	
<i>Graphium (Pazala) hoeneanus</i> Cotton & Hu, 2018	Sampled	Unconfirmed	Subspecies of <i>G. sichuanica</i> in Huang (2023). Unconfirmed status as <i>G. sichuanica</i> was not sampled in this study.
<i>Graphium (Pazala) mandarinus</i> (Oberthür, 1879)	Sampled	Valid	
<i>Graphium (Pazala) mullah</i> (Alphéraky, 1897)	Sampled	Valid	
<i>Graphium (Pazala) paphus</i> (de Nicéville, 1886)	Mito only	Valid	
<i>Graphium (Pazala) parus</i> (de Nicéville, 1900)	Sampled	Valid	
<i>Graphium (Pazala) sichuanica</i> (Koiwaya, 1993)	Unsampled	Valid	
<i>Graphium (Pazala) tamerlanus</i> (Oberthür, 1876)	Sampled	Valid	
<i>Graphium (Pazala) wenlingae</i> Hu, Cotton & Monastyrskii, 2019	COI-5P NCBI only	Unconfirmed	Subspecies of <i>G. mandarinus</i> in Huang (2023)

Genus <i>Iphiclides</i> Hübner, [1819]	Sampling	Taxonomic status	Comment
<i>Iphiclides feisthamelii</i> (Duponchel, 1832)	Sampled	Valid	
<i>Iphiclides podalirinus</i> (Oberthür, 1890)	Sampled	Valid	
<i>Iphiclides podalirius</i> (Linnaeus, 1758)	Sampled	Valid	

Genus <i>Lamproptera</i> Gray, 1832	Sampling	Taxonomic status	Comment
<i>Lamproptera curius</i> (Fabricius, 1787)	Sampled	Valid	
<i>Lamproptera meges</i> (Zinken, 1831)	Sampled	Valid	
<i>Lamproptera paracurius</i> Hu, Zhang & Cotton, 2014	Sampled	Valid	

Genus <i>Protographium</i> Munroe, 1961	Sampling	Taxonomic status	Comment
<i>Protographium leosthenes</i> (Doubleday, 1846)	Sampled	Valid	

Table 2: Summary of the five different phylogenomic analyses and their abbreviations. The asterisk corresponds to the analysis from which the matrix and the resulting topology were used in the concordance factors analysis.

	Mitogenome	Dataset 1	Dataset 2
Nucleotide	IQTREE_15_Mito	IQTREE_1402_NT*, ASTRAL_1402_NT	
Amino acid		IQTREE_1402_AA	IQTREE_4525_AA

Table 3 Assembly statistics for the five *de novo* reference genomes of Leptocircini. LR = long reads, SR = short reads. For BUSCO scores, abbreviations stand for S: Simple, D: Duplicated, F: Fragmented, M: Missing.

	<i>Iphiclides podalirius</i>	<i>Graphium</i>			
	FC536	<i>G. agamemnon</i> FC1381	<i>G. antheus</i> FC1382	<i>G. antiphates</i> FC1341	<i>G. doson</i> FC873
Raw data sequenced (Gb) (LR + SR)	40.0 + 20.0	31.1 + 103.1	30.9 + 103.8	101.9 + 105.3	20.6 + 71.1
Final mean coverage (LR + SR)	66x + 96x	19x + 110x	12x + 68x	32x + 68x	14x + 105x
Assembly size (bp)	468,946,765	960,973,235	1,685,715,539	2,052,007,334	989,610,395
Number of contigs	2,755	8,469	22,326	28,705	36,745
N50 (bp)	1,107,841	236,847	149,287	173,984	70,611
Max length (bp)	13,306,297	2,403,220	1,528,824	9,291,578	1,128,770
Nucleotide assembly BUSCO score (%)	S:97.0; D:1.8; F:0.3; M:0.9	S:96.5; D:1.9; F:0.8; M:0.8	S:85.1; D:13.1; F:0.9; M:0.9	S:85.8; D:12.3; F:0.9; M:1.0	S:93.2; D:4.1; F:1.5; M:1.2

Table 4. Summary of Aphid results for the four series of triplets within *Graphium (Paranticopsis)* and *Graphium (Pathysa)*. Each value is the mean of five replicates for each series of triplet. Values indicated in the ‘Posterior imbalance GFc triplet’ column correspond to the percentage of the predominant discordant topology (displayed in parenthesis) over the other one. ILS = incomplete lineage sorting, GF = gene flow. ILS_c and GF_c are for discordant topologies. Par = *Paranticopsis*, Pat = *Pathysa*.

Tested triplet	Number of analyzed genes	Events (%)					Posterior imbalance GFc triplet (%)
		none	ILS	GF	ILS _c	GF _c	
1 - A=Pat3; B=Par1; C=Par2	1034	23.3	3.4	12.6	14.1	46.7	((BC)A): 56.9
2 - A=Par1; B=Par2; C=Pat3	1038	22.5	4.5	6.4	13.7	52.9	((AC)B): 63.4
3 - A=Par2; B=Pat3; C=Pat2	1014	29.0	5.9	15.1	16.5	33.4	((AC)B): 55.8
4 - A=Par1; B=Pat3; C=Pat2	1023	31.1	5.9	20.5	16.7	25.7	((AC)B): 58.4