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A comprehensive phylogeny and revised taxonomy illuminate the origin and diversification of the global radiation of *Papilio* (Lepidoptera: Papilionidae)

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2

3 **Title**

4 **A comprehensive phylogeny and revised taxonomy illuminate the origin and**
5 **diversification of the global radiation of *Papilio* (Lepidoptera: Papilionidae)**

6

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36 **Running head:** *Global diversification of Papilio butterflies*

37 **Abstract**

38 The swallowtail genus *Papilio* (Lepidoptera: Papilionidae) is species rich, distributed
39 worldwide, and has broad morphological habits and ecological niches. Because of its elevated
40 species richness, it has been historically difficult to reconstruct a densely sampled phylogeny
41 for this clade. Here we provide a taxonomic working list for the genus, resulting in 235 *Papilio*
42 species, and assemble a molecular dataset of seven gene fragments representing ca. 80% of the
43 currently described diversity. Phylogenetic analyses reconstructed a robust tree with highly
44 supported relationships within subgenera, although a few nodes in the early history of the Old
45 World *Papilio* remain unresolved. Contrasting with previous results, we found that *Papilio*
46 *alexanor* is sister to all Old World *Papilio* and that the subgenus *Eleppone* is no longer
47 monotypic. The latter includes the recently described Fijian *Papilio natewa* with the Australian
48 *Papilio anactus* and is sister to subgenus *Araminta* (formerly included in subgenus *Menelaides*)
49 occurring in Southeast Asia. Our phylogeny also includes rarely studied (*P. antimachus*, *P.*
50 *benguetana*) or endangered species (*P. buddha*, *P. chikae*). Taxonomic changes resulting from
51 this study are elucidated. Molecular dating and biogeographic analyses indicate that *Papilio*
52 originated ca. 30 million years ago (Oligocene), in a northern region centered on Beringia. A
53 rapid early Miocene radiation in the Paleotropics is revealed within Old World *Papilio*,
54 potentially explaining their low early branch support. Most subgenera originated in the early to
55 middle Miocene followed by synchronous southward biogeographic dispersals and repeated
56 local extirpations in northern latitudes. This study provides a comprehensive phylogenetic
57 framework for *Papilio* with clarification of subgeneric systematics and species taxonomic
58 changes enumerated, which will facilitate further studies to address questions on their ecology
59 and evolutionary biology using this model clade.

60

61 *Keywords:*

62 Butterflies, Historical biogeography, Macroevolution, Paleotropics, Systematics, Taxonomy

63

64 1. Introduction

65 Insects are indisputably the most diverse terrestrial eukaryotic clade, with over a million insect
66 species described and many more awaiting discovery or formal description (Stork, 2018). This
67 staggering species diversity is unevenly distributed across the insect tree of life, with many
68 clades comprising substantially more species than their sister clades (Grimaldi and Engel, 2005;
69 Engel, 2015). For instance, within ants (Formicidae), some genera such as *Camponotus* and
70 *Pheidole* have over 1,500 and 1,100 species, respectively (Hölldobler and Wilson, 1990), while
71 their corresponding sister clades have less than 700 and 200 species, respectively (Economo *et*
72 *al.*, 2018). Within flies (Diptera), the most well-known case is the genus *Drosophila*, which has
73 more than 1600 species (Brake and Bächli, 2013; O’Grady and DeSalle, 2018), which is sister
74 to a clade composed of seven genera including about 600 species (Wiegmann *et al.*, 2011;
75 O’Grady and DeSalle, 2018). Such genera are difficult to resolve phylogenetically and manage
76 taxonomically. The genus rank is widely used in molecular, morphological and paleontological
77 systematics. However, species-rich genera that are difficult to delimit can also be treated using
78 the subgenus rank, rendering their relationships less complicated while allowing flexibility to
79 taxonomic ranks that are less frequently employed (Winston, 1999; Teta, 2019).

80 In Lepidoptera, swallowtail butterflies (Papilionidae) of the genus *Papilio* Linnaeus,
81 1758 include more than 200 species and represent more than one third of all Papilionidae (**Fig.**
82 **1**), which has about 600 recognized species (Zakharov *et al.*, 2004a; Häuser *et al.*, 2005;
83 Condamine *et al.*, 2012; Nakae, 2021a). As one of the most well-known and broadly studied
84 groups of insects, *Papilio* swallowtails are recognized as model organisms in evolutionary
85 biology, ecology, genomics, and conservation biology (e.g. Collins and Morris, 1985; Scriber
86 *et al.*, 1995; Kunte, 2009; Kunte *et al.*, 2014; Dupuis and Sperling, 2015). Yet the phylogeny
87 of *Papilio* is far from being resolved despite numerous studies (Ae, 1979; Hancock, 1983;
88 Igarashi, 1984; Miller, 1987; Tyler *et al.*, 1994; Scriber *et al.*, 1995; Aubert *et al.*, 1999;
89 Caterino and Sperling, 1999; Reed and Sperling, 1999; Yagi *et al.*, 1999; Caterino *et al.*, 2001;
90 Zakharov *et al.*, 2004a; Condamine *et al.*, 2013a; Lewis *et al.*, 2015; Wu *et al.*, 2015; Owens *et*
91 *al.*, 2017, 2020). Ecological and evolutionary hypotheses on their diversification rely on a
92 comprehensive and strongly supported phylogeny as well as accurate age estimates for
93 significant phylogenetic events like host-plant shifts or mimicry evolution.

94 The first classifications of *Papilio* species relied on morphological characters
95 (summarized in Zakharov *et al.*, 2004a: table 1). Munroe (1961) divided *Papilio* into five
96 sections but did not designate them as subgenera because they lacked a simple diagnosis with
97 adult characters. Using an explicitly cladistic estimation of relationships within *Papilio*,

98 Hancock (1983) recognized six genera (*Chilasa*, *Eleppone*, *Heraclides*, *Papilio*, *Princeps*, and
99 *Pterourus*) based on phylogenetic evidence and inferred evolutionary antiquity, but this
100 phylogeny also suffered from lack of character justification. Another classification was
101 proposed by Igarashi (1984) based on the morphology of immature stages, but this work did
102 not represent all of Hancock's genera. Igarashi (1984) nonetheless recognized seven genera
103 (*Achillides*, *Agehana*, *Chilasa*, *Euchenor*, *Menelaides*, *Papilio*, and *Pterourus*), with numerous
104 discrepancies between his treatment and that of Hancock (1983). Hancock's classification was
105 criticized by Miller (1987), who did not consider elevation of *Papilio* subdivisions to the genus
106 level to be justified. However, one group within *Papilio* was elevated in a widely available
107 checklist of swallowtail butterflies (Häuser *et al.*, 2005), where *Chilasa* was treated as a distinct
108 genus. It has been challenging to apply the rules of the PhyloCode in designating subgroups
109 within *Papilio* to generic status as it has proven difficult to find morphological synapomorphies
110 as required by the PhyloCode (Cantino and de Queiroz, 2020). The sole use of genetic data to
111 delimit taxa has not been adequately addressed by the PhyloCode.

112 Due to the limitations of traditional morphological approaches and with the
113 development of new molecular systematic approaches, the classification of *Papilio* has received
114 significant attention in the last three decades. Relationships among species within the *P.*
115 *machaon* and *P. glaucus-troilus* species groups were studied based on allozyme variation
116 (Sperling, 1987; Hagen and Scriber, 1991). Restriction fragment length polymorphism of
117 mitochondrial DNA was used to compare taxa within the same species groups in later studies
118 (Sperling, 1991, 1993a, 1993b; Sperling and Harrison, 1994, Tyler *et al.*, 1994). Phylogenetic
119 relationships within *Papilio* have also been analyzed using DNA sequences of a variety of
120 genes, but these studies have been confined to single species groups or local geographic areas
121 (e.g. Vane-Wright *et al.*, 1999; Yagi *et al.*, 1999; Zakharov *et al.*, 2004b; Condamine *et al.*,
122 2013; Lewis *et al.*, 2015; Owens *et al.*, 2017, 2020; Dupuis and Sperling, 2020; Joshi and Kunte,
123 2022) or have included limited sampling across *Papilio* subdivisions (e.g. Aubert *et al.*, 1999;
124 Caterino and Sperling, 1999; Reed and Sperling, 1999; Zakharov *et al.*, 2004a). Although the
125 two latest molecular phylogenetic studies of Papilionidae (Condamine *et al.*, 2012; Allio *et al.*,
126 2021) substantially increased the fraction of sampled species, they did not provide a sufficient
127 resolution to assess the fine-scale taxonomic delimitation within the genus. Yet, a number of
128 systematic enigmas remain in *Papilio*, starting with the number of valid species to consider in
129 the genus.

130 Here we establish a list of valid *Papilio* species based on previous molecular studies
131 and build a reliable and comprehensive time-calibrated species-level phylogeny for the genus

132 *Papilio* using seven gene fragments for ca. 80% of the total species diversity. Our study aims
133 at establishing a reference phylogenetic framework to evaluate both subgeneric monophyly and
134 species relationships within *Papilio*, for the enigmatic and long-debated placement of several
135 groups and species. The phylogeny includes species that are key for testing biogeographic
136 hypotheses (e.g. *P. anactus*, *P. benguetana*), evolution of mimicry (e.g. *Chilasa*, *P. nobilis*),
137 and host-plant associations (e.g. *P. alexanor*), as well as species that are rare and insufficiently
138 studied (e.g. *P. antimachus*, *P. himeros*), endangered (*P. buddha*, *P. chikae*) or recently
139 described (e.g. the Fijian *P. natewa*). The recent discovery of *P. natewa* (Tennent *et al.*, 2018)
140 may clarify the systematic position of *P. anactus*, presently placed in a monotypic subgenus
141 (*Eleppone*) but with an unstable phylogenetic position (Hancock, 1979; Zakharov *et al.*, 2004a;
142 Condamine *et al.*, 2012). Indeed, external morphology and genitalia of *P. natewa* suggest a
143 phylogenetic affinity with *P. anactus* (Tennent *et al.*, 2018), but this remains to be tested.
144 Without knowledge of its larva, the enigmatic African giant swallowtail, *P. antimachus*, has
145 often been placed in species groups of two distinct *Papilio* subgenera (*Druryia* or *Princeps*),
146 and the subgenus *Druryia* has never been studied with a molecular approach. The position of
147 the *nobilis* species-group also remains poorly resolved, wavering between the iconic *phorcas*
148 and *hesperus* species-groups (Munroe, 1961, and Hancock, 1983, respectively). Yet, its
149 placement has important implications for the understanding of mimicry evolution in the
150 *phorcas* group (Vane-Wright *et al.*, 1999) and evolution of iridescent wings (common origin or
151 convergence with the subgenus *Achillides*). Including the giant blue swallowtail, *P. zalmoxis*,
152 in the phylogeny could help solve this puzzle. Moreover, the monophyly and rank of the
153 danaine- and moth-mimicking *Chilasa* are uncertain. Munroe (1961) split its members among
154 two *Papilio* subunits, but Hancock (1983) placed them together in a single genus, considered
155 to be the sister taxon of *Eleppone*. Finally, we also revisited the placement of *P. alexanor*. The
156 relationships of this odd European Apiaceae feeder have been examined several times (Aubert
157 *et al.*, 1999; Caterino and Sperling, 1999; Reed and Sperling, 1999; Zakharov *et al.*, 2004a),
158 nearly reaching a consensus that *P. alexanor* is sister to a clade comprising *Pterourus* and
159 *Chilasa* (Zakharov *et al.*, 2004a; Condamine *et al.*, 2012). However, no strong resolution has
160 been obtained and this position has been questioned with phylogenomic analyses (Allio *et al.*,
161 2020), albeit with less-than-ideal sampling density. We not only resolve these systematic
162 conflicts and uncertainties, but also provide a phylogenetic framework to infer an evolutionary
163 timescale for *Papilio*, estimate historical biogeography, and investigate heterogeneity of
164 diversification dynamics.

165

166 2. Materials and methods

167 2.1. Taxon sampling and molecular data

168 We first established a taxonomic working list of *Papilio* species (**Table 1**). This species list
169 combines several previous studies (Zakharov *et al.*, 2004a, 2004b; Condamine *et al.*, 2012,
170 2013a, 2013b; Shiraiwa *et al.*, 2014; Lewis *et al.*, 2015; Wu *et al.*, 2015; Owens *et al.*, 2017,
171 2020; Allio *et al.*, 2021; Joshi and Kunte, 2022). Like all other working lists (Garnett *et al.*,
172 2020), we acknowledge that this species list remains provisional and is likely to evolve through
173 time (i.e. species are hypotheses, Pante *et al.*, 2015). Indeed, *Papilio* butterflies will inevitably
174 continue to receive attention as a model clade, and we expect many of the species' boundaries
175 to be tested with new genomic data and evolutionary models in further studies, which are very
176 likely to eventually modify the taxonomic list (e.g. Kunte *et al.*, 2011; Dupuis and Sperling,
177 2022). From the 235 species that are currently recognized in the new taxonomic list presented
178 here for the genus *Papilio*, we sampled 184 species representing 78.3% of the total diversity
179 (**Table 1**). However, the total number of species will evolve with further systematic studies,
180 especially of the African clades that are currently poorly represented in our analysis (**Fig. 2**).
181 We added 18 outgroup species representing several swallowtail genera to root the *Papilio* tree
182 and provide deeper relationships for secondary calibration of nodes based on previous dated
183 studies (Condamine *et al.*, 2012; Allio *et al.*, 2021). The outgroups included: (1) two species of
184 the genus *Meandrusa* (*M. payeni* and *M. sciron*) to represent the sister genus of *Papilio* and
185 define the crown of tribe Papilionini, (2) five species of the tribe Troidini (*Battus philenor*,
186 *Ornithoptera priamus*, *Parides photinus*, *Pharmacophagus antenor* and *Troides helena*), which
187 is sister to Papilionini, (3) two species of the tribe Leptocircini (*Graphium sarpedon* and
188 *Lamproptera meges*), which is sister to all other Papilioninae, (4) two species of the tribe
189 Parnassiini (*Hypermnestra helios* and *Parnassius apollo*), (5) four species of the tribe
190 Zerynthiini (*Allancastria louristana*, *Bhutanitis mansfieldi*, *Sericinus montela* and *Zerynthia*
191 *polyxena*), (6) two species of the tribe Luehdorfiini (*Archon apollinaris* and *Luehdorfia*
192 *puziloi*), and (7) the single species of the subfamily Baroniinae, *Baronia brevicornis*, which is
193 the sister lineage to all Papilionidae and was used as root of the phylogenetic tree (Condamine
194 *et al.*, 2012; Allio *et al.*, 2020). Overall, the molecular dataset comprised 202 species (184
195 ingroups and 18 outgroups).

196 We assembled a supermatrix dataset with data extracted from Sanger sequencing and
197 genome sequencing available on GenBank as of September 2021. The molecular data mainly
198 came from previous studies (e.g. Zakharov *et al.*, 2004a, 2004b; Condamine *et al.*, 2012, 2013a,
199 2013b; Lewis *et al.*, 2015; Wu *et al.*, 2015; Owens *et al.*, 2017, 2020; Allio *et al.*, 2021; Joshi

200 and Kunte, 2022). We used five mitochondrial gene fragments (*COI*, *COII*, *ND1*, *ND5* and
201 *rRNA 16S*) and two nuclear gene fragments (*EF-1a* and *Wg*), chosen based on their availability
202 among *Papilio* species. We aligned the DNA sequences for the rRNA 16S using MAFFT 7.110
203 (Kato and Standley, 2013) with the E-INS-i algorithm, while we aligned the coding genes
204 using MACSE 2.00 (Ranwez *et al.*, 2011) with the *alignSequences* subprogram and default
205 options. All the resulting alignments were checked for codon stops and eventually refined by
206 eye with Mesquite 3.7 (Maddison and Maddison, 2021). All gene alignments were concatenated
207 into a nucleotide supermatrix, which is available in FigShare (Data 1:
208 <https://figshare.com/s/a32288db7e6429714a62>).

209

210 **2.2. Inferring phylogenetic relationships**

211 We performed both maximum likelihood (ML) and Bayesian Inference (BI) to reconstruct
212 phylogenetic relationships. Although phylogenomic approaches have used amino acids on
213 Papilionidae at the genus level (Allio *et al.*, 2020), all our analyses relied on nucleotides for the
214 tree inference of *Papilio* because the molecular dataset is limited to seven gene fragments and
215 converting it to amino acids will result in a smaller dataset with limited phylogenetic
216 information given the species diversity of the focal clade. ML inference was implemented with
217 IQ-TREE 2.1.2 (Minh *et al.*, 2020) using ModelFinder to select the best-fit partition scheme
218 and the best-fitting substitution model for each partition (*-m MFP+MERGE* option, Chernomor
219 *et al.*, 2016; Kalyaanamoorthy *et al.*, 2017). For IQ-TREE analyses, we estimated the most
220 likely tree with 100 separate ML searches, which after initial model optimization on a
221 parsimony tree used 100 random tree topologies as starting trees for each search. As
222 recommended, we optimized ML searches to avoid local optima by (1) increasing the number
223 of unsuccessful iterations before stopping tree optimization to 500 (*-nstop 500* option), and (2)
224 decreasing the perturbation strength for randomized NNI to 0.2 (*-pers 0.2* option). Statistical
225 reliability of the ML tree was evaluated with 100 non-parametric bootstraps under the optimal
226 partitioned model to obtain ML bootstrap percentages (BP_{PART}). To compare branch supports,
227 a second ML analysis with IQ-TREE was carried out under the same conditions but with 2,000
228 ultrafast bootstraps (UFBS_{PART}; Hoang *et al.*, 2018). BS values and UFBS values were
229 considered strong when higher than 70% and 95%, respectively. We also assessed branch
230 support using Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT; Guindon *et*
231 *al.*, 2010), with SH-aLRT values above 80% considered as strong support for a clade.

232 BI analyses were performed using MrBayes 3.2.7a (Ronquist *et al.*, 2012). Because
233 ModelFinder includes more substitution models than BEAST or MrBayes, the most likely

234 partitioning scheme and substitution models can be altered, the molecular dataset was analyzed
235 with PartitionFinder 2.1.1 (Lanfear *et al.*, 2017) to estimate the best partition scheme with an
236 initial subset of 19 possible partitions (all three codon positions for coding sequences and non-
237 coding genes treated separately). Partitions and corresponding optimal substitution models
238 were searched using the *greedy* algorithm, the *mrBayes* set of models, and the Bayesian
239 Information Criterion (BIC) to compare the fit of different models. We used reversible-jump
240 Markov chain Monte Carlo (rjMCMC) to sample the entire space of possible models instead of
241 using the *a priori* substitution models recovered by PartitionFinder (Huelsenbeck *et al.*, 2004).
242 MrBayes analyses were performed with two separate runs, a random starting tree, and eight
243 rjMCMC (one cold and seven incrementally heated, *temp=0.1*) running for 30 million
244 generations with tree sampling occurring every 3,000 generations (resulting in 10,000 trees) to
245 calculate the clade posterior probabilities (PP_{PART}). We also specified (1) a uniform prior
246 probability of phylogenies (i.e. all possible trees are considered *a priori* equally probable), and
247 (2) a uniform prior probability distribution on branch lengths. Convergence of the Bayesian
248 runs was ensured by checking the average deviation of split frequencies (ADSF), the potential
249 scale reduction factor (PSRF) values, the effective sample size (ESS) of all parameters, and by
250 plotting the log-likelihood of the samples against the number of generations in Tracer 1.7.1
251 (Rambaut *et al.*, 2018). The runs had to have values of ADSF approaching zero, PSRF close to
252 1.0 and ESS above 200 to assume convergence. All trees that predated the time needed to reach
253 a log-likelihood plateau were discarded as burn-in, and the remaining samples were used to
254 generate a 50% majority rule consensus tree (option *halfcompat*). Branch support was estimated
255 and PP_{PART} ≥ 0.95 was considered to indicate strong support for a given clade (Douady *et al.*,
256 2003). All MrBayes analyses were performed on the computer cluster CIPRES Science
257 Gateway (Miller *et al.*, 2015), using BEAGLE (Ayres *et al.*, 2012) with default parameters.

258 BI was also conducted using PhyloBayes MPI 1.8 (Lartillot *et al.*, 2013) under the CAT-
259 GTR- Γ_4 mixture model (Lartillot and Philippe, 2004), which has proven to perform well on
260 large molecular datasets (e.g. Allio *et al.*, 2020). The analyses were conducted on the nucleotide
261 dataset. For each analysis, two independent MCMC starting from a random tree were run at
262 least 10,000 cycles, with trees and associated model parameters being sampled every 10 cycles.
263 The initial 2,000 trees sampled in each MCMC run were discarded as burn-in after checking
264 for convergence in both likelihood and model parameters (*tracecomp* subprogram), and clade
265 posterior probability (*bpcomp* subprogram). We checked the mean (*meandiff*) discrepancy
266 observed across all bipartitions, considering that *meandiff* < 0.01 indicates convergence. The

267 50% majority-rule Bayesian consensus tree and the associated posterior probabilities (PP_{CAT})
268 were then computed from the remaining trees using *bpcomp*.

269

270 **2.3. Testing topology hypotheses**

271 We conducted tests of topology hypotheses with MrBayes when phylogenetic analyses did not
272 recover the same relationships as those from previous studies (see in Zakharov *et al.*, 2004a;
273 Condamine *et al.*, 2012; Lewis *et al.*, 2015). To do so, we conducted topology hypotheses by
274 enforcing the clade (species, genera) to be sister to another clade or to be monophyletic in a
275 case of non-monophyly. Bayesian inferences were run with the exact same priors and
276 parameters (see above) but including constraints and a model to compute the marginal
277 likelihood estimate (MLE) to obtain the likelihood score of each constrained topology, which
278 was then compared to the score of an unconstrained topology.

279 We used stepping-stone sampling (Xie *et al.*, 2011) to estimate the marginal likelihood
280 of the specified topology and the unconstrained topology. Stepping-stone sampling (SS) is
281 considerably more accurate than the harmonic mean of the likelihoods from a standard MCMC
282 run, and has been shown to be more efficient than the thermodynamic integration (Baele *et al.*,
283 2013). SS estimates the model likelihood by sampling a series of distributions that represent
284 different mixtures of posterior distribution and prior distribution (Xie *et al.*, 2011). To obtain
285 an adequate sample from most of the steps in the algorithm, we used 100 steps with 300,000
286 generations each, for a total of 30 million generations. To monitor convergence during each
287 step, we set the diagnostics frequency to once every 1,000 generations. The MLE obtained with
288 the SS in MrBayes were used to calculate the Bayes factors (BF). The logarithm of the BF is
289 the difference in the logarithms of the marginal model likelihoods. The BF is calculated by
290 subtracting the MLE of the constrained topology and the MLE of the unconstrained topology.
291 We considered BF values >10 favoring one model over another as very significant (Nylander
292 *et al.*, 2004; Brown and Lemmon, 2007).

293

294 **2.4. Estimation of divergence times**

295 We first tested the hypothesis of a molecular clock with PATHd8 (Britton *et al.*, 2007). Since
296 a strict molecular clock was not supported for 72.7% of the nodes in this dataset at $P < 0.05$, a
297 Bayesian relaxed-clock approach considering rate variations across lineages was employed to
298 estimate divergence times (Drummond *et al.*, 2006). Bayesian MCMC analyses implemented
299 in BEAST 1.10.4 (Suchard *et al.*, 2018) were performed to approximate the posterior
300 distribution of rates and divergence times and infer their credibility intervals.

301 Molecular dating analyses can be sensitive to several parameters or priors (Alfaro and
302 Holder, 2006; Drummond and Bouckaert, 2015). For instance the prior governing the branching
303 process (Condamine *et al.*, 2015) or the number of molecular clocks (Angelis *et al.*, 2018;
304 Condamine *et al.*, 2018a) may impact estimates of divergence times. Accordingly, we
305 conducted analyses with the following non-default settings and priors: (1) the molecular dataset
306 was partitioned according to the best-fit scheme recovered by PartitionFinder, (2) substitution
307 models were set based on ModelFinder estimation in IQ-TREE (see above), (3) a birth-death
308 tree prior was set for the branching process, and (4) one clock model was set for the
309 mitochondrial partitions, and one clock for the nuclear partitions. Finally, we let the tree
310 topology be estimated by BEAST (classic operator mix) but enforced the monophyly of
311 subfamilies, tribes, and genus *Papilio* following the results of phylogenomic analyses (Allio *et*
312 *al.*, 2020).

313 Bayesian relaxed clocks were set up with an uncorrelated lognormal distribution clock
314 model, with the mean set to a uniform prior between 0 and 0.5 (starting value=0.1), and an
315 exponential prior ($\lambda=0.333$) for the standard deviation. The birth-death process
316 (Gernhard, 2008) is a more realistic branching tree prior than a Yule model for species-level
317 divergence times analysis. The birth-death process was set using the following uniform priors:
318 the mean growth rate ranged between 0 and 1 with a starting value at 0.1 births per lineage per
319 million years, and the relative death rate ranged between 0 and 1 deaths per lineage per million
320 years (starting value=0.5). We performed four independent BEAST runs (different seeds) for
321 50 million generations of MCMC each and with a sampling frequency of 5,000 generations.
322 We discarded the first 10% of generations as burn-in and checked for convergence using Tracer
323 ($ESS>200$). We combined the four runs using LogCombiner. Using TreeAnnotator, we
324 computed the maximum clade credibility tree with median ages and the 95% credibility
325 intervals (CI) at each node. The xml files are available in FigShare (Data 2:
326 <https://figshare.com/s/a32288db7e6429714a62>).

327

328 **2.5. Fossil and secondary calibrations**

329 To explore the effect of fossil calibrations versus secondary calibrations on estimating
330 divergence times, we designed two calibration sets. All node calibrations were assigned a
331 uniform prior distribution with hard bounds (Yang and Rannala, 2006).

332 First, we used three unambiguous fossil calibrations assigned to Papilionidae, two of
333 which are Parnassiinae (de Jong, 2017). The first is †*Thaites ruminiana* (Scudder, 1875), a
334 compression fossil from limestone in the Niveau du gypse d'Aix Formation of France (Aix-en-

335 Provence, Bouches-du-Rhône) within the Chattian (23.03–28.1 Ma) of the late Oligocene (Sohn
336 *et al.*, 2012). †*Thaites* is sister to Parnassiini, and occasionally sister to Luehdorfiini +
337 Zerynthiini (Condamine *et al.*, 2018b). Thus we constrained the crown age of Parnassiinae with
338 a uniform distribution bounded by a minimum age of 23.03 Ma. The second is †*Doritites*
339 *bosniaskii* (Rebel, 1898), an exoskeleton and compression fossil from Italy (Tuscany) from the
340 Messinian (5.33–7.25 Ma, late Miocene; Sohn *et al.*, 2012). †*Doritites* is sister to *Archon*
341 (Luehdorfiini, Condamine *et al.*, 2018b), in agreement with Carpenter (1992). The crown of
342 Luehdorfiini was thus constrained for divergence time estimation using a uniform distribution
343 bounded with 5.33 Ma. Third is the genus †*Praepapilio* with two fossil species †*P. colorado*
344 and †*P. gracilis* (Durden and Rose, 1978) found in the Green River Formation (Colorado,
345 U.S.A.). The age of †*Praepapilio* was used to constrain the crown age of Papilionidae with a
346 uniform distribution bounded by a minimum age of 47.8 Ma since the Green River Formation
347 encompasses a 5 million-year period between ~48.5 and 53.5 Ma, which falls within the
348 Ypresian (47.8–56 Ma) in the early Eocene (Smith *et al.*, 2003; de Jong, 2007). These three
349 fossil calibrations have been used in previous studies (e.g. Condamine *et al.*, 2012, 2013a,
350 2018a, 2018b; Allio *et al.*, 2020). Uniform distributions of the fossil calibrations were bounded
351 with a maximum age of 150 Ma, a conservative age congruent with the major radiation of
352 angiosperms (Magallón *et al.*, 2015; Foster *et al.*, 2017; Li *et al.*, 2019).

353 Second, we relied on secondary calibrations with uniform priors applied to the nodes
354 where we set the fossil calibrations plus nodes that are in common between our phylogeny and
355 the phylogeny of Papilionidae. We retrieved the 95% CI from recent estimations of divergence
356 times of the family (Allio *et al.*, 2021) as follows: (1) the crown of Papilionidae (root of the
357 tree) between 47.8 and 70.9 Ma, (2) the crown of Parnassiinae between 29.9 and 58.9 Ma, (3)
358 the crown of Luehdorfiini between 13.9 and 35.3 Ma, (4) the crown of Papilioninae between
359 34.4 and 62.9 Ma, (5) the crown of Leptocircini between 26.6 and 49.9 Ma, (6) the crown of
360 Papilionini + Troidini between 30.8 and 56.1 Ma, (7) the crown of Troidini between 26.9 and
361 50.4 Ma, and (8) the crown of Papilionini between 27.5 and 50.9 Ma (Allio *et al.*, 2021).

362

363 **2.6. Inference of historical biogeography**

364 We estimated the ancestral ranges of origin and geographic range evolution for *Papilio* using
365 the ML approach of dispersal-extinction-cladogenesis (DEC, Ree and Smith, 2008) as
366 implemented in the DEC eXtended version (DECX, Beeravolu and Condamine, 2016; available
367 at: <https://github.com/champost/DECX>). To infer the biogeographic history of a clade, DEC
368 requires a time-calibrated tree, the current distribution of each species for a set of geographic

369 areas, and a time-stratified geographic model that is represented by connectivity and dispersal
370 scalar matrices for specified time intervals spanning the entire evolutionary history of the group.
371 DECX allows classical vicariance as a cladogenetic event by using temporally flexible
372 constraints on the connectivity between any two given areas following the movement of
373 landmasses and dispersal opportunity over time. DECX can analyze phylogenies on the order
374 of several thousand tips with numerous areas (Rolland and Condamine, 2019; Kawahara *et al.*,
375 2023). DECX does not incorporate the founder-event speciation (+J parameter) because of
376 concerns with statistical validity of model choice among DEC-derived models (Ree and
377 Sanmartín, 2018). Also, founder-event speciation often leads to inferences that are decoupled
378 from time, with null or extremely low extinction rates, an effect of the model favoring
379 cladogenetic events over anagenetic events (Ree and Sanmartín, 2018), which makes it
380 inadequate for reconstructing the history of ancient groups with widespread distributions.

381 The geographic distribution for all 235 *Papilio* species was categorized by coding the
382 presence or the absence of each species in the following areas: (1) West Palearctic, defined as
383 Europe west of the Urals and the part of Asia west of this north-south line, (2) East Palearctic,
384 defined as everywhere considered Palearctic east of the Urals, above 3,000 m in the Himalayas
385 and north of Sichuan in China, (3) West Nearctic, defined as North America west of the Rocky
386 Mountains, (4) East Nearctic, defined as North America east of the Rocky Mountains, (5)
387 Central America, defined as from the northern border of Mexico southwards to the border
388 between Panama and Colombia, also including the Caribbean islands except Trinidad and
389 Tobago, (6) South America, defined as all countries from Colombia to Argentina and including
390 Trinidad and Tobago, (7) Africa, defined as the whole of the African continent and Arabian
391 Peninsula but excluding the islands in the Indian Ocean, (8) Madagascar, defined as the island
392 of Madagascar and all other Indian Ocean islands in the vicinity, (9) India, defined as the area
393 below 3,000 m from NW Pakistan to the border with Myanmar, (10) Indonesia and Wallacea,
394 defined as Myanmar, SE Asia, southern China, western Indonesia to Lydekker's Line; including
395 the Lesser Sunda Islands but excluding Timor, Wetar and associated islands, which are
396 Australasian in origin, and (11) Australasia, defined as everywhere east of Lydekker's Line but
397 including Timor, Wetar and small nearby islands. Species which only marginally enter an area
398 were excluded. We used data available in the literature (e.g. Collins and Morris, 1985; Tyler *et*
399 *al.*, 1994; Scriber *et al.*, 1995). The geographic distribution of all species and the species
400 sampled in this study is presented in **Fig. 2**. The resulting matrix of species distribution for
401 *Papilio* is available in Table S1.

402 A time-stratified geographic model was built using connectivity matrices that consider
403 paleogeographic changes through time with time slices indicating the possibility or not for a
404 species to colonize a new area (Beeravolu and Condamine, 2016). Based on paleogeographic
405 reconstructions (e.g. Scotese, 2004; Blakey, 2008; Seton *et al.*, 2012), we created a connectivity
406 matrix to represent major changes in tectonic conditions that may have affected the distribution
407 of these butterflies. We specified constraints on area connectivity by coding 0 if any two areas
408 are not connected or 1 if they are connected at a given period. We did not add dispersal matrices
409 because setting the values for dispersal rates between regions through time is highly subjective,
410 and it has been shown that dispersal probability categories had minor effects on ancestral state
411 estimation (Chacon and Renner, 2014). Therefore, we assumed a dispersal scalar matrix with
412 equal dispersal rates between areas through time. Biogeographic ranges larger than four areas
413 in size were disallowed as valid biogeographic states if they were not subsets of the terminal
414 species ranges; widespread ranges comprising areas that have never been geographically
415 connected were also removed.

416 We estimated the most likely ancestral states at each node by performing a DEC analysis
417 under an ML procedure as implemented in DECX (Beeravolu and Condamine, 2016) using
418 both species distribution matrix and connectivity matrices. The files for reproducing the
419 analyses are available in FigShare (Data 3: <https://figshare.com/s/a32288db7e6429714a62>).

420

421 **2.7. Investigating heterogeneity of diversification rates**

422 To provide an assessment of diversification rates through time, we used the ML approach of
423 Morlon *et al.* (2011), tested and automated in Mazet *et al.* (2023) and implemented in the R-
424 package *RPANDA* 2.0 (Morlon *et al.*, 2016). This method aims at capturing heterogeneity of
425 diversification by allowing preselected subclades to follow different birth-death models from
426 the deeper pruned tree (the backbone). For both subclades and backbones (different backbones
427 are tested because of the different combination of shifts), speciation and/or extinction rates can
428 change exponentially through time: $\lambda(t) = \lambda_0 \times e^{\alpha t}$ with λ_0 denoting speciation at present, α the
429 trend of rate variation of speciation through time t . Extinction rate can exceed speciation,
430 meaning that diversification rates can be negative (Morlon *et al.*, 2011), which results in a
431 declining paleodiversity dynamic that can be expected for the backbone because of the higher
432 proportion of long branches after isolating recently-originated subclades.

433 Following Mazet *et al.* (2023), for the analysis of *Papilio*, we first computed the clades'
434 sampling fractions based on our revised taxonomy with the *get.sampling.fraction* function. We
435 specified the nine following subclades: the subgenera *Achillides*, *Chilasa*, *Druryia*, *Heraclides*,

436 *Menelaides*, *Nireopapilio*, *Papilio*, *Pterourus*, and the monophyletic group of Lauraceae
437 feeders regrouping *Chilasa* and *Pterourus* (Apiaceae and Rutaceae feeders are not
438 monophyletic). We then estimated the number of possible shifts to be tested in combination
439 with corresponding backbones using the *get.comb.shift* function. The selection of subclades
440 created 319 combinations of subclade(s)/backbone that were compared to the clade-
441 homogeneous birth-death model. We designed and fitted five diversification models to each
442 clade and backbone with the *shift.estimate* function that determines the best fitting model and
443 most likely combination of shifts. The five models are: (1) a Yule model, where speciation is
444 constant and extinction is null (BCST); (2) a constant birth-death model, where speciation and
445 extinction rates are constant (BCST_DCST); (3) a variable speciation rate model without
446 extinction (BVAR); (4) a variable speciation rate model with constant extinction
447 (BVAR_BCST); and (5) a rate-constant speciation and variable extinction rate model
448 (BCST_BVAR). Diversification rates are defined backward in time such as a positive
449 dependency parameter (α for speciation and β for extinction) reflects a slowdown of rates
450 towards the present. Finally, based on the most likely rate estimates and best combination of
451 shifts, we estimated the diversity dynamics of each clade and resulting backbone recovered in
452 the best shift combination using the *apply_prob_dtt* and *paleodiv* function. The files for
453 reproducing the analyses are available in FigShare (Data 4:
454 <https://figshare.com/s/a32288db7e6429714a62>).

455

456 **3. Results and Discussion**

457 **3.1. Global phylogeny of *Papilio***

458 Partitioned phylogenetic analyses with IQ-TREE and MrBayes provided almost identical
459 phylogenetic trees, differing in branch length estimates (**Fig. 3**; Figs S1, S2 for IQ-TREE). The
460 genus *Papilio* was always recovered as monophyletic with maximal (PP_{CAT}=1, PP_{PART}=1,
461 BP_{PART}=100, UFBS_{PART}=100) branch support (**Table 3**), which was expected since molecular
462 data have never found it non-monophyletic (e.g. Aubert *et al.*, 1999; Zakharov *et al.*, 2004a;
463 Condamine *et al.*, 2012; Lewis *et al.*, 2015; Owens *et al.*, 2017, 2020; Allio *et al.*, 2020). The
464 Bayesian inference with MrBayes converged well (ADSF=0.007293, average PSRF for
465 parameter values=1.000, and ESS \gg 200 for all parameters). Bayesian analyses reconstructed a
466 robust phylogeny with 69.4% of the nodes recovered with strong support within *Papilio* (nodes
467 with PP_{PART} \geq 0.95, **Fig. 3**). Robustness was slightly lower for ML analysis with non-parametric
468 bootstrap: 67.4% of branches in the tree were strongly supported (nodes with BP_{PART} \geq 70, Fig.
469 S1). In comparison, IQ-TREE analysis with UFBS_{PART} recovered the most robust phylogeny

470 with 82.5% of branches supported by $UFBS_{PART} \geq 95$ (Fig. S2). PhyloBayes analysis under the
471 mixture (CAT-GTR- Γ_4) model ran during 11,350 cycles and converged well
472 ($meandiff=0.00814$). The topology (Fig. S3) was very similar to traditional partitioned analyses
473 with IQ-TREE and MrBayes, except within the Old World *Papilio* (see below). Overall, branch
474 support in PhyloBayes was also like IQ-TREE and MrBayes with 66.7% of branches having
475 $PP_{CAT} \geq 0.95$ (see Fig. S4 for a comparison of branch support across all analyses).

476 All phylogenetic analyses reconstructed a backbone topology with three main clades
477 (Clades 1 to 3 on **Fig. 3, Table 3**). Subgenus *Heraclides* (Clade 1) was sister to all remaining
478 *Papilio*, which is composed of a clade mostly including the New World *Papilio* (Clade 2,
479 subgenera *Chilasa* and *Pterourus*) and another clade comprising the Old World *Papilio* (Clade
480 3, the remaining subgenera). Although this topology was consistent across methods, branch
481 support for the large clade of *Papilio* excluding the subgenus *Heraclides* was not robust
482 ($PP_{CAT}=0.75$, $PP_{PART}=0.98$, $BP_{PART}=55$, and $UFBS_{PART}=90$). Subgenus *Heraclides* was always
483 monophyletic with high branch support ($PP_{CAT}=1$, $PP_{PART}=0.96$, $BP_{PART}=75$, and
484 $UFBS_{PART}=100$). The species relationships within *Heraclides* largely correspond to previous
485 works (Lewis *et al.*, 2015; Owens *et al.*, 2017, 2020).

486 New World *Papilio sensu stricto* (i.e. subgenera *Heraclides* and *Pterourus*) were not
487 inferred as monophyletic in all analyses. We always recovered the American subgenus
488 *Pterourus* within a clade including Asian subgenera *Chilasa* and ‘*Agehana*’ (Clade 2 on **Fig.**
489 **3**) with strong branch support ($PP_{CAT}=0.99$, $PP_{PART}=1$, $BP_{PART}=91$, and $UFBS_{PART}=100$). In
490 addition, ‘*Agehana*’ was internal to subgenus *Pterourus* in all analyses (**Table 3**). This topology
491 agrees with some phylogenetic work (Wu *et al.*, 2015) but contrasts with others (Zakharov *et*
492 *al.*, 2004a; Condamine *et al.*, 2012; Lewis *et al.*, 2015), which proposed that *Heraclides* is sister
493 to *Pterourus* + *Chilasa* + *Alexanoria*. The substantial increase of taxon sampling may account
494 for the difference between topologies: we sampled 64 species belonging to these subgenera,
495 while Zakharov *et al.* (2004a) and Condamine *et al.* (2012) analyzed only 21 species (including
496 *P. alexanor*). Bayesian topology tests provided strong support ($BF > 6$) for the non-monophyly
497 of the New World *Papilio* clade (*sensu* Zakharov *et al.*, 2004a; Condamine *et al.*, 2012; Lewis
498 *et al.*, 2015), and decisive support ($BF > 10$) for the non-monophyly of *Pterourus sensu lato*
499 (**Table 2**). These new phylogenetic arrangements have important biogeographic implications
500 (see below).

501 *Papilio alexanor*, a mysterious Eurasian lineage that is notoriously difficult to place
502 within *Papilio* (Zakharov *et al.*, 2004a; Wu *et al.*, 2015), was sister to the Old World clade
503 including all remaining species, with moderate to high branch support ($PP_{CAT}=1$, $PP_{PART}=0.99$,

504 BP_{PART}=58, and UFBS_{PART}=85). The Bayesian topology test constraining *P. alexanor* to be
505 sister to the clade *Pterourus* + *Chilasa* + ‘*Agehana*’ (Zakharov *et al.*, 2004a; Condamine *et al.*,
506 2012) yielded a worse MLE than the unconstrained topology with strong support (BF>10,
507 **Table 2**). Our unconstrained topology agrees with a recent but sparsely sampled phylogenomic
508 study (Allio *et al.*, 2020), suggesting that the phylogenetic position of *P. alexanor* is reaching
509 a consensus.

510 The Old World *Papilio* clade (Clade 3 on **Fig. 3**) includes the highest species diversity
511 of the genus. After the divergence with *P. alexanor*, partitioned phylogenetic analyses
512 recovered a series of five main clades (Clades 3a to 3e on **Fig. 3**) sustained by short internal
513 branches leading to different subgenera with moderate to high branch support (**Table 3**). These
514 internal branches were the source of discrepancy between the Bayesian analyses (under both
515 the mixture model and the partitioned analyses) and ML analyses. The main discrepancy was
516 that Clades 3a and 3b were recovered as sisters in ML analyses and weakly supported
517 (BP_{PART}=23, and UFBS_{PART}=58; Figs S1-2) but not recovered in Bayesian analyses (**Fig. 3**, Fig.
518 S3). Despite a substantially increased taxon sampling compared to previous studies (37% of
519 total species diversity in Condamine *et al.*, 2012 *versus* 78% in this study), these results suggest
520 that the systematic backbone of *Papilio* is still not definitely resolved, which impedes a higher-
521 level systematic revision of the genus. We also acknowledge the limited size of the Sanger-
522 based dataset and phylogenomic studies may illuminate the early evolutionary history of
523 *Papilio* in future studies to provide a definitive resolution of subgeneric classification.

524 Clade 3a was always composed of the subgenus *Euchenor* (Joshi and Kunte, 2022)
525 including two New Guinean species (*Papilio euchenor* and *P. depilis*), subtended by a long
526 branch, which was systematically recovered as sister to a clade comprising species of subgenus
527 *Druryia* (including the *antimachus* and *dardanus* species-groups) with moderate to strong
528 branch support (Clade 3a on **Fig. 3**; PP_{CAT}=0.82, PP_{PART}=0.99, BP_{PART}=74, and UFBS_{PART}=99).
529 We still have poor knowledge on subgenus *Druryia* because existing phylogenies only included
530 a handful of species. Here we found the *nireus*, *oribazus*, and *zalmoxis* species groups in a
531 separate clade sister to *Papilio nobilis* with strong branch support (PP_{CAT}=1, PP_{PART}=1,
532 BP_{PART}=76, UFBS_{PART}=98). This clade has recently been ranked as the subgenus *Nireopapilio*
533 (Cotton and Nakae, 2020). A Bayesian topology test provided decisive support (BF>10) for
534 non-monophyly of subgenus *Druryia* (**Table 2**), therefore lending support to the validity of
535 subgenus *Nireopapilio*. However, it is important to remain cautious because future studies with
536 more comprehensive sampling could recover subgenus *Druryia* as monophyletic, notably
537 through the inclusion of the *zenobia* species-group not sampled in this or previous studies.

538 *Papilio natewa*, the latest described *Papilio* species (Tennent *et al.*, 2018), was always
539 sister to the monotypic subgenus *Eleppone*, with maximal branch support in all analyses (**Fig.**
540 **3, Table 3**). This indicates that *Papilio natewa* can be placed in the subgenus *Eleppone*, together
541 with *P. anactus* from eastern Australia. The subgenus *Eleppone* was always found to be sister
542 to a strongly supported clade of five Indonesian species, the *demolion* species group, which was
543 previously considered to belong to the subgenus *Menelaides* but now assigned to the subgenus
544 *Araminta*. Although often recovered, this sister relationship was not highly supported (Clade
545 3b on **Fig. 3**; PP_{PART}=0.72, BP_{PART}=50, and UFBS_{PART}=93).

546 The next clade (Clades 3c + 3d + 3e on **Fig. 3**) included species classified in six
547 subgenera and was generally strongly supported in all analyses (PP_{CAT}=0.99, PP_{PART}=1,
548 BP_{PART}=72, and UFBS_{PART}=99). The first to branch off this clade were subgenus *Sinoprinceps*
549 (*Papilio xuthus* and *P. benguetana*) and subgenus *Papilio* (*machaon* species-group) found to
550 be sisters (Clade 3c on **Fig. 3**) in all analyses with maximal branch support (except BP_{PART}=97).
551 These two subgenera were both recovered as monophyletic with maximal branch supports. The
552 remaining subgenera comprised *Nireopapilio* + *Achillides* + *Princeps* + *Menelaides* (Clade 3d
553 + Clade 3e on **Fig. 3**) and formed a strongly supported clade (PP_{CAT}=0.99, PP_{PART}=1,
554 BP_{PART}=60, and UFBS_{PART}=99). The species *Papilio nobilis* (usually ranked in subgenus
555 *Princeps*, *nobilis* group) was always found as sister to *Nireopapilio* (PP_{CAT}=1, PP_{PART}=1,
556 BP_{PART}=76, and UFBS_{PART}=98; Clade 3d on **Fig. 3**), and the latter contained the species of the
557 *nireus*, *oribazus* and *zalmoxis* groups. The subgenus *Achillides* was strongly supported as
558 monophyletic in all analyses (PP_{CAT}=1, PP_{PART}=1, BP_{PART}=85, and UFBS_{PART}=99), and was
559 often found as sister to the clade *Princeps* + *Menelaides* with moderate nodal support (Clade
560 3e on **Fig. 3**). Within *Achillides*, the species relationships largely agree with the study of
561 Condamine *et al.* (2013b), but we added two endangered species (*P. buddha* and *P. chikae*;
562 Collins and Morris, 1985). Endemic to the Western Ghats biodiversity hotspot of Southern
563 India, *P. buddha* was always recovered in the *palinurus* group (*P. daedalus* and *P. palinurus*)
564 from Southeast Asia with strong support (PP_{CAT}=1, PP_{PART}=1, BP_{PART}=100, and
565 UFBS_{PART}=100), but its sister relationship with *P. daedalus* was weakly supported (PP_{CAT}=0.8,
566 PP_{PART}=0.72, BP_{PART}=64, and UFBS_{PART}=62). Such a relationship is interesting to study in
567 terms of wing morphological evolution between the *palinurus* group and the other *Achillides*
568 endemic to India, *P. crino*. *Papilio chikae* is endemic to the Philippines (North Luzon) and was
569 always sister to *P. hermeli* as expected (Cabusas *et al.*, 2020), also endemic to the Philippines
570 (North Mindoro) with maximal support in all analyses. They were together nested in the *bianor*
571 group with maximal branch support as previously found (Condamine *et al.*, 2013b). Subgenus

572 *Princeps*, containing five species of the *demoleus* species group, constituted a strongly
573 supported clade with maximal branch support, which was found to be sister to subgenus
574 *Menelaides* (PP_{CAT}=0.93, PP_{PART}=1, BP_{PART}=70, and UFBS_{PART}=99). A Bayesian topology test
575 rejected the hypothesis of a monophyletic origin for all species usually placed in subgenus
576 *Princeps* like the *dardanus* species-group (BF>10, **Table 2**). Finally, the species comprising
577 the subgenus *Menelaides* formed a solid monophyletic group with robust branch support in all
578 analyses (PP_{CAT}=1, PP_{PART}=0.99, BP_{PART}=99, and UFBS_{PART}=100). The species relationships
579 within *Menelaides* largely agree with the recent phylogenetic study of Joshi and Kunte (2022).
580 We constrained subgenera *Menelaides* and *Araminta* (species previously included in
581 *Menelaides*) to form a single clade, but the Bayesian analysis confirmed the non-monophyly of
582 such an artificially inclusive *Menelaides* with decisive support (BF>10, **Table 2**).

583

584 **3.2. Origin of *Papilio* and subgeneric diversification**

585 The four independent Bayesian runs of the two dating analyses converged well (ESS>>200 for
586 most of the parameters) and were therefore combined. The analyses yielded almost identical
587 estimates of divergence times with less than 0.5 million years of difference for all nodes,
588 regardless of the calibrations used: fossils or secondary (**Fig. 4, Table 3**, see Figs S5-6 for the
589 chronograms resulting from the BEAST analyses). The dating analyses estimated that *Papilio*
590 originated in the Oligocene ca. 30.06 Ma (95% CI=20.66-47.42 Ma) with the three-fossil-
591 calibrations analysis, and ca. 29.95 Ma (95% CI=23.97-37.34 Ma) with the eight-secondary-
592 calibrations analysis. These results indicate that fossil and secondary calibrations can provide
593 similar and consistent results in age estimates, which has not always been the case (Sauquet *et*
594 *al.*, 2012). For the subsequent analyses (biogeography and diversification), we selected the
595 maximum clade credibility tree with median ages estimated with a Bayesian uncorrelated
596 lognormal method calibrated with fossils (**Fig. 4**).

597 We estimated that the origin of subgenera ranges from the early Miocene (e.g. *Chilasa*,
598 *Heraclides*, *Pterourus*), middle Miocene (e.g. *Achillides*), to the late Miocene (e.g. *Araminta*,
599 *Menelaides*, *Papilio*) (**Fig. 4, Table 3**). These age estimates are slightly younger than previous
600 analyses with age differences ranging from ca. 1 to 2 million years younger, but it is important
601 to note that 95% CIs for these nodes strongly overlap with earlier studies. For instance, we
602 estimated the origin of the clade ‘*Agehana*’ + *Chilasa* + *Pterourus* at 22.73 Ma (95% CI=15.36-
603 35.9 Ma), whereas we previously estimated this age at 20.9 Ma (95% CI=16.9-25.6 Ma; Lewis
604 *et al.*, 2015) or 19.7 Ma (95% CI=17.2-22.9 Ma, Owens *et al.*, 2017, 2020) but we have a similar
605 estimation to Wu *et al.* (2015) who found an age of 22.63 Ma (95% CI=18.93-26.58 Ma). Slight

606 differences are found in (1) subgenus *Heraclides* recovered at 21.22 Ma (95% CI=13.95-33.86
607 Ma) compared to our previous estimation of 22.1 Ma (95% CI=18.0-26.9 Ma; Lewis *et al.*,
608 2015) or 21.9 Ma (95% CI=17.5-26.4 Ma; Wu *et al.*, 2015); and (2) subgenus *Achillides*
609 estimated at 17.1 Ma (95% CI=11.45-26.88 Ma) whereas we previously recovered a 2-million-
610 year older age at 19.3 Ma (95% CI=16.4-21.8 Ma; Condamine *et al.*, 2013). We argue that these
611 slight age discrepancies mostly come from the differences in taxon sampling resulting in new
612 phylogenetic placements (e.g. *P. alexanor*) and potentially from practices in dating techniques
613 both influencing divergence time estimates.

614

615 **3.3. Northern origin and dynamic dispersal into the tropics**

616 DEC analyses recovered a region including West Nearctic, Central America, East Palearctic,
617 and Sundaland as the most likely ancestral geographic origin (relative probability=0.467), when
618 Asia and North America were connected by the Bering land bridge in the Oligocene (**Fig. 4**).
619 The second best ancestral area was composed of West Nearctic, Central America, and East
620 Palearctic (relative probability=0.215). Hence, a Northern (Laurasian) origin is preferred over
621 a Southern (Gondwanan) origin. This is not unexpected given the age of the genus and the
622 results of previous biogeographic analyses of the genus (e.g. Condamine *et al.*, 2012, 2013;
623 Lewis *et al.*, 2015; Wu *et al.*, 2015), although some studies estimated an older age and
624 Gondwanan origin (Zakharov *et al.*, 2004a). The DEC analyses indicate a dynamic
625 biogeographic history with numerous dispersal events inferred ($n=64$) in comparison to
626 vicariance events ($n=22$). Dispersal events were mostly southward ($n=32$) from a northern
627 origin (or dispersal *into the tropics*, Condamine *et al.*, 2012; Rolland *et al.*, 2015) than
628 northward ($n=17$, when including northwestward dispersals) from the equator (or dispersal *out*
629 *of the tropics*, Jablonski *et al.*, 2006). Northward dispersals are only estimated in the last 10
630 million years. Excluding vicariance events involving areas around the Bering Strait ($n=2$), we
631 found more vicariance in the Old World ($n=13$) than in the New World ($n=7$). We also
632 estimated numerous local extirpation events ($n=51$), which tend to be more numerous in the
633 Old World subgenera ($n=27$) than in the New World subgenera ($n=15$), likely due to the
634 Miocene fragmentation of the Boreotropical forest in the Holarctic (Pound *et al.*, 2012).

635

636 **3.4. The Paleotropics as a biogeographic crossroad**

637 In the non-monophyletic New World *Papilio*, subgenus *Heraclides* originated in Central
638 America (very likely including Caribbean Islands; Lewis *et al.*, 2015) and clade *Chilasa* +
639 *Pterourus* originated in a region comprising the West Nearctic, Central America, East

640 Palearctic, and Sundaland. The clade of Old World *Papilio* originated in East Palearctic with
641 *P. alexanor* being sister to all remaining Old World *Papilio*, which soon after their divergence
642 colonized the Paleotropics through West and East Palearctic + Sundaland and extended to
643 Africa (see shaded area on **Fig. 4**).

644 We found the Paleotropics to be an important ancestral area for the historical
645 biogeography of *Papilio*. It is striking that, within the Old World clade (Clade 3), all the main
646 nodes of the backbone (seven in total out of 26, **Table 3**) are estimated to originate within the
647 Paleotropics in the early Miocene (23 to 15 Ma, **Fig. 4**). During this time period, Africa, West
648 and East Palearctic, and Sundaland were mostly covered by tropical-adapted or paratropical
649 forests providing an almost continuous tropical habitat between these large regions, which
650 likely facilitated biotic movements within the Paleotropics (e.g. Ziegler *et al.*, 2003; Morley,
651 2011). However, starting after the middle Miocene climatic optimum (Steinthorsdottir *et al.*,
652 2021), the global cooling of the Cenozoic fostered the geographic contraction of the tropical
653 belt toward the equator that disappeared from higher latitudes (Pound *et al.*, 2012). Our
654 biogeographic estimates indicated widespread geographic extinctions in the Paleotropics,
655 especially in the Holarctic, and at least seven different lineages were able to disperse
656 southwards to track their preferred macroclimatic conditions, supposedly tropical climates
657 (Condamine *et al.*, 2012). Like crematogastrine ants (Blaimer *et al.*, 2018), we show that the
658 Paleotropics had a central role in the origin and evolution of *Papilio*. The vast and stable
659 ecological opportunity offered by the tropical rainforests likely explained the *into-the-tropics*
660 dispersal trend to track tropical contractions as climate cooled down toward the present. This
661 supports the hypothesis that potentially many clades, particularly inhabitants of Boreotropical
662 floras, were likely extirpated from the Holarctic and persist today in more southern tropical
663 locations (Meseguer *et al.*, 2018).

664

665 **3.5. Tempo and mode of *Papilio* diversification**

666 The diversification analyses investigating rate heterogeneity across *Papilio* revealed four best
667 equally-likely scenarios of diversification ($\Delta\text{AICc} \leq 2$, Table S2), which refutes the hypothesis
668 of a single diversification rate for the whole genus ($\Delta\text{AICc} = 14.06$; Table S2). These shift-
669 configuration scenarios include three shifts located at subgenera *Achillides*, *Menelaides* and
670 *Papilio* for the first best scenario (**Fig. 5A**), two shifts (*Achillides* and *Menelaides*) for the
671 second best scenario, five shifts (*Achillides*, *Heraclides*, *Menelaides*, *Papilio* and *Pterourus*)
672 for the third best scenario (Fig. S7A), and four shifts (*Achillides*, *Heraclides*, *Menelaides* and
673 *Papilio*) for the fourth best scenario. Subgenera *Achillides* and *Menelaides* are always found as

674 significant shifts. All subclades are better explained by a pure-birth model (BCST), except
675 subgenus *Menelaides* that follows a model with a decreasing speciation rate through time
676 (BVAR; **Fig. 5B**, Fig. S7B, Table S3).

677 Interestingly, after isolating the subclades that significantly diversify at different rates,
678 two patterns emerge from the backbone (remaining lineages) of best combinations. For the two
679 first best combinations, the backbone is explained by a model with a decreasing speciation rate
680 over time without extinction (**Fig. 5B**), while the backbone in the two other scenarios follows
681 a model with the same decreasing speciation rate and includes a constant extinction rate (Fig.
682 S7B). In the latter case, net diversification rate becomes negative in the Pliocene onward (ca. 5
683 Ma), leading to a waxing-waning pattern of diversification (Fig. S7C). This short diversity
684 decline near the present did not affect the trend of the global diversity dynamics because it
685 happens when subclades are already diversifying, thus compensating the decline (Fig. S7B, C,
686 D). The diversity dynamics of these two different patterns in the backbone (decline or not) are
687 similar except with a faster accumulation of lineages during the early Miocene for the scenarios
688 with a decline (**Fig. 5**, Fig. S7).

689 These four scenarios highlight common features related to adaptive radiation. First, all
690 scenarios agree to show a two-step diversification history. The first phase of the *Papilio*
691 radiation proceeded at a high net diversification (ranging from 0.224 to 0.426
692 events/Myr/lineage depending on the scenario), while the second period of diversification is
693 supported by subclade dynamics having lower speciation rates than at the origin of *Papilio* (e.g.
694 0.122 for *Heraclides*, 0.178 for *Papilio*), except for *Menelaides* (0.386 events/Myr/lineage).
695 The first radiation phase reaches an equilibrium before a short declining phase in half of the
696 best scenarios. For the two other scenarios, the backbones have lower speciation rates at the
697 origin but also contain more lineages (only three or two shifts). These results agree with the
698 general tendency for diversification to slow down as evolution proceeds, considered as one of
699 the most pervasive macroevolutionary principles (Rabosky, 2009; Morlon *et al.*, 2010; Morlon
700 and Moen, 2014; Condamine *et al.*, 2019). Such diversification slowdowns have often been
701 interpreted as the effect of competition for resources or niche availability (Rabosky, 2009) or
702 the role of past environmental changes (Condamine *et al.*, 2019). It is thus possible that the
703 diversity of some *Papilio* lineages can be at equilibrium or limited by ecological resources,
704 although these lineages are still expanding toward the present but at a slower pace than in the
705 past, supporting the ‘damped increase’ hypothesis (Cornell, 2013).

706 Clade-specific rates of diversification can further explain differences in clades’ species
707 richness. Although the number of clade shifts varies from one scenario to another, this pattern

708 of radiating subclades within the genus *Papilio* seems to be supported by a strong signal (Table
709 S2). Clade-heterogeneous diversification has been unveiled across Papilionidae as a whole
710 (Condamine *et al.*, 2012; Allio *et al.*, 2021) or for other swallowtail clades (Condamine *et al.*,
711 2018b), which has been then linked to species' traits or environments. In the case of *Papilio*,
712 the two most important shifts in diversification are recovered for subgenera *Achillides* and
713 *Menelaides*. These two subclades are island-dwelling groups in the Indo-Malayan and
714 Australasian Archipelagos (Condamine *et al.*, 2013; Joshi and Kunte, 2022), a region where
715 species diversity is the highest at the global scale for this genus (**Fig. 2**). Their diversification
716 proceeded through repeated island colonizations since the middle Miocene leading to rampant
717 allopatric speciation across the entire archipelago (Condamine *et al.*, 2013; Joshi and Kunte
718 2022). In addition, the subgenus *Menelaides* shows an early-burst pattern with high speciation
719 rate when it originated (0.386 events/Myr/lineage), followed by a decrease toward the present
720 (0.145 events/Myr/lineage, **Fig. 5**). Besides their island distribution, *Menelaides* are well-
721 known for their Batesian mimicry of aposematic and toxic troidine swallowtails (Kunte, 2009;
722 Palmer and Kronforst, 2020; Kizhakke and Kunte, 2022), which may have spurred their high
723 speciation rates. The subgenus *Menelaides* diversified faster than any other subgenus, and yet
724 is the most recent clade with subgenus *Papilio* (Table S3). The latter is often found as a
725 significant shift (**Fig. 5**), which may be linked to the host-plant shift on Apiaceae (Allio *et al.*,
726 2021) and/or to the glaciation cycles initiated in the late Pliocene (Dupuis and Sperling, 2020).

727 We did not recover a model incorporating extinction rate in any subclade, which might
728 be artifactual due to the difficulty of estimating extinction rates from phylogenies of extant
729 species alone, or this may be biologically realistic if the nascent subclades did not have enough
730 time to experience extinction to be detectable (e.g. Morlon *et al.*, 2011). Assuming these
731 estimates are not biased, this may suggest that subclades of *Papilio* evolved under a 'museum
732 model of diversity' with a very low extinction rate. Altogether, while their geographic ranges
733 contracted toward the equator (**Fig. 4**), the genus sustained high rates of species diversification
734 thanks to multiple speciation shifts leading to a global increase of species accumulation toward
735 the present (**Fig. 5**). This suggests that the tropics are not only the evolutionary source of the
736 *Papilio* diversity but have also played an important role in mitigating their extinction.

737

738 **3.6. Should more than one genus be recognized within *Papilio*?**

739 The rank of genus is the most visible rung in the Linnaean hierarchy. It forms part of every
740 species name, indicating shared relationships when there are multiple species in a genus, or
741 unusual distinctness of a species when it constitutes a monotypic genus. Other than monophyly

742 (evidenced by one or more synapomorphies), there are no objective criteria for determining
743 genus boundaries, and even monophyly does not determine how high up on its tree a branch
744 should be cut. Further, when subclades within a genus are elevated to the rank of genus, the
745 information provided by the name about closer relationships is balanced by the lost information
746 about the broader relationships of the group. Nonetheless, numerous attempts have been made
747 to provide general guidelines for recognizing a genus (Talavera *et al.*, 2012; Dorchin *et al.*,
748 2018; Sigward *et al.*, 2018; Zhang *et al.*, 2019; Nakahara *et al.*, 2020), with criteria including
749 the compactness of a group, its distinctness from other such groups, the number of species it
750 contains, its estimated age of divergence, comparability to related genera, consistency with
751 established usage of a name, and degree of confidence in the assessment of its phylogenetic
752 relationships (Ashlock and Mayr, 1991). Balancing and prioritizing potential conflicts among
753 these criteria, while at the same time conveying as much information as possible about
754 relationships between species to non-expert end-users of the names, remains one of the most
755 subjective aspects of systematics.

756 It is clear that taxonomic stability is a primary aim, if not *the* primary aim, of the
757 International Code of Zoological Nomenclature (ICZN, 1999, 2012). The genus *Papilio sensu*
758 *lato* has been stable and unambiguously defined by morphology since Munroe (1961), and later
759 supported by molecular evidence (e.g. Aubert *et al.*, 1999; Caterino and Sperling, 1999;
760 Zakharov *et al.*, 2004a), although the clades within that genus have continued to be volatile
761 (Hancock, 1983; Miller, 1987; Zakharov *et al.*, 2004a). Even *Chilasa* and ‘*Agehana*’, which
762 Hauser *et al.* (2005) treated as distinct, have continued to move back and forth with each new
763 phylogeny (Zakharov *et al.*, 2004a; Wu *et al.*, 2015). Consequently, we have chosen here to
764 retain the use of the genus *Papilio* in its broad sense, pending a more rigorous and objective
765 integration of the multiple criteria that may be used to determine the boundary of a genus. For
766 widely recognized and previously stable taxonomic groups, we consider it to be in the best
767 interests of systematists to be conservative in proposing new name changes for anything other
768 than well supported cases of non-monophyly. In our experience, continued name changes for
769 high-profile taxa will consistently elicit frustration and disrespect from the larger community
770 of biologists, conservationists, and the general public. At the same time, if names reflect current
771 knowledge, then advances based on new evidence or even different weighting of evidence will
772 inevitably result in name changes. Fortunately, a solution to this conflict is available through
773 the use of subgeneric names, which allow systematists to refer clearly to their refined taxonomic
774 concepts without putting the burden of increased confusion from name changes onto the users
775 of these species and genus names in other fields.

776

777 **4. Conclusion**

778 Building a comprehensive species-level dated phylogeny for a globally distributed insect clade
779 is challenging. We addressed this challenge with the genus *Papilio*, which currently includes
780 235 species worldwide. Our study assembles ~80% of the species diversity in a molecular
781 supermatrix and provides a generally robust time-calibrated phylogenetic reference for *Papilio*.
782 This new tree confirms previous results such as the early-diverging position of New World
783 *Papilio* and the sister relationships between some subgenera and unveils novel relationships
784 like the placement of *P. alexanor* and the non-monophyly of several subgenera. This
785 phylogenetic framework provides the foundation for a systematic revision, but we urge
786 specialists to refrain from changing the status of subgenera to the rank of genus. Deep nodes
787 within *Papilio* remain poorly resolved and some subgenera are still poorly sampled, especially
788 in Africa. Future studies with denser taxon sampling and full genomic data will undoubtedly
789 provide a more accurate phylogeny for *Papilio* and justify a thorough systematic revision. Here
790 we used this dated phylogeny to assess the evolutionary history of *Papilio*, with estimated
791 divergence times that place its origin in the Oligocene (~30 Ma). Biogeographic analyses
792 suggest a Beringian origin followed by southward dispersals into the tropics, with a pivotal role
793 of the Paleotropics as a biogeographic crossroad for the worldwide colonization of *Papilio*.

794

795 **5. Formal taxonomic changes**

796 Our results confirm the status of ‘*Agehana*’ (two species, *P. elwesi* and *P. maraho*) within
797 subgenus *Pterourus* as proposed by Wu *et al.* (2015). *Papilio zalmoxis* Hewitson, 1864 is
798 transferred from subgenus *Druryia* to subgenus *Nireopapilio*. This finding is also supported
799 morphologically by Huxley (1976), who showed that the wing scale structure of *P. zalmoxis* is
800 identical to *P. bromius* (valid name: *P. chrapkowskoides* Storace, 1952), both also containing
801 blue-fluorescent pigment.

802 Two taxa in subgenus *Druryia* are recognized as separate species to *Papilio dardanus*
803 Yeats, 1776, namely *Papilio meriones* C. Felder & R. Felder, 1864 (**stat. rev.**) from
804 Madagascar and *Papilio humbloti* Oberthür, 1888 (**stat. rev.**) from Comoros Islands.

805 In subgenus *Pterourus*, Tyler *et al.* (1994) placed *Papilio victorinus* Doubleday, 1844
806 from Mexico within *Pterourus menatius* (Hübner, [1819]), but we consider this Central
807 American taxon as specifically distinct from the South American *Papilio menatius* (Owens *et*
808 *al.* 2017, 2020), and we reinstate *Papilio victorinus* Doubleday, 1844 as a separate species (**stat.**
809 **rev.**).

810 In subgenus *Papilio* two North American species are confirmed as separate from *P.*
811 *machaon* Linnaeus, 1758, namely *Papilio kahli* F. & R. Chermock, 1937 (**stat. nov.**) and
812 *Papilio bairdii* Edwards, 1866 (**stat. rev.**). *Papilio bairdii* includes two subspecies, *oregonia*
813 Edwards, 1876 and *dodi* McDunnough, 1939 (**comb. nov.**) as well as the nominate subspecies.
814 *Papilio saharae* Oberthür, 1879 is treated as a subspecies of *P. machaon* as per Dupuis and
815 Sperling (2020), subject to further investigation.

816 We found two commonly recurrent patterns in several Asian groups, with speciation
817 between taxa from mainland southern Asia and Sundaland, and between taxa in the Bismarck
818 Archipelago from those in New Guinea, as detailed below.

819 Within subgenus *Achillides*, five taxa, three with more than one subspecies, are
820 separated at species level based on molecular results from Condamine *et al.* (2013b) and
821 Cabusas *et al.* (2020). *Papilio polyctor* Boisduval, 1836 (**stat. rev.**) from northern Pakistan and
822 NW India is separated from *Papilio bianor* Cramer, 1777, and *Papilio hermeli* Nuyda, 1992
823 (**stat. rev.**) from Mindoro, Philippines is reinstated as a separate species to *P. chikae* Igarashi,
824 1965 from Luzon. *Papilio daedalus* C. Felder & R. Felder, 1861 (**stat. rev.**), with subspecies
825 *angustatus* Staudinger, 1888, is confirmed as a separate species to *Papilio palinurus* Fabricius,
826 1787. Hiura and Alagar (1971) first separated *P. daedalus* from *P. palinurus* based on
827 morphology, but Page and Treadaway (2003a) placed them as conspecific based on perceived
828 similarity of genitalia. Molecular phylogenies clearly show they are separate species, and all
829 subspecies of the two species can easily be separated based on the position of the postdiscal
830 green hindwing band in relation to the anal eyespot. In *P. palinurus* the lowest point of the band
831 is always above the eyespot, whereas in *P. daedalus* the band meets the eyespot. The *Papilio*
832 *ulysses* group was found to consist of three separate species, *Papilio ulysses* Linnaeus, 1758
833 (South Moluccas, New Guinea and most associated islands, and Australia), *Papilio telegonus*
834 C. Felder & R. Felder, 1860 (**stat. rev.**) from Northern Moluccas, and *Papilio orsippus* Godman
835 & Salvin, 1888 (**stat. rev.**) from the Bismarck Archipelago and Solomon Islands. Nakae (2021)
836 separated *Papilio arjuna* Horsfield, 1828, found on Sumatra and Java, from mainland Asian *P.*
837 *paris* based on the findings of Condamine *et al.* (2013b), which is confirmed here due to
838 paraphyly with *P. karna*. That study of *Achillides* also suggested that *P. maackii* and *P. syfanius*
839 may be conspecific; but a recent genomic study clarified that mitochondrial gene exchange
840 occurs between these two species in western China without significant exchange of nuclear
841 genes (Xiong *et al.* 2022). As a result, we retain *P. maackii* and *P. syfanius* as separate species.

842 Subgenus *Euchenor* has previously been regarded as monobasic, but DNA analysis
843 shows that the subgenus consists of two distinct species (Joshi and Kunte 2022): *Papilio*

844 *euchenor* Guérin-Ménéville, 1830 and *Papilio depilis* Rothschild, 1895 (**stat. rev.**). Jordan, in
845 Rothschild (1895), stated that forewing scale structure in these two taxa are different but
846 refrained from treating them as separate species. Jordan (1896) then separated the two species,
847 citing several morphological differences including genitalia. Jordan (1908-09) without
848 explanation reunited *P. depilis* with *P. euchenor*, which has been followed by all authors until
849 now. This specific separation of Bismarck Archipelago taxa from New Guinea taxa mirrors the
850 separation of *P. orsippus* from *P. ulysses* in subgenus *Achillides*, and similar separation is found
851 in subgenus *Menelaides* below.

852 In the *helenus* group of subgenus *Menelaides*, both Munroe (1961 - *nepheus*, *nubilus*
853 and *chaon*) and Hancock (1985 - *noblei* and *antonio*) included species which have been found
854 not to be monophyletic. *Papilio noblei* Nicéville, [1889] and *P. antonio* Hewitson, 1875 are
855 shown here to belong to subgenus *Araminta*, which is also supported by morphology and wing
856 pattern, particularly on the underside. *Papilio nubilus* has been shown to be a natural hybrid
857 between *P. nepheus* and *P. polytes* rather than a valid species (Tsukada and Nishiyama 1980:
858 307). We confirmed that *Papilio hystaspes* C. Felder & R. Felder, 1862, separated from *helenus*
859 by Hiura and Alagar (1971) based on male genitalia and treated as separate by Hancock (1983)
860 but placed within *P. helenus* by Page and Treadaway (2003b), is a distinct species (**stat. rev.**)
861 which branches off before the traditional *helenus* taxa and *sataspes*. However, we also found
862 that several taxa always considered to belong to *P. helenus* are separate species. The first
863 species is *Papilio daksha* (**stat. rev.**) from Southern India. Joshi and Kunte (2022) analyzed
864 specimens of ssp. *enganius* Doherty, 1891 from Sumatra, Java and Borneo and found that they
865 are sister to *P. sataspes* from Sulawesi and associated islands, not *P. helenus* from mainland
866 SE Asia and the Malay Peninsula. The oldest name for the taxon in the Sundaic islands of
867 Sumatra, Java, Borneo and Palawan, is *Papilio palawanicus* Staudinger, 1888 (**stat. nov.**).

868 In the Lesser Sunda Islands, two more taxa in the *helenus* group are also separate
869 species, *Papilio mangarinus* Rothschild, 1908 (**stat. nov.**) and *Papilio biseriatus* Rothschild,
870 1895 (**stat. rev.**). *P. biseriatus* from Timor was previously treated as a separate species by
871 Hancock (1983) and differs from the other species in the postdiscal white hindwing patch
872 extending across four hindwing cells as in *P. hystaspes* from the Philippines, whereas in *P.*
873 *helenus*, *palawanicus* and *mangarinus* the hindwing patch only covers three cells. As a result
874 of this analysis the range of *P. helenus* is restricted to mainland Asia and the Malay Peninsula,
875 Taiwan and Japan.

876 Within the *polytes* group, *Papilio protenor* Cramer, 1775 is sister to all other species.
877 This does not correspond to its expected position, as the early stages are very similar to *P.*

878 *memnon*, not *polytes*; presumably this similarity is plesiomorphic. Five more species are
879 recognised within the *polytes* group, two of which are newly separated in this work. The two
880 easternmost species, *Papilio ambrax* Boisduval, 1832 and *Papilio phestus* Guérin-Ménéville,
881 1830, were treated as distinct species until Fujioka *et al.* (1997) combined them based on
882 morphology and allopatry. However, molecular phylogenies (Joshi and Kunte, 2022) and
883 population genetic analyses (Zhang *et al.*, 2017; Deshmukh *et al.*, 2022) show *P. ambrax* and
884 *P. phestus* to be specifically distinct (**stat. rev.**). *Papilio alphenor* Cramer, 1776 was separated
885 from *P. polytes* based on genitalia by Hiura and Alagar (1971), but subsequently sunk by Page
886 and Treadaway (2003a) without explanation. Molecular phylogenies suggest that *P. alphenor*
887 is sister to *phestus* + *ambrax*, not *polytes* (Joshi and Kunte, 2022), and thus must be treated as
888 a separate species (**stat. rev.**). The remaining taxa placed in *P. polytes* also belong to two
889 separate species: the mainland Asian populations are specifically distinct from the Sundaic
890 island taxa, the oldest name for which is *Papilio javanus* C. Felder, 1862 (**stat. nov.**). *Papilio*
891 *polytes*, *alphenor* and *javanus* also show prezygotic and postzygotic barriers to hybridization
892 including assortative mating and low fitness of hybrid progeny, thus being reproductively
893 isolated, with genome-wide and population genetic signatures of being highly diverged distinct
894 species (Zhang *et al.*, 2017; Deshmukh *et al.*, 2022).

895 Specific separation between the mainland Asian taxa and those in the Sundaic islands
896 was also found in the *memnon* group, but the status of taxa within this group is shown to be
897 further complicated by several taxa traditionally considered as separate species being
898 conspecific with related species (Joshi and Kunte, 2022). The larger *memnon* group then split
899 into two clades, one containing the *bootes* and *alcmenor* species groups and the other *P.*
900 *memnon* and close relatives. There are two branches within the first clade, one branch
901 containing just two species, *Papilio bootes* Westwood, 1842 and *Papilio janaka* Moore, 1857
902 (**stat. rev.**). Originally these were considered separate species, but they were treated as
903 conspecific by Evans (1923), followed by Talbot (1939) and subsequent authors. Previous
904 molecular phylogenies show that *P. bootes* and *P. janaka* are significantly genetically distinct
905 (Joshi and Kunte, 2022), and are treated as different species although they are sympatric in NE
906 Myanmar. The other branch of the first clade contains *Papilio acheron* Grose-Smith, 1887,
907 *forbesi* Grose-Smith, 1883 and *lampsacus* Boisduval, 1836 (this last taxon not sequenced due
908 to rarity) with *Papilio alcmenor* C. Felder & R. Felder, 1865 and *thaiwanus* Rothschild, 1898
909 sisters within this group. Previously *P. acheron*, *forbesi* and *lampsacus* were considered as very
910 close to *P. memnon* due to their similar appearance, but this relationship was not confirmed by
911 our analysis.

912 Molecular phylogenies confirmed that the Philippine taxon *rumanzovia* Eschscholtz,
913 1821 is genetically conspecific with Moluccan *P. deiphobus* (Joshi and Kunte, 2022), as stated
914 on morphological grounds by Page and Treadaway (2003a,b). There is a wide genetic
915 divergence between the mainland Asian and the Sundaland taxa previously united under *P.*
916 *memnon*, which clearly represent two separate species, *Papilio agenor* Linnaeus, 1758 (**stat.**
917 **rev.**) and *P. memnon* (Joshi and Kunte, 2022). Two traditionally well-regarded species, *Papilio*
918 *polymnestor* Cramer, 1775 from peninsular India and Sri Lanka, and *Papilio mayo* Atkinson,
919 [1874] from the Andaman Islands, do not merit species status. *Papilio polymnestor* was nested
920 within *P. agenor* (Joshi and Kunte, 2022) and should therefore be treated as a subspecies,
921 *Papilio agenor polymnestor* Cramer, 1775 (**stat. rev.**). Likewise, *P. mayo* was nested within
922 and therefore confirmed as conspecific with *P. memnon*, and should be treated as its subspecies,
923 *Papilio memnon mayo* Atkinson, [1874] (**stat. rev.**).

924 The *nephelus* group comprises four species. *Papilio castor* Westwood, 1842 and *P.*
925 *dravidarum* Wood-Mason, 1880 are sister species within this group, and the taxon *Papilio*
926 *mahadeva* Moore, [1879] is confirmed to be conspecific with *P. castor* as stated on
927 morphological grounds by Cotton and Racheli (2007). *Papilio chaon* Westwood, 1844 and *P.*
928 *nephelus* Boisduval, 1836, from mainland SE Asia and Sundaland respectively, were originally
929 described as separate species but were treated as conspecific by Igarashi (1979) based on early
930 stages. Molecular phylogenies showed that genetically *nephelus* and *chaon* are highly divergent
931 (Joshi and Kunte, 2022), and thus must be treated as separate species, *P. nephelus* and *P. chaon*
932 (**stat. rev.**).

933 Within the *aegeus* clade, *P. godeffroyi* was found to be the sister taxon to *Papilio oritas*
934 Godman & Salvin, 1879 (**stat. rev.**) from New Britain, New Ireland and New Hannover, which
935 was placed within *P. aegeus* by Jordan (1909). In molecular phylogenies, *P. oritas* diverged
936 before the remaining species in the *aegeus* group (Joshi and Kunte, 2022), and thus is not
937 conspecific with *P. aegeus*. This is another example of speciation within the Bismarck Islands.
938 *Papilio inopinatus* Butler, 1883 from Timor was found to be nested within *P. aegeus* (**syn.**
939 **nov.**), thus it becomes *Papilio aegeus inopinatus* (**comb. nov.**).

940 The most complex clade within subgenus *Menelaides* is the *fuscus* group. The species
941 *Papilio fuscus* Goeze, 1779 as recognised by Hancock (1992) in the most recent revision of this
942 species is not a monophyletic entity. Hancock placed many taxa in his single species *Princeps*
943 *fuscus* (Goeze, 1779) which we here recognise as five different species in two subclades of the
944 *fuscus* group. Hancock placed *Papilio canopus* Westwood, 1842 and *Papilio hypsicles*
945 Hewitson, 1868 as species level synonyms of *P. fuscus*, but we found that this arrangement is

946 not monophyletic, and these two taxa represent separate species (**stat. rev.**). He also placed four
947 taxa traditionally treated within *P. fuscus* with two taxa previously known as *Papilio pitmani*
948 Elwes & Nicéville, [1887] under the species name *Princeps prexaspes* (C. Felder & R. Felder,
949 1865). We confirmed that these six taxa form a single species which we treat as *Papilio*
950 *prexaspes*, restricting the name *Princeps* Hübner, [1807] as the subgeneric name for the *Papilio*
951 *demoleus* clade.

952 As stated above, Hancock (1992) treated *P. canopus* and *P. hypsicles* within *P. fuscus*,
953 but molecular phylogenies showed that this would result in a paraphyletic species. Two groups
954 of taxa traditionally treated within *Papilio fuscus* (e.g. Jordan 1909) were found to be the sister
955 to *P. hypsicles*, representing two distinct species not directly related to true *P. fuscus* (Joshi and
956 Kunte, 2022). One of these consists of two taxa from New Britain (*lamponius* Fruhstorfer,
957 1904) and New Ireland (*cilix* Godman & Salvin, 1879) which represent a distinct species,
958 *Papilio cilix* Godman & Salvin, 1879 (**stat. rev.**). This follows a pattern of speciation of New
959 Britain and New Ireland taxa seen in other *Papilio* species as discussed above. The sister to *P.*
960 *cilix* consists of the taxa traditionally placed in *P. fuscus* from eastern Australia, New Guinea
961 and the Solomon Islands. The oldest available name for this species is *Papilio capaneus*
962 Westwood, 1843 (**stat. rev.**).

963

964 **CRedit authorship contribution statement**

965 **Fabien L. Condamine:** Conceptualization, Methodology, Validation, Taxonomy,
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982

983 **Declaration of Competing Interest**

984 The authors declare that they have no known competing financial interests or personal
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- 1398

1399 **Figure Legends**

1400 **Fig. 1.** Illustration of swallowtail butterfly diversity in the genus *Papilio*, showing several
1401 subgenera that have been widely used since Munroe (1961). Specimens are not uniformly
1402 scaled. Pictures from Fabien L. Condamine.



P. (Alexanoria) alexanor



P. (Eleppone) anactus



P. (Sinoprinceps) bengueta



P. (Menelaides) bootes



P. (Papilio) joanae



P. (Chilasa) laglaize



P. (Heraclides) thoas



P. (Achillides) ulysses



P. (Pterourus) zagreus

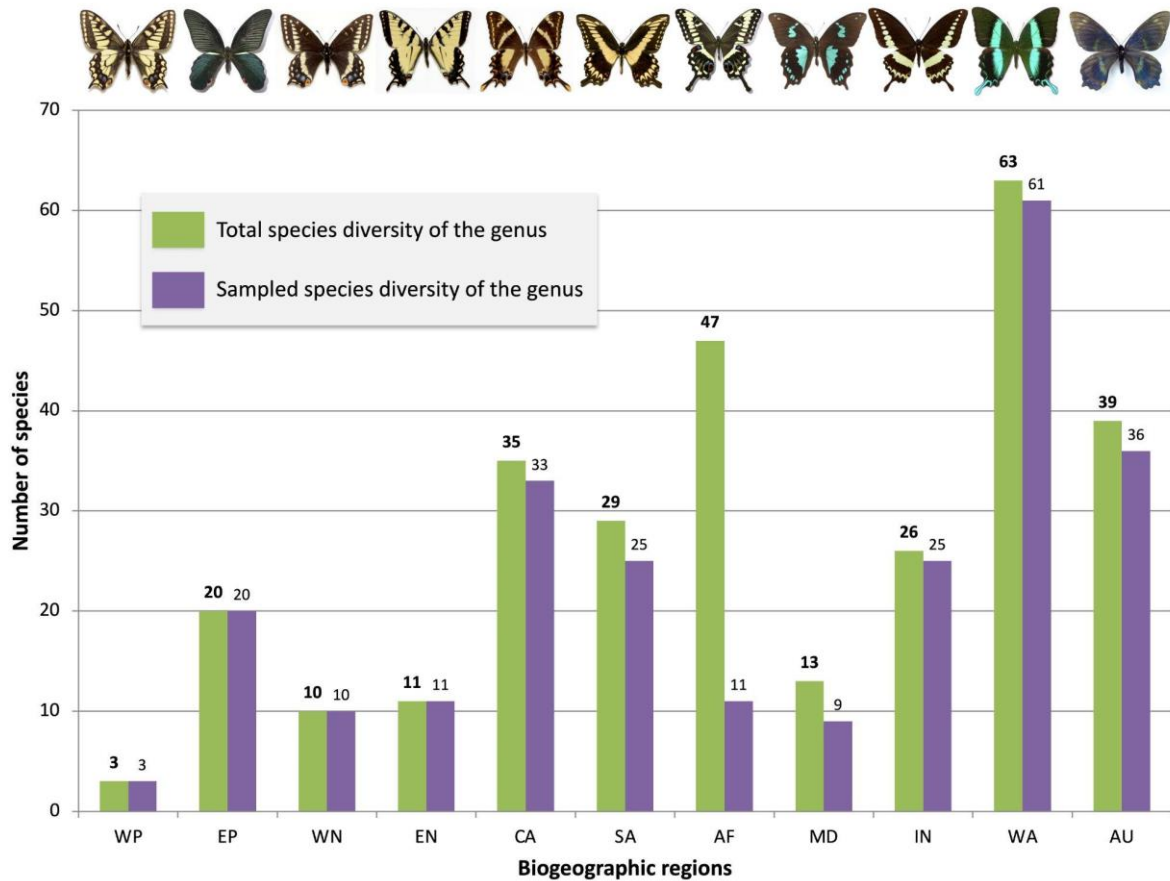


P. (Druryia) antimachus

1403

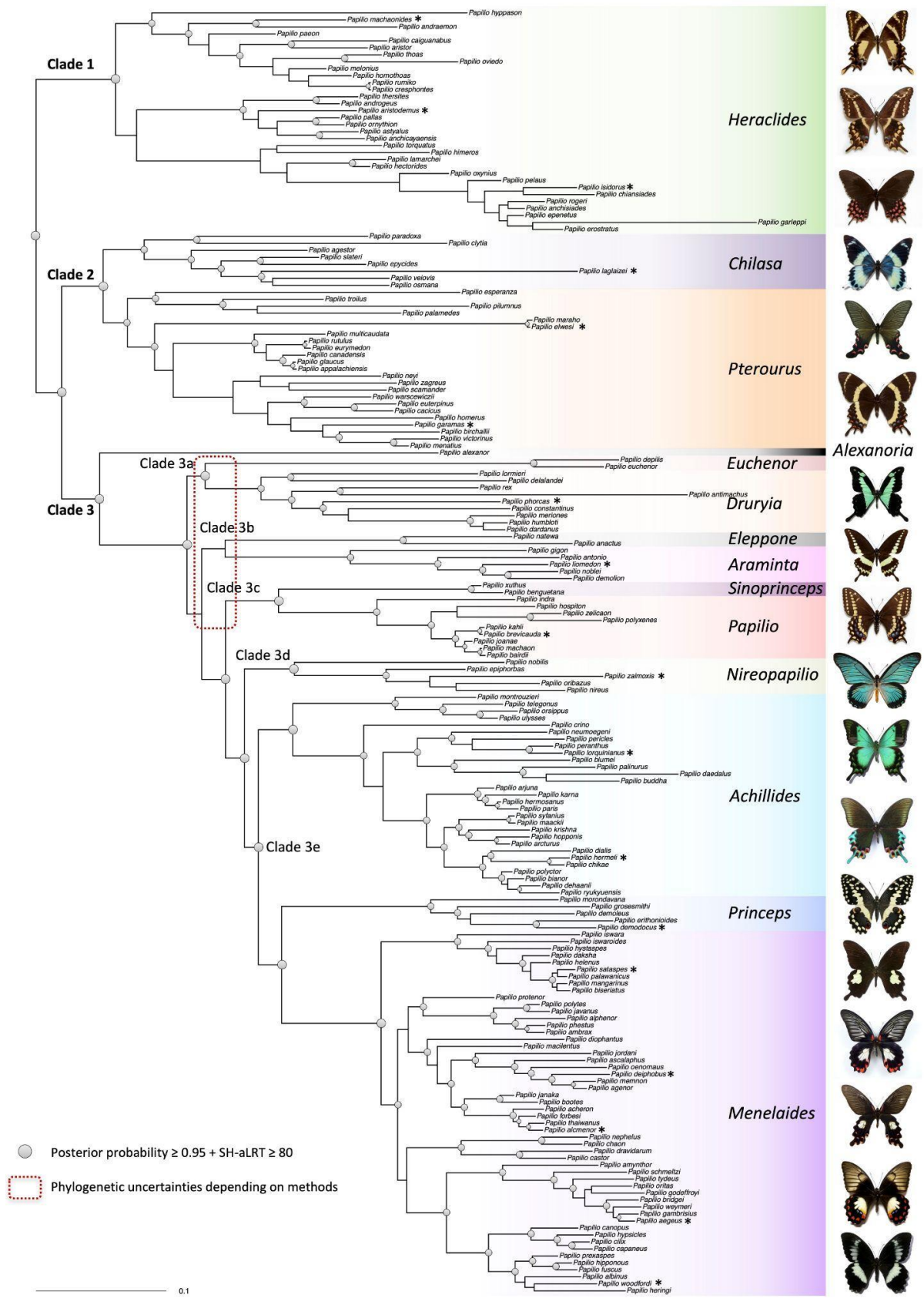
1404

1405 **Fig. 2.** Geographic distribution and sampling of *Papilio*. Histogram shows the number of
 1406 species occurring in 11 biogeographic regions and sampled in the current phylogenetic tree;
 1407 African species diversity is clearly under sampled. WP: Western Palearctic, EP: Eastern
 1408 Palearctic, WN: Western Nearctic, EN: Eastern Nearctic, CA: Central America and Caribbean
 1409 Islands, SA: South America, AF: Africa, MD: Madagascar, IN: India and Himalayan foothills,
 1410 WA: Southeast Asia and Wallacea, and AU: Australasia. Pictures from Fabien L. Condamine.
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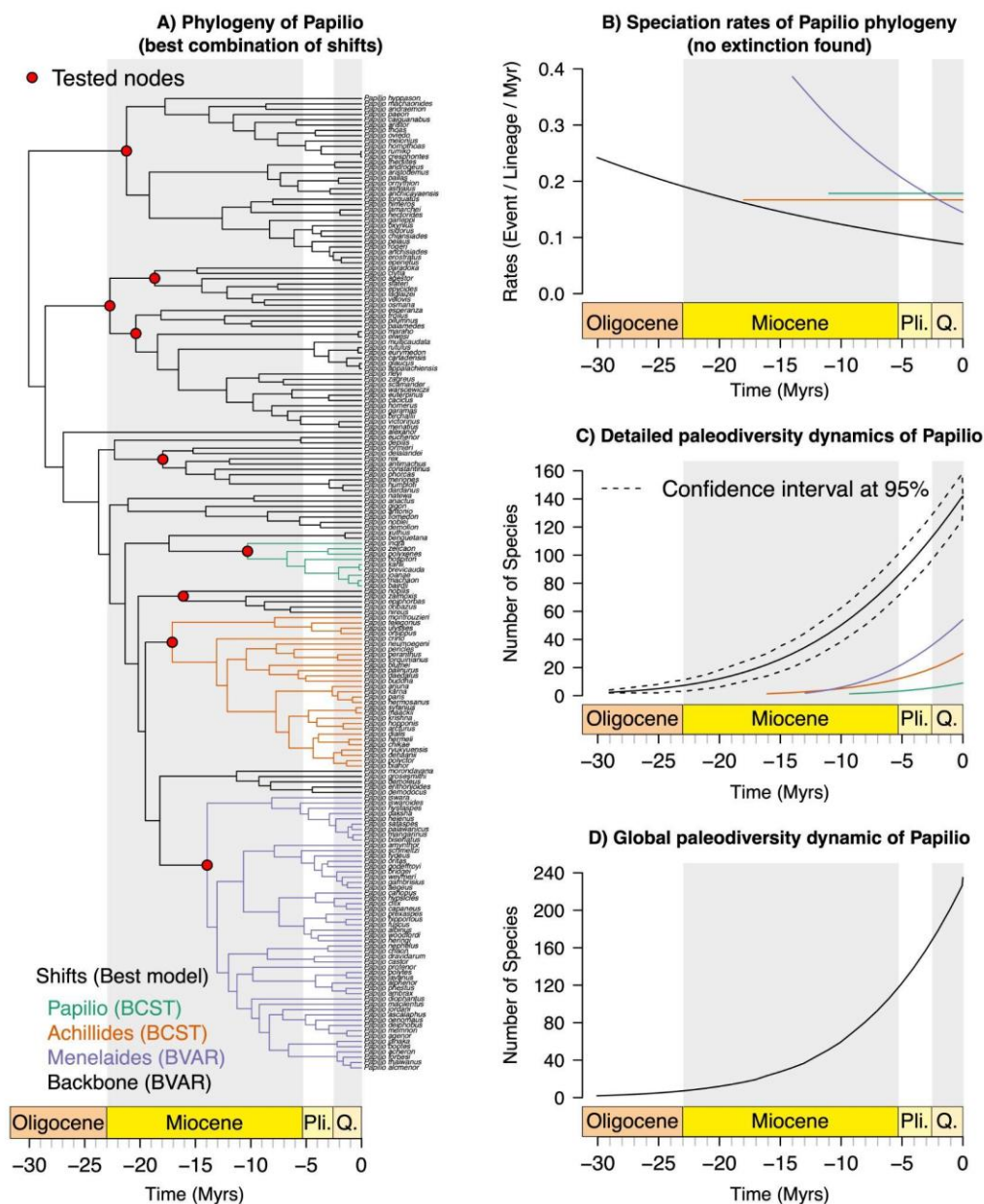
1414 **Fig. 3.** Bayesian molecular phylogeny of *Papilio*. The phylogeny was inferred with MrBayes
1415 using a traditional partitioning strategy and a reversible-jump MCMC approach for selecting
1416 the best fitting substitution models. Posterior probabilities ≥ 0.95 are indicated at nodes with
1417 filled circles. The red dashed rectangle indicates phylogenetic uncertainties between methods.
1418 Existing subgeneric classification is shown with colored rectangles delineating subgenera. The
1419 outgroups are removed. Asterisks indicate species illustrated on the right. Pictures from Fabien
1420 L. Condamine.



1421
1422

1423 **Fig. 4.** Dated phylogeny and historical biogeography of *Papilio*. The maximum clade credibility
1424 tree shows median ages estimated with a Bayesian uncorrelated lognormal method calibrated
1425 with fossils (see Figs S5-7 for additional results). The bottom-left corner map represents the
1426 global paleogeography about 25 Ma with continents delimited into 11 areas. Colored areas on
1427 the map correspond to colored squares for each node, representing inferred ancestral area(s)
1428 with the DEC model, and colored circles at tips, representing present-day distributions. The
1429 outgroups are removed. Asterisks indicate species illustrated on the right. Pictures from Fabien
1430 L. Condamine.

1434 **Fig. 5.** Diversification shifts and diversity dynamics estimated for *Papilio* as estimated by the
 1435 best-fitting combination of shifts. A) The phylogeny of *Papilio* with shifts highlighted in colors
 1436 and best models in parenthesis. Red dots correspond to all tested nodes. B) The evolution of
 1437 diversification rates through time for the backbone and all subclades that are found as
 1438 significant shifts. C) Diversity dynamics for the backbone and subclade trees as estimated with
 1439 the probabilistic approach (dotted line represents the confidence interval of diversity estimates
 1440 for the backbone). For the sake of clarity, confidence intervals of diversity estimates for
 1441 subclades are not represented. D) Global diversity dynamics of *Papilio* obtained by summing
 1442 all the diversity dynamics for the backbone and subclade trees. Pli.=Pliocene, Q=Quaternary,
 1443 Myrs=million years.



1444

1445 **Table 1.** Taxonomic working list for *Papilio* species. The list includes subgenera that are
 1446 currently recovered as monophyletic in molecular phylogenies, and species that belong to each
 1447 subgenus. We also indicate the ratio of species sampled in the phylogeny presented in this study,
 1448 which highlights subgenera that are well sampled versus poorly sampled. In total, genus *Papilio*
 1449 Linnaeus, 1758 includes 235 species, and we sampled 184 species in this study (=78.3%).

<i>Achillides</i> Hübner, [1819] [30 spp.]: 29 spp. sampled in the current study (=96.6%)	Status	In the tree
<i>Papilio (Achillides) arcturus</i> Westwood, 1842	Valid	Sampled
<i>Papilio (Achillides) arjuna</i> Horsfield, 1828	Valid	Sampled
<i>Papilio (Achillides) bianor</i> Cramer, 1777	Valid	Sampled
<i>Papilio (Achillides) blumei</i> Boisduval, 1836	Valid	Sampled
<i>Papilio (Achillides) buddha</i> Westwood, 1872	Valid	Sampled
<i>Papilio (Achillides) chikae</i> Igarashi, 1965	Valid	Sampled
<i>Papilio (Achillides) crino</i> Fabricius, 1793	Valid	Sampled
<i>Papilio (Achillides) daedalus</i> Felder & Felder, 1861	stat. rev. (formerly a subspecies of <i>palinurus</i>)	Sampled
<i>Papilio (Achillides) dehaanii</i> Felder & Felder, 1864	Valid	Sampled
<i>Papilio (Achillides) dialis</i> Leech, 1893	Valid	Sampled
<i>Papilio (Achillides) elephenor</i> Doubleday, 1845	Valid	Unsampled
<i>Papilio (Achillides) hermeli</i> Nuyda, 1992	stat. rev. (formerly a subspecies of <i>chikae</i>)	Sampled
<i>Papilio (Achillides) hermosanus</i> Rebel, 1906	Valid	Sampled
<i>Papilio (Achillides) hopponis</i> Matsumura, 1907	Valid	Sampled
<i>Papilio (Achillides) karna</i> Felder & Felder, 1865	Valid	Sampled
<i>Papilio (Achillides) krishna</i> Moore, [1858]	Valid	Sampled
<i>Papilio (Achillides) lorquinianus</i> Felder & Felder, 1865	Valid	Sampled
<i>Papilio (Achillides) maackii</i> Ménétriés, 1858	Valid	Sampled
<i>Papilio (Achillides) montrouzieri</i> Boisduval, 1859	Valid	Sampled
<i>Papilio (Achillides) neumogeni</i> Honrath, 1890	Valid	Sampled
<i>Papilio (Achillides) orsippus</i> Godman & Salvin, 1888	stat. rev. (formerly a subspecies of <i>ulysses</i>)	Sampled
<i>Papilio (Achillides) palinurus</i> Fabricius, 1787	Valid	Sampled
<i>Papilio (Achillides) paris</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Achillides) peranthus</i> Fabricius, 1787	Valid	Sampled
<i>Papilio (Achillides) pericles</i> Wallace, 1865	Valid	Sampled
<i>Papilio (Achillides) polyctor</i> Boisduval, 1836	stat. rev. (formerly a subspecies of <i>bianor</i>)	Sampled
<i>Papilio (Achillides) ryukyuensis</i> Fujioka, 1975	Valid	Sampled
<i>Papilio (Achillides) syfanius</i> Oberthür, 1886	Valid	Sampled
<i>Papilio (Achillides) telegonus</i> Felder & Felder, 1860	stat. rev. (formerly a subspecies of <i>ulysses</i>)	Sampled
<i>Papilio (Achillides) ulysses</i> Linnaeus, 1758	Valid	Sampled
<i>Alexanoria</i> Koçak and Kemal, 2002 [1 sp.]: 1 sampled in the current study (=100%)	Status	In the tree
<i>Papilio (Alexanoria) alexanor</i> Esper, [1800]	Valid	Sampled
<i>Araminta</i> Moore, 1886 [5 spp.]: 5 sampled in the current study (=100%)	Status	In the tree
<i>Papilio (Araminta) antonio</i> Hewitson, 1875	Valid	Sampled
<i>Papilio (Araminta) demolition</i> Cramer, 1776	Valid	Sampled
<i>Papilio (Araminta) gigon</i> Felder & Felder, 1865	Valid	Sampled
<i>Papilio (Araminta) liomedon</i> Moore, [1875]	Valid	Sampled
<i>Papilio (Araminta) noblei</i> Nicéville, [1889]	Valid	Sampled

<i>Chilasa</i> Moore, [1881] [11 spp.]: 8 sampled in the current study (=72.7%)	Status	In the tree
<i>Papilio (Chilasa) agestor</i> Gray, 1831	Valid	Sampled
<i>Papilio (Chilasa) carolinensis</i> (Jumalon, 1967)	Valid	Unsampled
<i>Papilio (Chilasa) clytia</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Chilasa) epycides</i> Hewitson, 1864	Valid	Sampled
<i>Papilio (Chilasa) laglaizei</i> Depuiset, 1877	Valid	Sampled
<i>Papilio (Chilasa) moerneri</i> Aurivillius, 1919	Valid	Unsampled
<i>Papilio (Chilasa) osmana</i> (Jumalon, 1967)	Valid	Sampled
<i>Papilio (Chilasa) paradoxa</i> Zincken, 1831	Valid	Sampled
<i>Papilio (Chilasa) slateri</i> Hewitson, 1859	Valid	Sampled
<i>Papilio (Chilasa) toboroi</i> Ribbe, 1907	Valid	Unsampled
<i>Papilio (Chilasa) veiovis</i> Hewitson, 1865	Valid	Sampled
<i>Druryia</i> Aurivillius, 1881 [30 spp.]: 9 sampled in the current study (=30%)	Status	In the tree
<i>Papilio (Druryia) andronicus</i> Ward, 1871	Valid	Unsampled
<i>Papilio (Druryia) antimachus</i> Drury, [1782]	Valid	Sampled
<i>Papilio (Druryia) arnoldiana</i> Vane-Wright, 1995	Valid	Unsampled
<i>Papilio (Druryia) bacelarae</i> Bivar de Sousa & Mendes, 2009	Valid	Unsampled
<i>Papilio (Druryia) constantinus</i> Ward, 1871	Valid	Sampled
<i>Papilio (Druryia) cynorta</i> Fabricius, 1793	Valid	Unsampled
<i>Papilio (Druryia) cyproeofila</i> Butler, 1868	Valid	Unsampled
<i>Papilio (Druryia) dardanus</i> Brown, 1776	Valid	Sampled
<i>Papilio (Druryia) delalandei</i> Godart, 1823	Valid	Sampled
<i>Papilio (Druryia) echerioides</i> Trimen, 1868	Valid	Unsampled
<i>Papilio (Druryia) fernandus</i> Fruhstorfer, 1903	Valid	Unsampled
<i>Papilio (Druryia) filaprae</i> Süffert, 1904	Valid	Unsampled
<i>Papilio (Druryia) fuelleborni</i> Karsch, 1900	Valid	Unsampled
<i>Papilio (Druryia) gallienus</i> Distant, 1879	Valid	Unsampled
<i>Papilio (Druryia) humbloti</i> Oberthür, 1888	stat. rev. (formerly a subspecies of <i>dardanus</i>)	Sampled
<i>Papilio (Druryia) jacksoni</i> Sharpe, 1891	Valid	Unsampled
<i>Papilio (Druryia) leucotaenia</i> Rothschild, 1908	Valid	Unsampled
<i>Papilio (Druryia) lormieri</i> Distant, 1874	Valid	Sampled
<i>Papilio (Druryia) mangoura</i> Hewitson, 1875	Valid	Unsampled
<i>Papilio (Druryia) mechowii</i> Dewitz, 1881	Valid	Unsampled
<i>Papilio (Druryia) mechowianus</i> Dewitz, 1885	Valid	Unsampled
<i>Papilio (Druryia) menestheus</i> Drury, [1773]	Valid	Unsampled
<i>Papilio (Druryia) meriones</i> Felder & Felder, 1864	stat. rev. (formerly a subspecies of <i>dardanus</i>)	Sampled
<i>Papilio (Druryia) nobicea</i> Suffert, 1904	Valid	Unsampled
<i>Papilio (Druryia) ophidicephalus</i> Oberthür, 1878	Valid	Unsampled
<i>Papilio (Druryia) phorcus</i> Cramer, 1775	Valid	Sampled
<i>Papilio (Druryia) plagiatus</i> Aurivillius, 1898	Valid	Unsampled
<i>Papilio (Druryia) rex</i> Oberthür, 1886	Valid	Sampled
<i>Papilio (Druryia) sjoestedti</i> Aurivillius, 1908	Valid	Unsampled
<i>Papilio (Druryia) zenobia</i> Fabricius, 1775	Valid	Unsampled
<i>Eleppone</i> Hancock, 1979 [2 spp.]: 2 sampled in the current study (=100%)	Status	In the tree
<i>Papilio (Eleppone) anactus</i> Macleay, 1826	Valid	Sampled

<i>Papilio (Eleppone) natewa</i> Tennent, Chandra & Müller, 2018	Valid	Sampled
<i>Euchenor</i> Igarashi, 1979 [2 spp.]: 2 sampled in the current study (=100%)	Status	In the tree
<i>Papilio (Euchenor) depilis</i> Rothschild, 1895	stat. rev. (formerly a subspecies of <i>euchenor</i>)	Sampled
<i>Papilio (Euchenor) euchenor</i> Guérin-Méneville, 1830	Valid	Sampled
<i>Heraclides</i> Hübner, [1819] [32 spp.]: 32 sampled in the current study (=100%)	Status	In the tree
<i>Papilio (Heraclides) anchicayaensis</i> Constantino, Le Crom & Salazar, 2002	Valid	Sampled
<i>Papilio (Heraclides) anchisiades</i> Esper, [1788]	Valid	Sampled
<i>Papilio (Heraclides) andraemon</i> Hübner, [1823]	Valid	Sampled
<i>Papilio (Heraclides) androgeus</i> Cramer, 1775	Valid	Sampled
<i>Papilio (Heraclides) aristodemus</i> Esper, 1794	Valid	Sampled
<i>Papilio (Heraclides) aristor</i> Godart, 1819	Valid	Sampled
<i>Papilio (Heraclides) astyalus</i> Godart, 1819	Valid	Sampled
<i>Papilio (Heraclides) caiguanabus</i> Poey, 1852	Valid	Sampled
<i>Papilio (Heraclides) chiansiades</i> Westwood, 1872	Valid	Sampled
<i>Papilio (Heraclides) cresphontes</i> Cramer, 1777	Valid	Sampled
<i>Papilio (Heraclides) epenetus</i> Hewitson, 1861	Valid	Sampled
<i>Papilio (Heraclides) erostratus</i> Westwood, 1847	Valid	Sampled
<i>Papilio (Heraclides) garleppi</i> Staudinger, 1892	Valid	Sampled
<i>Papilio (Heraclides) hectorides</i> Esper, 1794	Valid	Sampled
<i>Papilio (Heraclides) himeros</i> Hopffer, 1865	Valid	Sampled
<i>Papilio (Heraclides) homothoas</i> Rothschild & Jordan, 1906	Valid	Sampled
<i>Papilio (Heraclides) hyppason</i> Cramer, 1775	Valid	Sampled
<i>Papilio (Heraclides) isidorus</i> Doubleday, 1846	Valid	Sampled
<i>Papilio (Heraclides) lamarchei</i> Staudinger, 1892	Valid	Sampled
<i>Papilio (Heraclides) machaonides</i> Esper, 1796	Valid	Sampled
<i>Papilio (Heraclides) melonius</i> Rothschild & Jordan, 1906	Valid	Sampled
<i>Papilio (Heraclides) ornythion</i> Boisduval, 1836	Valid	Sampled
<i>Papilio (Heraclides) oviedo</i> Gundlach, 1866	Valid	Sampled
<i>Papilio (Heraclides) oxynius</i> (Geyer, 1827)	Valid	Sampled
<i>Papilio (Heraclides) paeon</i> Boisduval, 1836	Valid	Sampled
<i>Papilio (Heraclides) pallas</i> Gray, [1853]	Valid	Sampled
<i>Papilio (Heraclides) pelaus</i> Fabricius, 1775	Valid	Sampled
<i>Papilio (Heraclides) rogeri</i> Boisduval, 1836	Valid	Sampled
<i>Papilio (Heraclides) rumiko</i> (Shiraiwa & Grishin, 2014)	Valid	Sampled
<i>Papilio (Heraclides) thersites</i> Fabricius, 1775	Valid	Sampled
<i>Papilio (Heraclides) thoas</i> Linnaeus, 1771	Valid	Sampled
<i>Papilio (Heraclides) torquatus</i> Cramer, 1777	Valid	Sampled
<i>Menelaides</i> Hübner, [1819] [54 spp.]: 52 sampled in the current study (=96.5%)	Status	In the tree
<i>Papilio (Menelaides) acheron</i> Grose-Smith, 1887	Valid	Sampled
<i>Papilio (Menelaides) aegaeus</i> Donovan, 1805	Valid	Sampled
<i>Papilio (Menelaides) agenor</i> Linnaeus, 1758	stat. rev. (formerly a subspecies of <i>memnon</i>)	Sampled
<i>Papilio (Menelaides) albinus</i> Wallace, 1865	Valid	Sampled
<i>Papilio (Menelaides) alcmenor</i> Felder & Felder, 1865	Valid	Sampled
<i>Papilio (Menelaides) alphenor</i> Cramer, 1776	stat. rev. (formerly a subspecies of <i>polytes</i>)	Sampled
<i>Papilio (Menelaides) ambrax</i> Boisduval, 1832	stat. rev. (formerly a subspecies of <i>phestus</i>)	Sampled

<i>Papilio (Menelaides) amynthor</i> Boisduval, 1859	Valid	Sampled
<i>Papilio (Menelaides) ascalaphus</i> Boisduval, 1836	Valid	Sampled
<i>Papilio (Menelaides) biseriatus</i> Rothschild, 1895	stat. rev. (formerly a subspecies of <i>helenus</i>)	Sampled
<i>Papilio (Menelaides) bootes</i> Westwood, 1842	Valid	Sampled
<i>Papilio (Menelaides) bridgei</i> Mathew, 1886	Valid	Sampled
<i>Papilio (Menelaides) canopus</i> Westwood, 1842	stat. rev. (formerly a subspecies of <i>fuscus</i>)	Sampled
<i>Papilio (Menelaides) capaneus</i> Westwood, 1843	stat. rev. (formerly a subspecies of <i>fuscus</i>)	Sampled
<i>Papilio (Menelaides) castor</i> Westwood, 1842	Valid	Sampled
<i>Papilio (Menelaides) chaon</i> Westwood, 1844	stat. rev. (formerly a subspecies of <i>nepheles</i>)	Sampled
<i>Papilio (Menelaides) cilix</i> Godman & Salvin, 1879	stat. rev. (formerly a subspecies of <i>fuscus</i>)	Sampled
<i>Papilio (Menelaides) daksha</i> Moore, [1889]	stat. rev. (formerly a subspecies of <i>helenus</i>)	Sampled
<i>Papilio (Menelaides) deiphobus</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Menelaides) diophantus</i> Grose-Smith, 1883	Valid	Sampled
<i>Papilio (Menelaides) dravidarum</i> Wood-Mason, 1880	Valid	Sampled
<i>Papilio (Menelaides) erskinei</i> Mathew, 1886	Valid	Unsampled
<i>Papilio (Menelaides) forbesi</i> Grose-Smith, 1883	Valid	Sampled
<i>Papilio (Menelaides) fuscus</i> Goeze, 1779	Valid	Sampled
<i>Papilio (Menelaides) gambrisius</i> Cramer, 1777	Valid	Sampled
<i>Papilio (Menelaides) godeffroyi</i> Semper, 1866	Valid	Sampled
<i>Papilio (Menelaides) helenus</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Menelaides) heringi</i> Niepelt, 1924	Valid	Sampled
<i>Papilio (Menelaides) hipponous</i> Felder & Felder, 1862	Valid	Sampled
<i>Papilio (Menelaides) hypsicles</i> Hewitson, 1868	stat. rev. (formerly a subspecies of <i>fuscus</i>)	Sampled
<i>Papilio (Menelaides) hystaspes</i> Felder & Felder, 1862	stat. rev. (formerly a subspecies of <i>helenus</i>)	Sampled
<i>Papilio (Menelaides) iswara</i> White, 1842	Valid	Sampled
<i>Papilio (Menelaides) iswaroides</i> Fruhstorfer, 1898	Valid	Sampled
<i>Papilio (Menelaides) janaka</i> Moore, 1857	stat. rev. (formerly a subspecies of <i>bootes</i>)	Sampled
<i>Papilio (Menelaides) javanus</i> Felder, 1862	stat. nov. (formerly a subspecies of <i>polytes</i>)	Sampled
<i>Papilio (Menelaides) jordani</i> Fruhstorfer, 1902	Valid	Sampled
<i>Papilio (Menelaides) lampsacus</i> Boisduval, 1836	Valid	Unsampled
<i>Papilio (Menelaides) macilentus</i> Janson, 1877	Valid	Sampled
<i>Papilio (Menelaides) mangarinus</i> Rothschild, 1908	stat. nov. (formerly a subspecies of <i>helenus</i>)	Sampled
<i>Papilio (Menelaides) memnon</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Menelaides) nepheles</i> Boisduval, 1836	Valid	Sampled
<i>Papilio (Menelaides) oenomaus</i> Godart, 1819	Valid	Sampled
<i>Papilio (Menelaides) oritas</i> Godman & Salvin, 1879	stat. rev. (formerly a subspecies of <i>aegeus</i>)	Sampled
<i>Papilio (Menelaides) palawanicus</i> Staundinger 1888	stat. nov. (formerly a subspecies of <i>helenus</i>)	Sampled
<i>Papilio (Menelaides) phestus</i> Guérin-Ménéville, 1830	Valid	Sampled
<i>Papilio (Menelaides) polytes</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Menelaides) prexaspes</i> Felder & Felder, 1865	Valid	Sampled
<i>Papilio (Menelaides) protenor</i> Cramer, 1775	Valid	Sampled
<i>Papilio (Menelaides) sataspes</i> Felder & Felder, 1865	Valid	Sampled
<i>Papilio (Menelaides) schmeltzi</i> Herrich-Schäffer, 1869	Valid	Sampled
<i>Papilio (Menelaides) thaiwanus</i> Rothschild, 1898	Valid	Sampled
<i>Papilio (Menelaides) tydeus</i> Felder & Felder, 1860	Valid	Sampled
<i>Papilio (Menelaides) weymeri</i> Niepelt, 1914	Valid	Sampled

<i>Papilio (Menelaides) woodfordi</i> Godman & Salvin, 1888	Valid	Sampled
<i>Nireopapilio</i> Cotton & Nakae, 2020 [24 spp.]: 5 sampled in the current study (=20.8%)	Status	In the tree
<i>Papilio (Nireopapilio) aristophontes</i> Oberthür, 1897	Valid	Unsampled
<i>Papilio (Nireopapilio) charopus</i> Westwood, 1843	Valid	Unsampled
<i>Papilio (Nireopapilio) chitondensis</i> Bivar de Sousa & Fernandes, 1966	Valid	Unsampled
<i>Papilio (Nireopapilio) chrapkowskii</i> Suffert, 1904	Valid	Unsampled
<i>Papilio (Nireopapilio) chrapkowskoides</i> Storace, 1952	Valid	Unsampled
<i>Papilio (Nireopapilio) desmondi</i> van Someren, 1939	Valid	Unsampled
<i>Papilio (Nireopapilio) epiphorbas</i> Boisduval, 1833	Valid	Sampled
<i>Papilio (Nireopapilio) euphranor</i> Trimen, 1868	Valid	Unsampled
<i>Papilio (Nireopapilio) hesperus</i> Westwood, 1843	Valid	Unsampled
<i>Papilio (Nireopapilio) hornimani</i> Distant, 1879	Valid	Unsampled
<i>Papilio (Nireopapilio) horribilis</i> Butler, [1872]	Valid	Unsampled
<i>Papilio (Nireopapilio) interjectana</i> Vane-Wright, 1995	Valid	Unsampled
<i>Papilio (Nireopapilio) mackinnoni</i> Sharpe, 1891	Valid	Unsampled
<i>Papilio (Nireopapilio) manlius</i> Fabricius, 1798	Valid	Unsampled
<i>Papilio (Nireopapilio) microps</i> Storace, 1951	Valid	Unsampled
<i>Papilio (Nireopapilio) nireus</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Nireopapilio) nobilis</i> Rogenhofer, 1891	Valid	Sampled
<i>Papilio (Nireopapilio) oribazus</i> Boisduval, 1836	Valid	Sampled
<i>Papilio (Nireopapilio) pelodurus</i> Butler, [1896]	Valid	Unsampled
<i>Papilio (Nireopapilio) phorbanta</i> Linnaeus, 1771	Valid	Unsampled
<i>Papilio (Nireopapilio) sosia</i> Rothschild & Jordan, 1903	Valid	Unsampled
<i>Papilio (Nireopapilio) thurau</i> Karsch, 1900	Valid	Unsampled
<i>Papilio (Nireopapilio) ufipa</i> Carcasson, 1961	Valid	Unsampled
<i>Papilio (Nireopapilio) zalmoxis</i> Hewitson, [1864]	Valid	Sampled
<i>Papilio</i> Linnaeus, 1758 [9 spp.]: 9 sampled in the current study (=100%)	Status	In the tree
<i>Papilio (Papilio) bairdii</i> Edwards, 1866	stat. rev. (formerly a subspecies of <i>machaon</i>)	Sampled
<i>Papilio (Papilio) brevicauda</i> Saunders, 1868	Valid	Sampled
<i>Papilio (Papilio) hospiton</i> Gén�, 1839	Valid	Sampled
<i>Papilio (Papilio) indra</i> Reakirt, 1866	Valid	Sampled
<i>Papilio (Papilio) joanae</i> Heitzman, 1974	Valid	Sampled
<i>Papilio (Papilio) kahli</i> Chermock & Chermock, 1937	stat. nov. (formerly a subspecies of <i>machaon</i>)	Sampled
<i>Papilio (Papilio) machaon</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Papilio) polyxenes</i> Fabricius, 1775	Valid	Sampled
<i>Papilio (Papilio) zelicaon</i> Lucas, 1852	Valid	Sampled
<i>Princeps</i> H�bner, [1807] [5 spp.]: 5 sampled in the current study (=100%)	Status	In the tree
<i>Papilio (Princeps) demodocus</i> Esper, 1799	Valid	Sampled
<i>Papilio (Princeps) demoleus</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Princeps) erithonioides</i> Grose-Smith, 1891	Valid	Sampled
<i>Papilio (Princeps) grosesmithi</i> Rothschild, 1926	Valid	Sampled
<i>Papilio (Princeps) morondavana</i> Grose-Smith, 1891	Valid	Sampled
<i>Pterourus</i> Scopoli, 1777 [28 spp.]: 23 sampled in the current study (=82.1%)	Status	In the tree
<i>Papilio (Pterourus) alexiaries</i> Hopffer, 1865	Valid	Unsampled
<i>Papilio (Pterourus) appalachiensis</i> (Pavulaan & Wright, 2002)	Valid	Sampled

<i>Papilio (Pterourus) ascolius</i> Felder & Felder, 1864	Valid	Unsampled
<i>Papilio (Pterourus) bachus</i> Felder & Felder, 1865	Valid	Unsampled
<i>Papilio (Pterourus) birchallii</i> Hewitson, 1863	Valid	Sampled
<i>Papilio (Pterourus) cacicus</i> Lucas, 1852	Valid	Sampled
<i>Papilio (Pterourus) canadensis</i> Rothschild & Jordan, 1906	Valid	Sampled
<i>Papilio (Pterourus) elwesi</i> Leech, 1889	Valid	Sampled
<i>Papilio (Pterourus) esperanza</i> Beutelspacher, 1975	Valid	Sampled
<i>Papilio (Pterourus) eurymedon</i> Lucas, 1852	Valid	Sampled
<i>Papilio (Pterourus) euterpinus</i> Salvin & Godman, 1868	Valid	Sampled
<i>Papilio (Pterourus) garamas</i> (Geyer, [1829])	Valid	Sampled
<i>Papilio (Pterourus) glaucus</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Pterourus) hellanichus</i> Hewitson, 1868	Valid	Unsampled
<i>Papilio (Pterourus) homerus</i> Fabricius, 1793	Valid	Sampled
<i>Papilio (Pterourus) maraho</i> Shiraki & Sonan, 1934	Valid	Sampled
<i>Papilio (Pterourus) menatius</i> (Hübner, [1819])	Valid	Sampled
<i>Papilio (Pterourus) multicaudata</i> Kirby, 1884	Valid	Sampled
<i>Papilio (Pterourus) neyi</i> Niepelt, 1909	Valid	Sampled
<i>Papilio (Pterourus) palamedes</i> Drury, 1773	Valid	Sampled
<i>Papilio (Pterourus) pilumnus</i> Boisduval, 1836	Valid	Sampled
<i>Papilio (Pterourus) rutulus</i> Lucas, 1852	Valid	Sampled
<i>Papilio (Pterourus) scamander</i> Boisduval, 1836	Valid	Sampled
<i>Papilio (Pterourus) troilus</i> Linnaeus, 1758	Valid	Sampled
<i>Papilio (Pterourus) victorinus</i> Doubleday, 1844	stat. rev. (formerly a subspecies of <i>menatius</i>)	Sampled
<i>Papilio (Pterourus) warscewiczii</i> Hopffer, 1865	Valid	Sampled
<i>Papilio (Pterourus) xanthopleura</i> Salvin & Godman, 1868	Valid	Unsampled
<i>Papilio (Pterourus) zagreus</i> Doubleday, 1847	Valid	Sampled

***Sinoprinceps* Hancock, 1983 [2 spp.]: 2 sampled in the current study (=100%)**

Status

In the tree

<i>Papilio (Sinoprinceps) benguetana</i> Joicey & Talbot, 1923	stat. rev. (formerly a subspecies of <i>xuthus</i>)	Sampled
<i>Papilio (Sinoprinceps) xuthus</i> Linnaeus, 1767	Valid	Sampled

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1452 **Table 2.** Bayesian tests of topology hypotheses using the stepping-stone sampling (SS). The topology was constrained with previously inferred
1453 relationships (Zakharov *et al.*, 2004) that were not recovered in our best topology. The SS estimated the marginal likelihood for each topology and
1454 was compared to the marginal likelihood of the best topology (unconstrained). The marginal likelihood is used to calculate Bayes factors to select
1455 the topology for the dataset. Results for BF are as follows: non-significant ($0 < \text{BF} < 2$), positive support ($2 < \text{BF} < 6$), strong support ($6 < \text{BF} < 10$), and
1456 very strong support ($\text{BF} > 10$).
1457

Hypothesis tests on various systematic positions	Marginal likelihood (SS)	Bayes factor
Unconstrained MrBayes phylogenetic analysis	-97,079.39	-
Monophyly of the subgenus <i>Pterourus</i> (i.e. excluding <i>Agehana</i>)	-97,127.68	48.29
Monophyly of the subgenus <i>Druryia</i> (i.e. <i>Druryia</i> + <i>Nireopapilio</i>)	-97,269.70	190.31
Monophyly of the subgenus <i>Princeps</i> (i.e. <i>Princeps</i> + <i>dardanus</i> sp. gr.)	-97,277.63	198.24
Monophyly of the subgenus <i>Menelaides</i> (i.e. <i>Menelaides</i> + <i>Araminta</i>)	-97,145.29	65.9
Monophyly of the New World <i>Papilio</i>	-97,094.08	14.69
<i>P. alexanor</i> sister to <i>Agehana</i> + <i>Chilasa</i> + <i>Pterourus</i>	-97,141.38	61.99

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1460 **Table 3.** Phylogenetic, dating, and biogeographic results for the main nodes of *Papilio*. Clades 1 to 3 are shown in Fig. 3.

Clades	Node supports				Median node ages, Ma (95% CI)		Ancestral area estimates	Biogeographic interpretation
	PP _{CAT}	PP _{PART}	BS _{PART}	UFBS _{PART}	Fossil calibrations	Secondary calibrations		
<i>Papilio sensu lato</i>	1	1	100	100	30.06 (20.66 – 47.42)	29.95 (23.97 – 37.34)	EP + WN + CA + WA	Origin centred on Beringia
Clade 1: <i>Heraclides</i>	1	0.96	75	100	21.22 (13.95 – 33.86)	21.2 (16.07 – 27.48)	CA	Central America
Clade 2: <i>Papilio sensu lato</i> excl. <i>Heraclides</i>	0.75	0.98	55	90	28.57 (19.98 – 45.45)	28.5 (22.89 – 35.55)	EP + WN + CA + WA	Origin centred on Beringia
<i>Chilasa</i> + <i>Pterourus</i> + ‘ <i>Agehana</i> ’	0.99	1	91	100	22.73 (15.36 – 35.9)	22.64 (17.33 – 28.74)	EP + WN + CA + WA	Origin centred on Beringia
<i>Chilasa</i>	1	1	99	100	16.68 (12.49 – 29.71)	18.63 (14.02 – 24.44)	WA	Indonesia
<i>Pterourus</i> + ‘ <i>Agehana</i> ’	1	1	79	99	20.38 (13.8 – 32.28)	20.3 (15.3 – 25.92)	EP + WN + CA	Origin centred on Beringia
‘ <i>Agehana</i> ’	1	1	100	100	0.28 (0.09 – 0.63)	0.27 (0.09 – 0.53)	EP + WA	Asia and Indonesia
Clade 3: Old World <i>Papilio</i>	1	0.99	58	85	26.93 (18.62 – 42.62)	26.86 (21.52 – 33.51)	EP	East Palearctic
Old World <i>Papilio</i> excl. <i>Alexanoria</i>	1	1	86	100	23.74 (16.45 – 37.49)	23.67 (18.96 – 29.58)	WP + EP + AF + WA	Paleotropics
Clade 3a: <i>Druryia</i> + <i>Euchenor</i>	0.82	0.99	74	99	22.32 (15.3 – 35.23)	22.23 (17.46 – 27.95)	WP + EP + AF + WA	Paleotropics
<i>Euchenor</i>	1	1	100	100	5.49 (2.74 – 9.71)	5.33 (2.84 – 8.42)	AU	Australasia
<i>Druryia</i>	1	1	99	100	17.95 (12.07 – 28.62)	17.88 (13.61 – 22.95)	AF	Afrotropics
Clade 3b: <i>Eleppone</i> + <i>Araminta</i>	-	0.72	50	93	21.09 (14.82 – 33.9)	20.99 (16.4 – 26.47)	WA	Indonesia
<i>Eleppone</i>	1	1	97	100	9.72 (4.41 – 17.0)	9.54 (4.77 – 15.03)	AU	Australasia
<i>Araminta</i>	1	1	100	100	14.07 (8.87 – 22.59)	13.9 (9.89 – 18.61)	WA	Indonesia
Clade 3c + Clade 3d + Clade 3e	0.99	1	72	99	21.35 (15.08 – 33.97)	21.25 (16.97 – 26.59)	WP + EP + AF + WA	Paleotropics
Clade 3c: <i>Sinoprinceps</i> + <i>Papilio sensu stricto</i>	1	1	97	100	17.39 (11.36 – 27.85)	17.27 (13.1 – 22.34)	EP	East Palearctic
<i>Sinoprinceps</i>	1	1	100	100	1.5 (0.63 – 2.82)	1.44 (0.67 – 2.45)	EP + WA	Asia and Indonesia
<i>Papilio sensu stricto</i>	1	1	100	100	10.3 (6.26 – 16.69)	10.2 (7.01 – 13.85)	EP + WN	Origin centred on Beringia
Clade 3d + Clade 3e	0.99	1	60	99	20.17 (14.01 – 31.92)	20.09 (16.09 – 25.23)	WP + EP + AF + WA	Paleotropics
Clade 3d: <i>Nireopapilio</i>	1	1	76	98	16.1 (10.21 – 25.51)	15.98 (11.78 – 20.65)	AF	Afrotropics
Clade 3e: <i>Achillides</i> + <i>Princeps</i> + <i>Menelaides</i>	-	0.91	54	96	19.52 (13.5 – 30.98)	19.41 (15.57 – 24.39)	WP + EP + AF + WA	Paleotropics
<i>Achillides</i>	1	1	85	99	17.1 (11.45 – 26.88)	17.0 (13.31 – 21.62)	WA + AU	Indonesia and Australasia
<i>Princeps</i> + <i>Menelaides</i>	0.93	1	70	99	18.21 (12.6 – 29.05)	18.15 (14.37 – 22.86)	WP + EP + AF + WA	Paleotropics
<i>Princeps</i>	1	1	100	100	11.29 (6.93 – 18.01)	11.21 (8.0 – 14.97)	WP + EP + AF + MD	Paleotropics
<i>Menelaides</i>	1	1	99	100	13.94 (9.4 – 21.98)	13.94 (10.9 – 17.65)	WA	Indonesia

1462 **Table 4.** Changes to subspecies nomenclature resulting from literature review and this study.
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Species	New subspecies combinations
<i>Papilio (Achillides) orsippus</i> Godman & Salvin, 1888 (stat. rev.)	<i>Papilio orsippus orsippus</i> Godman & Salvin, 1888 <i>Papilio orsippus ambiguus</i> Rothschild, 1895 (comb. nov.) <i>Papilio orsippus gabrielis</i> Rothschild, 1898 (comb. nov.) <i>Papilio orsippus kallinikos</i> Fruhstorfer, 1903 (comb. nov.) <i>Papilio orsippus rothschildianus</i> Fruhstorfer, 1909 (comb. nov.)
<i>Papilio (Achillides) telegonus</i> C. Felder & R. Felder, 1860 (stat. rev.)	<i>Papilio telegonus telegonus</i> C. Felder & R. Felder, 1860 <i>Papilio telegonus dohertius</i> Rothschild, 1898 (comb. nov.) <i>Papilio telegonus morotaicus</i> Rothschild, 1908 (comb. nov.)
<i>Papilio (Euchenor) depilis</i> Rothschild, 1895 (stat. rev.)	<i>Papilio depilis depilis</i> Rothschild, 1895 <i>Papilio depilis neohannoveranus</i> Rothschild, 1898 (comb. nov.) <i>Papilio depilis novohibernicus</i> Rothschild, 1898 (comb. nov.)
<i>Papilio (Menelaides) aegeus</i> Donovan, 1805	<i>Papilio aegeus inopinatus</i> Butler, 1883 (comb. nov.) <i>Papilio aegeus komos</i> Fruhstorfer, 1904 (comb. nov.)
<i>Papilio (Menelaides) agenor</i> Linnaeus, 1758 (stat. rev.)	<i>Papilio agenor agenor</i> Linnaeus, 1758 <i>Papilio agenor polymnestor</i> Cramer, 1775 (comb. nov.) <i>Papilio agenor parinda</i> (Moore, 1881) (comb. nov.) <i>Papilio agenor nicobarensis</i> Hachitani, 1986 (comb. nov.) <i>Papilio agenor heronus</i> Fruhstorfer, 1902 (comb. nov.) <i>Papilio agenor iriomotensis</i> Fujioka, 2012 (comb. nov.) <i>Papilio agenor thunbergii</i> Siebold, 1824 (comb. nov.)
<i>Papilio (Menelaides) capaneus</i> Westwood, 1843 (stat. rev.)	<i>Papilio capaneus capaneus</i> Westwood, 1843 <i>Papilio capaneus beccarii</i> Oberthür, 1880 (comb. nov.) <i>Papilio capaneus gyrei</i> Tennent, 1999 (comb. nov.) <i>Papilio capaneus hasterti</i> Ribbe, 1907 (comb. nov.) <i>Papilio capaneus indicatus</i> Butler, 1876 (comb. nov.) <i>Papilio capaneus relmae</i> Tennent, 1999 (comb. nov.) <i>Papilio capaneus rotalita</i> (Swinhoe, 1893) (comb. nov.)

	<i>Papilio capaneus xenophilus</i> Mathew, 1886 (comb. nov.)
<i>Papilio (Menelaides) chaon</i> Westwood, 1844 (stat. rev.)	<i>Papilio chaon chaon</i> Westwood, 1844 <i>Papilio chaon annulus</i> Pendlebury, 1936 (comb. nov.) <i>Papilio chaon chaonulus</i> Fruhstorfer, 1902 (comb. rev.) <i>Papilio chaon rileyi</i> Fruhstorfer, 1913 (comb. rev.)
<i>Papilio (Menelaides) cilix</i> Godman & Salvin, 1879 (stat. rev.)	<i>Papilio cilix cilix</i> Godman & Salvin, 1879 <i>Papilio cilix lamponius</i> Fruhstorfer, 1904 (comb. nov.)
<i>Papilio (Menelaides) daksha</i> Moore, [1889] (stat. rev.)	<i>Papilio daksha daksha</i> Moore, [1889] <i>Papilio daksha mooreanus</i> Rothschild, 1895 (comb. nov.)
<i>Papilio (Menelaides) javanus</i> C. Felder, 1862 (stat. nov.)	<i>Papilio javanus javanus</i> C. Felder, 1862 <i>Papilio javanus theseus</i> Cramer, 1777 (comb. nov.) <i>Papilio javanus melanides</i> Haan, 1840 (comb. nov.) <i>Papilio javanus vigellius</i> Fruhstorfer, 1909 (comb. nov.) <i>Papilio javanus messius</i> Fruhstorfer, 1909 (comb. nov.) <i>Papilio javanus sotira</i> Jordan, 1909 (comb. nov.) <i>Papilio javanus timorensis</i> C. Felder & R. Felder, 1864 (comb. nov.) <i>Papilio javanus alcindor</i> Oberthür, 1879 (comb. nov.) <i>Papilio javanus kurokawai</i> Nakae, 2013 (comb. nov.) <i>Papilio javanus tucanus</i> Jordan, 1909 (comb. nov.)
<i>Papilio (Menelaides) mangarinus</i> Rothschild, 1908 (stat. nov.)	<i>Papilio mangarinus mangarinus</i> Rothschild, 1908 <i>Papilio mangarinus jindanus</i> Rothschild, 1908 (comb. nov.) <i>Papilio mangarinus tambora</i> Rothschild, 1908 (comb. nov.)
<i>Papilio (Menelaides) memnon</i> Linnaeus, 1758	<i>Papilio memnon memnon</i> Linnaeus, 1758 <i>Papilio memnon mayo</i> Atkinson, 1874 (comb. nov.)
<i>Papilio (Menelaides) oritas</i> Godman & Salvin, 1879 (stat. rev.)	<i>Papilio oritas oritas</i> Godman & Salvin, 1879 <i>Papilio oritas websteri</i> Grose-Smith, 1894 (comb. nov.) <i>Papilio oritas byronensis</i> Talbot, 1932 (comb. nov.)
<i>Papilio (Menelaides) palawanicus</i> Staudinger, 1888 (stat. nov.)	<i>Papilio palawanicus palawanicus</i> Staudinger, 1888 <i>Papilio palawanicus enganius</i> Doherty, 1891 (comb. nov.) <i>Papilio palawanicus sinabangana</i> Goode & Burk, 2013 (comb. nov.) <i>Papilio palawanicus boloboca</i> Page & Treadaway, 1996 (comb. nov.)

Papilio (Papilio) bairdii Edwards, 1866 (**stat. rev.**)

Papilio bairdii bairdii Edwards, 1866

Papilio bairdii oregonia Edwards, 1876 (**comb. nov.**)

Papilio bairdii dodi McDunnough, 1939 (**comb. nov.**)

Papilio (Pterourus) victorinus Doubleday, 1844 (**stat. rev.**)

Papilio victorinus victorinus Doubleday, 1844

Papilio victorinus morelius Rothschild & Jordan, 1906 (**stat. rev.**)

Papilio victorinus vulneratus Butler, 1872 (**stat. rev.**)

1464

1465

1466 **Supplementary Information**

1467

1468 **Figure S1.** Maximum-likelihood phylogeny of *Papilio*. This phylogeny was inferred with IQ-
1469 TREE using a traditional partitioning strategy and non-parametric bootstraps (BS) to estimate
1470 branch supports (values ≥ 70 are considered as strong support). The outgroups are removed.

1471

1472 **Figure S2.** Maximum-likelihood phylogeny of *Papilio*. This phylogeny was inferred with IQ-
1473 TREE using a traditional partitioning strategy and ultrafast bootstraps (UFBS) to estimate
1474 branch supports (values ≥ 95 are considered as strong support). The outgroups are removed.

1475

1476 **Figure S3.** Bayesian phylogeny of *Papilio*. This phylogeny was inferred with PhyloBayes using
1477 a mixture model for site heterogeneity and posterior probabilities to estimate branch supports
1478 (values ≥ 0.95 are considered as strong support). The outgroups are removed.

1479

1480 **Figure S4.** Branch support for phylogenetic analyses of *Papilio*. Histograms show that the
1481 phylogeny of *Papilio* is generally robust, but several branches, in particular in the backbone,
1482 remain unresolved. Percentages of strongly supported branches and branches with maximal
1483 support as well as mean and median branch supports are reported for each analysis with
1484 corresponding thresholds considered as strong supports.

1485

1486 **Figure S5.** Bayesian divergence times of *Papilio* estimated with three fossil calibrations. The
1487 time-calibrated tree was inferred with BEAST and uniform priors set on fossil ages. The same
1488 partitioning strategy used for phylogenetic reconstructions was used, and an uncorrelated
1489 lognormal clock model was used for each partition.

1490

1491 **Figure S6.** Bayesian divergence times of *Papilio* estimated with eight secondary calibrations.
1492 The time-calibrated tree was inferred with BEAST and uniform priors set on secondary
1493 calibrations. Secondary calibrations were retrieved from a study of Papilionidae (Allio *et al.*,
1494 2021; see *Material and Methods*). The same partitioning strategy used for phylogenetic
1495 reconstructions was used, and an uncorrelated lognormal clock model was used for each
1496 partition.

1497

1498 **Figure S7.** Diversification shifts and diversity dynamics estimated for *Papilio* as estimated by
1499 the third best-fitting combination of shifts. A) The phylogeny of *Papilio* with shifts highlighted

1500 in colors and best models in parenthesis. Red dots correspond to all tested nodes. B) The
1501 evolution of diversification rates through time for the backbone and all subclades that are found
1502 as significant shifts. C) Diversity dynamics for the backbone and subclade trees as estimated
1503 with the probabilistic approach (dotted line represents the confidence interval of diversity
1504 estimates for the backbone). For the sake of clarity, confidence intervals of diversity estimates
1505 for subclades are not represented. D) Global diversity dynamics of *Papilio* obtained by
1506 summing all the diversity dynamics for the backbone and subclade trees.

1507

1508 **Table S1.** Geographic distribution of *Papilio* species. The tables include the geographic data
1509 for (1) all species listed in Table 1, and (2) the species that have been sampled in the current
1510 phylogenetic tree. We coded the presence (1) or absence (0) in each of the 11 defined
1511 biogeographic regions. Histogram plots show the number of species per region.

1512

1513 **Table S2.** Results of macroevolutionary analyses. A) Global comparison of combinations of
1514 diversification shifts for the *Papilio* genus (shifts are tested at the crown) with B) the rates of
1515 the diversification model for their backbones. The best combination of shift and the phylogeny
1516 analyzed with no shift are highlighted in bold. NP=Number of parameters,
1517 $\log L = \log(\text{Likelihood})$, λ =speciation rate (at present if variable), α =dependency parameter of
1518 speciation rate, μ =extinction rate, β =dependency parameter of extinction rate.

1519

1520 **Table S3.** Comparisons of diversification models for each subclade. The best models are
1521 highlighted in bold. NP=Number of parameters, $\log L = \log(\text{Likelihood})$, λ =speciation rate (at
1522 present if variable), α =dependency parameter of speciation rate, μ =extinction rate,
1523 β =dependency parameter of extinction rate.

1524