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Title

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

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

Abstract

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

Keywords:

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

1. Introduction

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

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

The first classifications of *Papilio* species relied on morphological characters (summarized in Zakharov *et al.*, 2004a: table 1). Munroe (1961) divided *Papilio* into five sections but did not designate them as subgenera because they lacked a simple diagnosis with adult characters. Using an explicitly cladistic estimation of relationships within *Papilio*, Hancock (1983) recognized six genera (*Chilasa*, *Eleppone*, *Heraclides*, *Papilio*, *Princeps*, and *Pterourus*) based on phylogenetic evidence and inferred evolutionary antiquity, but this phylogeny also suffered from lack of character justification. Another classification was proposed by Igarashi (1984) based on the morphology of immature stages, but this work did not represent all of Hancock's genera. Igarashi (1984) nonetheless recognized seven genera (*Achillides*, *Agehana*, *Chilasa*, *Euchenor*, *Menelaides*, *Papilio*, and *Pterourus*), with numerous discrepancies between his treatment and that of Hancock (1983). Hancock's classification was criticized by Miller (1987), who did not consider elevation of *Papilio* subdivisions to the genus level to be justified. However, one group within *Papilio* was elevated in a widely available checklist of swallowtail butterflies (Haüser *et al.*, 2005), where *Chilasa* was treated as a distinct genus. It has been challenging to apply the rules of the PhyloCode in designating subgroups within *Papilio* to generic status as it has proven difficult to find morphological synapomorphies as required by the PhyloCode (Cantino and de Queiroz, 2020). The sole use of genetic data to delimit taxa has not been adequately addressed by the PhyloCode.

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

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

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

2. Materials and methods

2.1. Taxon sampling and molecular data

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

We assembled a supermatrix dataset with data extracted from Sanger sequencing and genome sequencing available on GenBank as of September 2021. The molecular data mainly came from previous studies (e.g. Zakharov *et al.*, 2004a, 2004b; Condamine *et al.*, 2012, 2013a, 2013b; Lewis *et al.*, 2015; Wu *et al.*, 2015; Owens *et al.*, 2017, 2020; Allio *et al.*, 2021; Joshi and Kunte, 2022). We used five mitochondrial gene fragments (*COI*, *COII*, *ND1*, *ND5* and *rRNA 16S*) and two nuclear gene fragments (*EF-1a* and *Wg*), chosen based on their availability among *Papilio* species. We aligned the DNA sequences for the rRNA 16S using MAFFT 7.110 (Katoh and Standley, 2013) with the E-INS-i algorithm, while we aligned the coding genes using MACSE 2.00 (Ranwez *et al.*, 2011) with the *alignSequences* subprogram and default options. All the resulting alignments were checked for codon stops and eventually refined by eye with Mesquite 3.7 (Maddison and Maddison, 2021). All gene alignments were concatenated into a nucleotide supermatrix, which is available in FigShare (Data 1: https://figshare.com/s/a32288db7e6429714a62).

2.2. Inferring phylogenetic relationships

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

BI analyses were performed using MrBayes 3.2.7a (Ronquist *et al.*, 2012). Because ModelFinder includes more substitution models than BEAST or MrBayes, the most likely partitioning scheme and substitution models can be altered, the molecular dataset was analyzed with PartitionFinder 2.1.1 (Lanfear *et al.*, 2017) to estimate the best partition scheme with an initial subset of 19 possible partitions (all three codon positions for coding sequences and non-coding genes treated separately). Partitions and corresponding optimal substitution models were searched using the *greedy* algorithm, the *mrbayes* set of models, and the Bayesian Information Criterion (BIC) to compare the fit of different models. We used reversible-jump Markov chain Monte Carlo (rjMCMC) to sample the entire space of possible models instead of using the *a priori* substitution models recovered by PartitionFinder (Huelsenbeck *et al.*, 2004). MrBayes analyses were performed with two separate runs, a random starting tree, and eight rjMCMC (one cold and seven incrementally heated, *temp=0.1*) running for 30 million generations with tree sampling occurring every 3,000 generations (resulting in 10,000 trees) to calculate the clade posterior probabilities (PP_{PART}). We also specified (1) a uniform prior probability of phylogenies (i.e. all possible trees are considered *a priori* equally probable), and (2) a uniform prior probability distribution on branch lengths. Convergence of the Bayesian runs was ensured by checking the average deviation of split frequencies (ADSF), the potential scale reduction factor (PSRF) values, the effective sample size (ESS) of all parameters, and by plotting the log-likelihood of the samples against the number of generations in Tracer 1.7.1 (Rambaut *et al.*, 2018). The runs had to have values of ADSF approaching zero, PSRF close to 1.0 and ESS above 200 to assume convergence. All trees that predated the time needed to reach a log-likelihood plateau were discarded as burn-in, and the remaining samples were used to generate a 50% majority rule consensus tree (option *halfcompat*). Branch support was estimated and $PP_{PART} \geq 0.95$ was considered to indicate strong support for a given clade (Douady *et al.*, 2003). All MrBayes analyses were performed on the computer cluster CIPRES Science Gateway (Miller *et al.*, 2015), using BEAGLE (Ayres *et al.*, 2012) with default parameters.

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

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

2.3. Testing topology hypotheses

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

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

2.4. Estimation of divergence times

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

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

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

2.5. Fossil and secondary calibrations

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

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

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

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

2.6. Inference of historical biogeography

We estimated the ancestral ranges of origin and geographic range evolution for *Papilio* using the ML approach of dispersal-extinction-cladogenesis (DEC, Ree and Smith, 2008) as implemented in the DEC eXtended version (DECX, Beeravolu and Condamine, 2016; available at: https://github.com/champost/DECX). To infer the biogeographic history of a clade, DEC requires a time-calibrated tree, the current distribution of each species for a set of geographic areas, and a time-stratified geographic model that is represented by connectivity and dispersal scalar matrices for specified time intervals spanning the entire evolutionary history of the group. DECX allows classical vicariance as a cladogenetic event by using temporally flexible constraints on the connectivity between any two given areas following the movement of landmasses and dispersal opportunity over time. DECX can analyze phylogenies on the order of several thousand tips with numerous areas (Rolland and Condamine, 2019; Kawahara *et al.*, 2023). DECX does not incorporate the founder-event speciation (+J parameter) because of concerns with statistical validity of model choice among DEC-derived models (Ree and Sanmartín, 2018). Also, founder-event speciation often leads to inferences that are decoupled from time, with null or extremely low extinction rates, an effect of the model favoring cladogenetic events over anagenetic events (Ree and Sanmartín, 2018), which makes it inadequate for reconstructing the history of ancient groups with widespread distributions.

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

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

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

2.7. Investigating heterogeneity of diversification rates

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

Following Mazet *et al.* (2023), for the analysis of *Papilio*, we first computed the clades' sampling fractions based on our revised taxonomy with the *get.sampling.fraction* function. We specified the nine following subclades: the subgenera *Achillides*, *Chilasa*, *Druryia*, *Heraclides*, *Menelaides*, *Nireopapilio*, *Papilio*, *Pterourus*, and the monophyletic group of Lauraceae feeders regrouping *Chilasa* and *Pterourus* (Apiaceae and Rutaceae feeders are not monophyletic). We then estimated the number of possible shifts to be tested in combination with corresponding backbones using the *get.comb.shift* function. The selection of subclades created 319 combinations of subclade(s)/backbone that were compared to the clade-homogeneous birth-death model. We designed and fitted five diversification models to each clade and backbone with the *shift.estimate* function that determines the best fitting model and most likely combination of shifts. The five models are: (1) a Yule model, where speciation is constant and extinction is null (BCST); (2) a constant birth-death model, where speciation and extinction rates are constant (BCST_DCST); (3) a variable speciation rate model without extinction (BVAR); (4) a variable speciation rate model with constant extinction (BVAR_BCST); and (5) a rate-constant speciation and variable extinction rate model (BCST_BVAR). Diversification rates are defined backward in time such as a positive dependency parameter (α for speciation and β for extinction) reflects a slowdown of rates towards the present. Finally, based on the most likely rate estimates and best combination of shifts, we estimated the diversity dynamics of each clade and resulting backbone recovered in the best shift combination using the *apply_prob_dtt* and *paleodiv* function. The files for reproducing the analyses are available in FigShare (Data 4: https://figshare.com/s/a32288db7e6429714a62).

3. Results and Discussion

3.1. Global phylogeny of **Papilio**

Partitioned phylogenetic analyses with IQ-TREE and MrBayes provided almost identical phylogenetic trees, differing in branch length estimates (**Fig. 3**; Figs S1, S2 for IQ-TREE). The genus *Papilio* was always recovered as monophyletic with maximal (PP_{CAT}=1, PP_{PART}=1, BP_{PART}=100, $UFBS_{PART}$=100) branch support (**Table 3**), which was expected since molecular data have never found it non-monophyletic (e.g. Aubert *et al.*, 1999; Zakharov *et al.*, 2004a; Condamine *et al.*, 2012; Lewis *et al.*, 2015; Owens *et al.*, 2017, 2020; Allio *et al.*, 2020). The Bayesian inference with MrBayes converged well (ADSF=0.007293, average PSRF for parameter values=1.000, and ESS>>200 for all parameters). Bayesian analyses reconstructed a robust phylogeny with 69.4% of the nodes recovered with strong support within *Papilio* (nodes with PP_{PART}≥0.95, **Fig. 3**). Robustness was slightly lower for ML analysis with non-parametric bootstrap: 67.4% of branches in the tree were strongly supported (nodes with BP_{PART}≥70, Fig. S1). In comparison, IQ-TREE analysis with $UFBS_{PART}$ recovered the most robust phylogeny with 82.5% of branches supported by $\text{UFBS}_{\text{PART}}\geq95$ (Fig. S2). PhyloBayes analysis under the mixture (CAT-GTR-Γ_4) model ran during 11,350 cycles and converged well (*meandiff*=0.00814). The topology (Fig. S3) was very similar to traditional partitioned analyses with IQ-TREE and MrBayes, except within the Old World *Papilio* (see below). Overall, branch support in PhyloBayes was also like IQ-TREE and MrBayes with 66.7% of branches having $\text{PP}_{\text{CAT}}\geq0.95$ (see Fig. S4 for a comparison of branch support across all analyses).

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

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

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

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

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

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

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

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

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

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

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

We estimated that the origin of subgenera ranges from the early Miocene (e.g. *Chilasa*, *Heraclides*, *Pterourus*), middle Miocene (e.g. *Achillides*), to the late Miocene (e.g. *Araminta*, *Menelaides*, *Papilio*) (**Fig. 4**, **Table 3**). These age estimates are slightly younger than previous analyses with age differences ranging from ca. 1 to 2 million years younger, but it is important to note that 95% CIs for these nodes strongly overlap with earlier studies. For instance, we estimated the origin of the clade '*Agehana*' + *Chilasa* + *Pterourus* at 22.73 Ma (95% CI=15.36-35.9 Ma), whereas we previously estimated this age at 20.9 Ma (95% CI=16.9-25.6 Ma; Lewis *et al.*, 2015) or 19.7 Ma (95% CI=17.2-22.9 Ma, Owens *et al.*, 2017, 2020) but we have a similar estimation to Wu *et al.* (2015) who found an age of 22.63 Ma (95% CI=18.93-26.58 Ma). Slight differences are found in (1) subgenus *Heraclides* recovered at 21.22 Ma (95% CI=13.95-33.86 Ma) compared to our previous estimation of 22.1 Ma (95% CI=18.0-26.9 Ma; Lewis *et al.*, 2015) or 21.9 Ma (95% CI=17.5-26.4 Ma; Wu *et al.*, 2015); and (2) subgenus *Achillides* estimated at 17.1 Ma (95% CI=11.45-26.88 Ma) whereas we previously recovered a 2-million-year older age at 19.3 Ma (95% CI=16.4-21.8 Ma; Condamine *et al.*, 2013). We argue that these slight age discrepancies mostly come from the differences in taxon sampling resulting in new phylogenetic placements (e.g. *P. alexanor*) and potentially from practices in dating techniques both influencing divergence time estimates.

3.3. Northern origin and dynamic dispersal into the tropics

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

3.4. The Paleotropics as a biogeographic crossroad

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

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

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

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

The diversification analyses investigating rate heterogeneity across *Papilio* revealed four best equally-likely scenarios of diversification (ΔAICc≤2, Table S2), which refutes the hypothesis of a single diversification rate for the whole genus (ΔAICc=14.06; Table S2). These shift-configuration scenarios include three shifts located at subgenera *Achillides*, *Menelaides* and *Papilio* for the first best scenario (**Fig. 5A**), two shifts (*Achillides* and *Menelaides*) for the second best scenario, five shifts (*Achillides*, *Heraclides*, *Menelaides*, *Papilio* and *Pterourus*) for the third best scenario (Fig. S7A), and four shifts (*Achillides*, *Heraclides*, *Menelaides* and *Papilio*) for the fourth best scenario. Subgenera *Achillides* and *Menelaides* are always found as significant shifts. All subclades are better explained by a pure-birth model (BCST), except subgenus *Menelaides* that follows a model with a decreasing speciation rate through time (BVAR; **Fig. 5B**, Fig. S7B, Table S3).

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

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

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

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

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

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

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

4. Conclusion

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

5. Formal taxonomic changes

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

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

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

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

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

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

Subgenus *Euchenor* has previously been regarded as monobasic, but DNA analysis shows that the subgenus consists of two distinct species (Joshi and Kunte 2022): *Papilio* *euchenor* Guérin-Méneville, 1830 and *Papilio depilis* Rothschild, 1895 (**stat. rev.**). Jordan, in Rothschild (1895), stated that forewing scale structure in these two taxa are different but refrained from treating them as separate species. Jordan (1896) then separated the two species, citing several morphological differences including genitalia. Jordan (1908-09) without explanation reunited *P. depilis* with *P. euchenor*, which has been followed by all authors until now. This specific separation of Bismarck Archipelago taxa from New Guinea taxa mirrors the separation of *P. orsippus* from *P. ulysses* in subgenus *Achillides*, and similar separation is found in subgenus *Menelaides* below.

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

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

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

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

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

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

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

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

The most complex clade within subgenus *Menelaides* is the *fuscus* group. The species *Papilio fuscus* Goeze, 1779 as recognised by Hancock (1992) in the most recent revision of this species is not a monophyletic entity. Hancock placed many taxa in his single species *Princeps fuscus* (Goeze, 1779) which we here recognise as five different species in two subclades of the *fuscus* group. Hancock placed *Papilio canopus* Westwood, 1842 and *Papilio hypsicles* Hewitson, 1868 as species level synonyms of *P. fuscus*, but we found that this arrangement is not monophyletic, and these two taxa represent separate species (**stat. rev.**). He also placed four taxa traditionally treated within *P. fuscus* with two taxa previously known as *Papilio pitmani* Elwes & Nicéville, [1887] under the species name *Princeps prexaspes* (C. Felder & R. Felder, 1865). We confirmed that these six taxa form a single species which we treat as *Papilio prexaspes,* restricting the name *Princeps* Hübner, [1807] as the subgeneric name for the *Papilio demoleus* clade.

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

CRediT authorship contribution statement

Fabien L. Condamine: Conceptualization, Methodology, Validation, Taxonomy, Investigation, Resources, Data curation, Writing – original draft, Project administration, Funding acquisition.

Rémi Allio: Conceptualization, Methodology, Data curation, Writing – review & editing.

Eliette L. Reboud: Conceptualization, Methodology, Writing – review & editing.

Julian R. Dupuis: Resources, Validation, Writing – review & editing.

Emmanuel F.A. Toussaint: Resources, Conceptualization, Methodology, Validation, Writing – review & editing.

Nathan Mazet: Methodology, Software, Writing – review & editing.

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Delano S. Lewis: Resources, Validation, Writing – review & editing.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figure Legends

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

P. (Alexanoria) alexanor
P. (Eleppone) anactus
P. (Sinoprinceps) benguetana
P. (Menelaides) bootes
P. (Papilio) joanae
P. (Chilasa) laglaizei
P. (Heraclides) thoas
P. (Achillides) ulysses
P. (Pterourus) zagreus
P. (Druryia) antimachus

Fig. 2. Geographic distribution and sampling of *Papilio*. Histogram shows the number of species occurring in 11 biogeographic regions and sampled in the current phylogenetic tree; African species diversity is clearly under sampled. WP: Western Palearctic, EP: Eastern Palearctic, WN: Western Nearctic, EN: Eastern Nearctic, CA: Central America and Caribbean Islands, SA: South America, AF: Africa, MD: Madagascar, IN: India and Himalayan foothills, WA: Southeast Asia and Wallacea, and AU: Australasia. Pictures from Fabien L. Condamine.

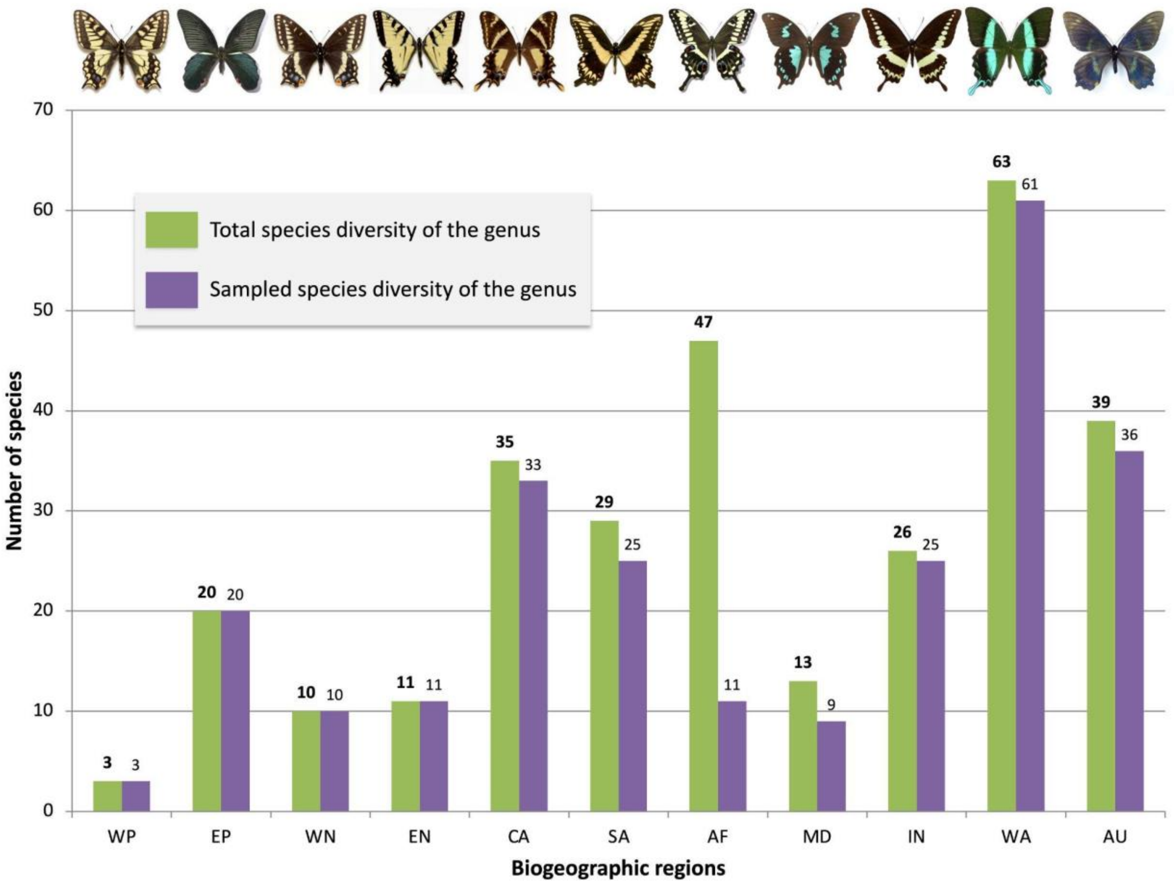

Fig. 3. Bayesian molecular phylogeny of *Papilio*. The phylogeny was inferred with MrBayes using a traditional partitioning strategy and a reversible-jump MCMC approach for selecting the best fitting substitution models. Posterior probabilities ≥0.95 are indicated at nodes with filled circles. The red dashed rectangle indicates phylogenetic uncertainties between methods. Existing subgeneric classification is shown with colored rectangles delineating subgenera. The outgroups are removed. Asterisks indicate species illustrated on the right. Pictures from Fabien L. Condamine.

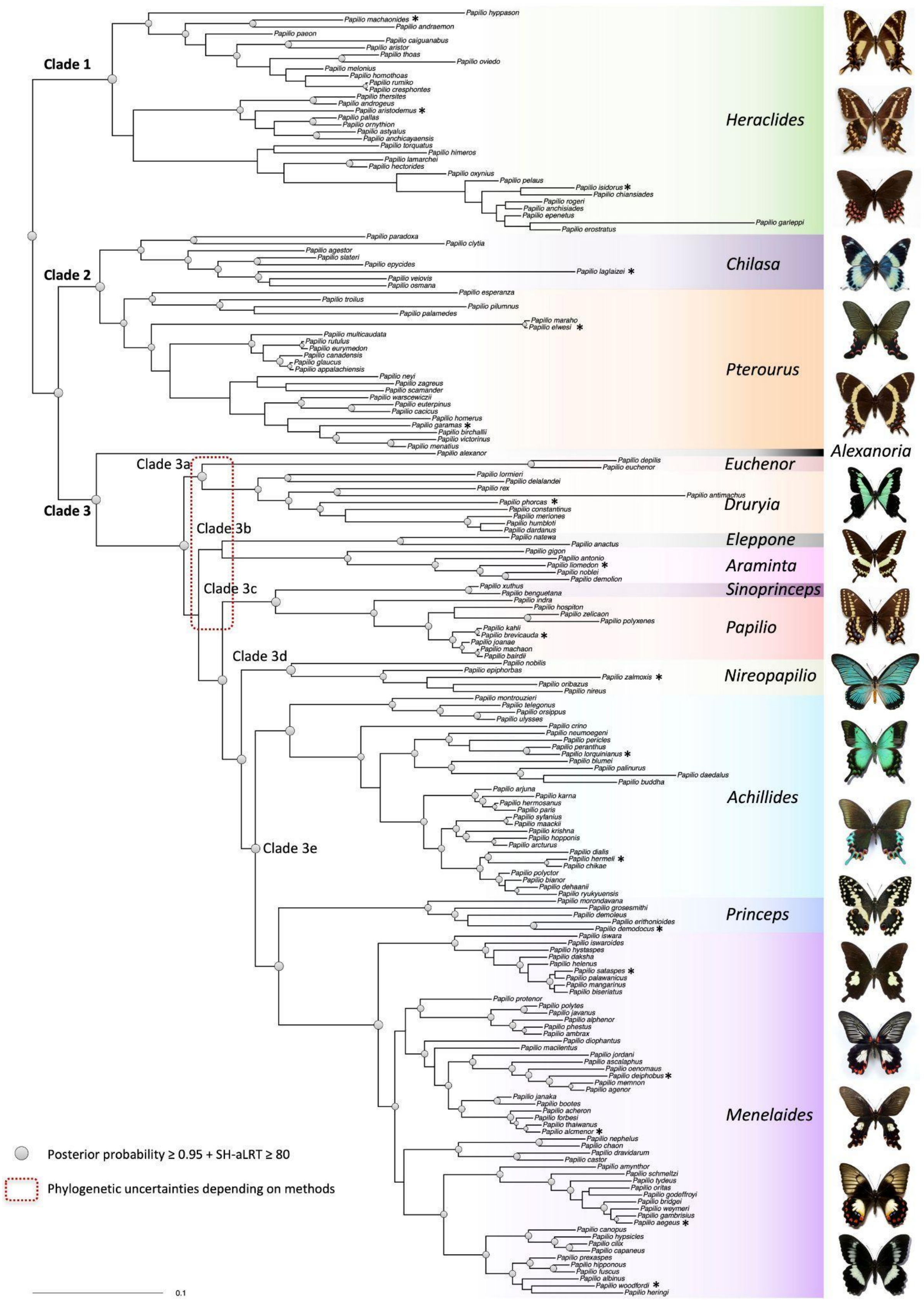
Clade 1
Clade 2
Clade 3
Clade 3a
Clade 3b
Clade 3c
Clade 3d
Clade 3e
Papilio hyppason
Papilio machaonides *
Papilio andraemon
Papilio paeon
Papilio caiguanabus
Papilio aristor
Papilio thoas
Papilio oviedo
Papilio melonius
Papilio homothoas
Papilio rumiko
Papilio cresphontes
Papilio thersites
Papilio androgeus
Papilio aristodemus *
Papilio pallas
Papilio ornythion
Papilio astyalus
Papilio anchicayaensis
Papilio torquatus
Papilio himeros
Papilio lamarchei
Papilio hectorides
Papilio oxynius
Papilio pelaus
Papilio isidorus *
Papilio chiansiades
Papilio rogeri
Papilio anchisiades
Papilio epenetus
Papilio garleppi
Papilio erostratus
Heraclides
Papilio paradoxa
Papilio clytia
Papilio agestor
Papilio slateri
Papilio epycides
Papilio laglaizei *
Papilio veiovis
Papilio osmana
Chilasa
Papilio esperanza
Papilio troilus
Papilio pilumnus
Papilio palamedes
Papilio maraho
Papilio elwesi *
Papilio multicaudata
Papilio rutulus
Papilio eurymedon
Papilio canadensis
Papilio glaucus
Papilio appalachiensis
Papilio neyi
Papilio zagreus
Papilio scamander
Papilio warscewiczii
Papilio euterpinus
Papilio cacicus
Papilio homerus
Papilio garamas *
Papilio birchallii
Papilio victorinus
Papilio menatius
Pterourus
Papilio alexanor
Alexanoria
Papilio deplilis
Papilio euchenor
Euchenor
Papilio lormieri
Papilio delalandei
Papilio rex
Papilio antimachus
Papilio phorcas *
Papilio constantinus
Papilio meriones
Papilio humbloti
Papilio dardanus
Papilio nalewa
Druryia
Papilio anactus
Eleppone
Papilio gigon
Papilio antonio
Papilio liomedon *
Papilio noblei
Papilio demolion
Araminta
Papilio xuthus
Papilio benguetana
Sinoprinceps
Papilio indra
Papilio hospiton
Papilio zelicaon
Papilio polyxenes
Papilio kahli
Papilio brevicauda *
Papilio joanae
Papilio machaon
Papilio bairdii
Papilio
Papilio nobilis
Papilio epiphorbas
Papilio zalmoxis *
Papilio oribazus
Papilio nireus
Nireopapilio
Papilio montrouzieri
Papilio telegonus
Papilio orsippus
Papilio ulysses
Papilio crino
Papilio neumoegeni
Papilio pericles
Papilio peranthus
Papilio lorquinianus *
Papilio blumei
Papilio palinurus
Papilio daedalus
Papilio buddha
Papilio arjuna
Papilio karna
Papilio hermosanus
Papilio paris
Papilio syfanius
Papilio maackii
Papilio krishna
Papilio hopponis
Papilio arcturus
Papilio dialis
Papilio hermeli *
Papilio chikae
Papilio polyctor
Papilio bianor
Papilio dehaanii
Papilio ryukyuensis
Achillides
Papilio morondavana
Papilio grosesmithi
Papilio demoleus
Papilio erithonioides
Papilio demodocus *
Princeps
Papilio iswara
Papilio iswaroides
Papilio hystaspes
Papilio daksha
Papilio helenus
Papilio sataspes *
Papilio palawanicus
Papilio mangarinus
Papilio biseriatus
Papilio protenor
Papilio polytes
Papilio javanus
Papilio alphenor
Papilio phestus
Papilio ambrax
Papilio diophantus
Papilio macilentus
Papilio jordani
Papilio ascalaphus
Papilio oenomaus
Papilio deiphobus *
Papilio memnon
Papilio agenor
Papilio janaka
Papilio bootes
Papilio acheron
Papilio forbesi
Papilio thaiwanus
Papilio alcmenor *
Papilio nephelus
Papilio chaon
Papilio dravidarum
Papilio castor
Papilio amynthor
Papilio schmeltzi
Papilio tydeus
Papilio oritas
Papilio godeffroyi
Papilio bridgei
Papilio weymeri
Papilio gambrisius
Papilio aegeus *
Papilio canopus
Papilio hypsicles
Papilio cilix
Papilio capaneus
Papilio prexaspes
Papilio hipponous
Papilio fuscus
Papilio albinus
Papilio woodfordi *
Papilio heringi
Menelaides
Posterior probability ≥ 0.95 + SH-aLRT ≥ 80
Phylogenetic uncertainties depending on methods
0.1

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

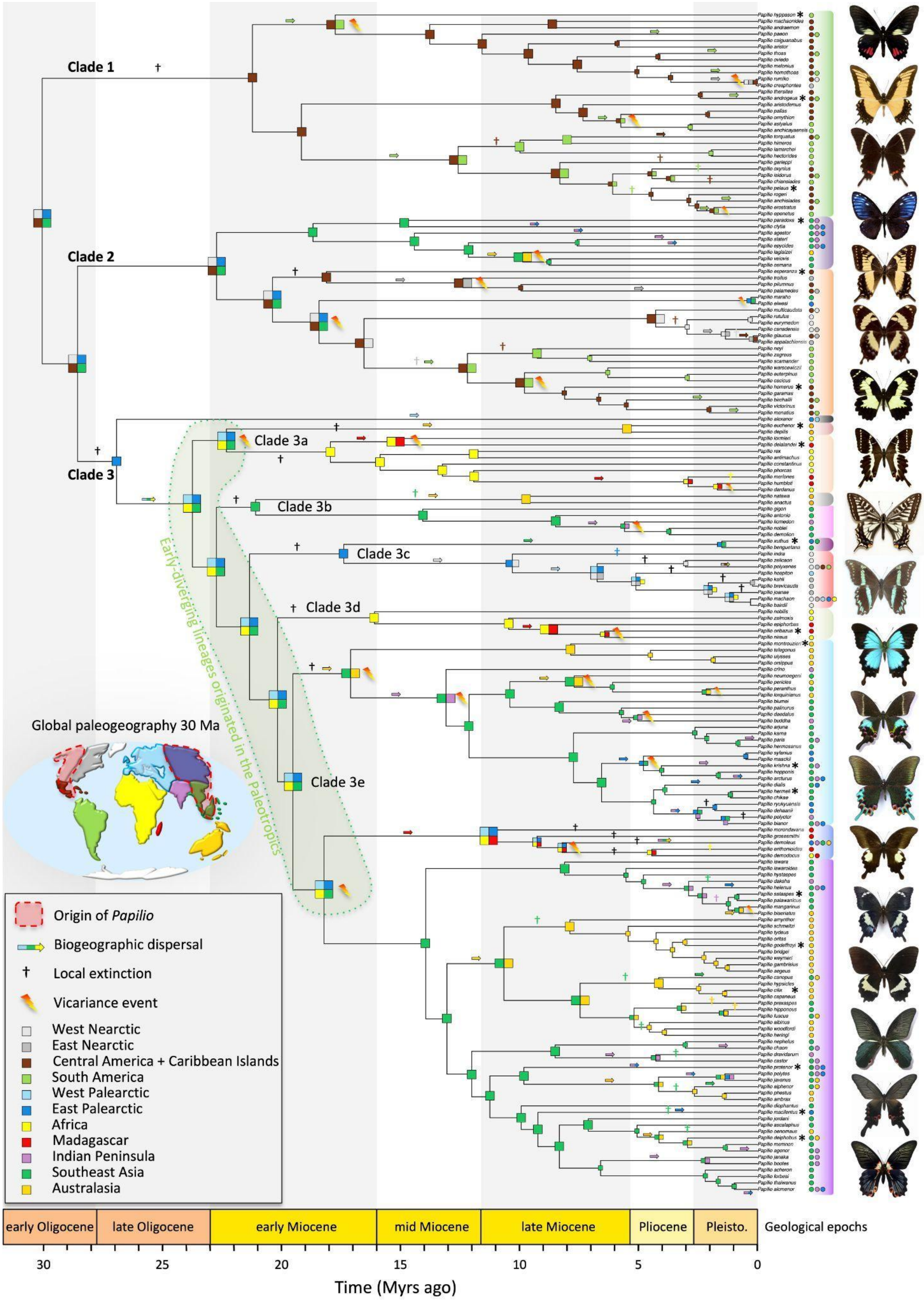
Clade 1
Clade 2
Clade 3
Clade 3a
Clade 3b
Clade 3c
Clade 3d
Clade 3e
Early-diverging lineages originated in the paleotropics
Global paleogeography 30 Ma
Origin of Papilio
Biogeographic dispersal
Local extinction
Vicariance event
West Nearctic
East Nearctic
Central America + Caribbean Islands
South America
West Palearctic
East Palearctic
Africa
Madagascar
Indian Peninsula
Southeast Asia
Australasia
early Oligocene
late Oligocene
early Miocene
mid Miocene
late Miocene
Pliocene
Pleisto.
Geological epochs
30
25
20
15
10
5
0
Time (Myrs ago)

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

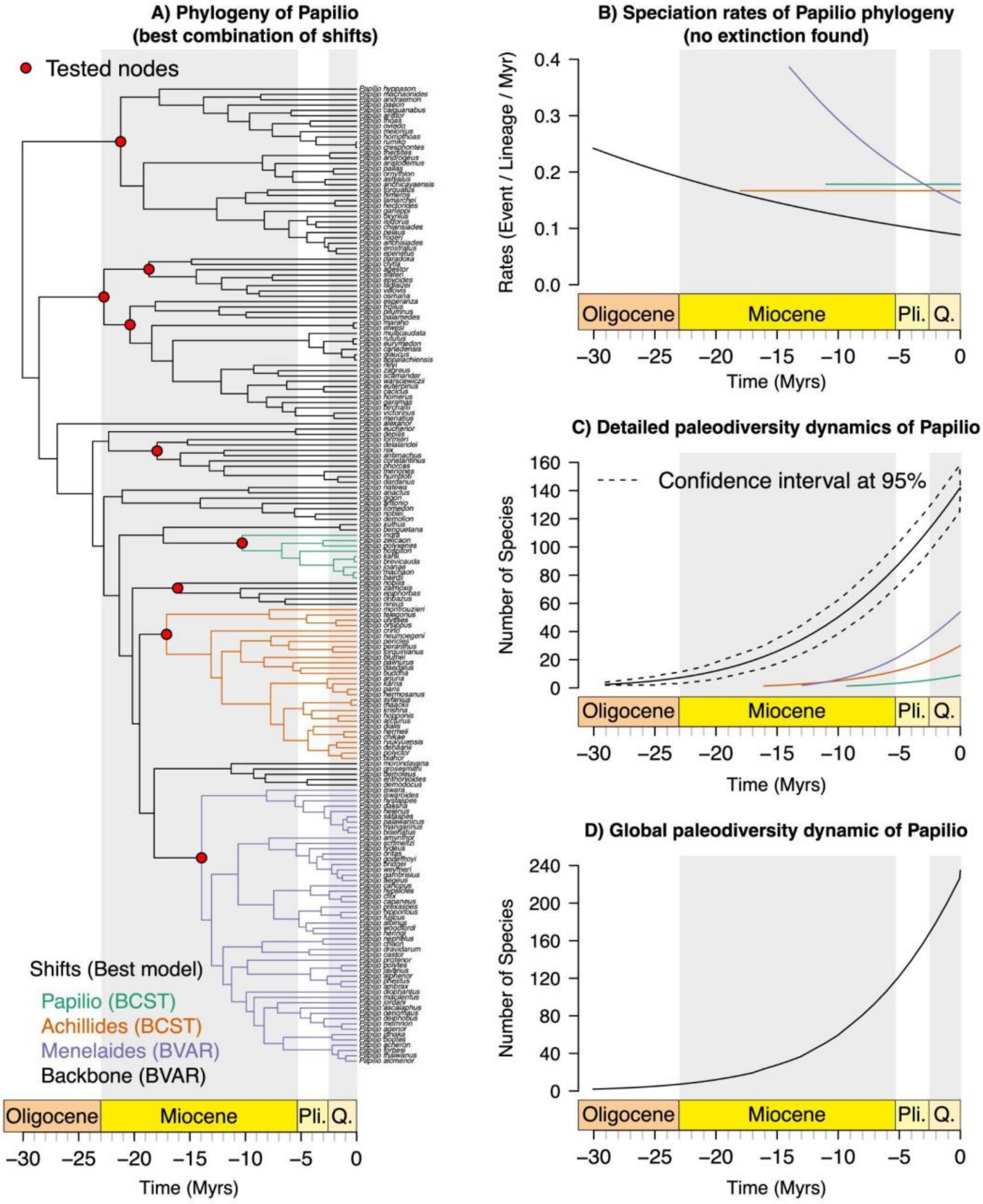

Table 1. Taxonomic working list for *Papilio* species. The list includes subgenera that are currently recovered as monophyletic in molecular phylogenies, and species that belong to each subgenus. We also indicate the ratio of species sampled in the phylogeny presented in this study, which highlights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

***Achillides* Hübner, [1819] [30 spp.]: 29 spp. sampled in the current study (=96.6%)**	**Status**	**In the tree**
Papilio (*Achillides*) *arcturus* Westwood, 1842	Valid	Sampled
Papilio (*Achillides*) *arjuna* Horsfield, 1828	Valid	Sampled
Papilio (*Achillides*) *bianor* Cramer, 1777	Valid	Sampled
Papilio (*Achillides*) *blumei* Boisduval, 1836	Valid	Sampled
Papilio (*Achillides*) *buddha* Westwood, 1872	Valid	Sampled
Papilio (*Achillides*) *chikae* Igarashi, 1965	Valid	Sampled
Papilio (*Achillides*) *crino* Fabricius, 1793	Valid	Sampled
Papilio (*Achillides*) *daedalus* Felder & Felder, 1861	**stat. rev.** (formerly a subspecies of *palinurus*)	Sampled
Papilio (*Achillides*) *dehaanii* Felder & Felder, 1864	Valid	Sampled
Papilio (*Achillides*) *dialis* Leech, 1893	Valid	Sampled
Papilio (*Achillides*) *elephenor* Doubleday, 1845	Valid	**Unsampled**
Papilio (*Achillides*) *hermeli* Nuyda, 1992	**stat. rev.** (formerly a subspecies of *chikae*)	Sampled
Papilio (*Achillides*) *hermosanus* Rebel, 1906	Valid	Sampled
Papilio (*Achillides*) *hopponis* Matsumura, 1907	Valid	Sampled
Papilio (*Achillides*) *karna* Felder & Felder, 1865	Valid	Sampled
Papilio (*Achillides*) *krishna* Moore, [1858]	Valid	Sampled
Papilio (*Achillides*) *lorquinianus* Felder & Felder, 1865	Valid	Sampled
Papilio (*Achillides*) *maackii* Ménétriés, 1858	Valid	Sampled
Papilio (*Achillides*) *montrouzieri* Boisduval, 1859	Valid	Sampled
Papilio (*Achillides*) *neumoegeni* Honrath, 1890	Valid	Sampled
Papilio (*Achillides*) *orsippus* Godman & Salvin, 1888	**stat. rev.** (formerly a subspecies of *ulysses*)	Sampled
Papilio (*Achillides*) *palinurus* Fabricius, 1787	Valid	Sampled
Papilio (*Achillides*) *paris* Linnaeus, 1758	Valid	Sampled
Papilio (*Achillides*) *peranthus* Fabricius, 1787	Valid	Sampled
Papilio (*Achillides*) *pericles* Wallace, 1865	Valid	Sampled
Papilio (*Achillides*) *polyctor* Boisduval, 1836	**stat. rev.** (formerly a subspecies of *bianor*)	Sampled
Papilio (*Achillides*) *ryukyuensis* Fujioka, 1975	Valid	Sampled
Papilio (*Achillides*) *syfanius* Oberthür, 1886	Valid	Sampled
Papilio (*Achillides*) *telegonus* Felder & Felder, 1860	**stat. rev.** (formerly a subspecies of *ulysses*)	Sampled
Papilio (*Achillides*) *ulysses* Linnaeus, 1758	Valid	Sampled

***Alexanoria* Koçak and Kemal, 2002 [1 sp.]: 1 sampled in the current study (=100%)**	**Status**	**In the tree**
Papilio (*Alexanoria*) *alexanor* Esper, [1800]	Valid	Sampled

***Araminta* Moore, 1886 [5 spp.]: 5 sampled in the current study (=100%)**	**Status**	**In the tree**
Papilio (*Araminta*) *antonio* Hewitson, 1875	Valid	Sampled
Papilio (*Araminta*) *demolion* Cramer, 1776	Valid	Sampled
Papilio (*Araminta*) *gigon* Felder & Felder, 1865	Valid	Sampled
Papilio (*Araminta*) *liomedon* Moore, [1875]	Valid	Sampled
Papilio (*Araminta*) *noblei* Nicéville, [1889]	Valid	Sampled

***Chilasa* Moore, [1881] [11 spp.]: 8 sampled in the current study (=72.7%)**	**Status**	**In the tree**
Papilio (*Chilasa*) *agestor* Gray, 1831	Valid	Sampled
Papilio (*Chilasa*) *carolinensis* (Jumalon, 1967)	Valid	**Unsampled**
Papilio (*Chilasa*) *clytia* Linnaeus, 1758	Valid	Sampled
Papilio (*Chilasa*) *epycides* Hewitson, 1864	Valid	Sampled
Papilio (*Chilasa*) *laglaizei* Depuiset, 1877	Valid	Sampled
Papilio (*Chilasa*) *moerneri* Aurivillius, 1919	Valid	**Unsampled**
Papilio (*Chilasa*) *osmana* (Jumalon, 1967)	Valid	Sampled
Papilio (*Chilasa*) *paradoxa* Zincken, 1831	Valid	Sampled
Papilio (*Chilasa*) *slateri* Hewitson, 1859	Valid	Sampled
Papilio (*Chilasa*) *toboroi* Ribbe, 1907	Valid	**Unsampled**
Papilio (*Chilasa*) *veiovis* Hewitson, 1865	Valid	Sampled

***Druryia* Aurivillius, 1881 [30 spp.]: 9 sampled in the current study (=30%)**	**Status**	**In the tree**
Papilio (Druryia) andronicus Ward, 1871	Valid	**Unsampled**
Papilio (*Druryia*) *antimachus* Drury, [1782]	Valid	Sampled
Papilio (*Druryia*) *arnoldiana* Vane-Wright, 1995	Valid	**Unsampled**
Papilio (*Druryia*) *bacelarae* Bivar de Sousa & Mendes, 2009	Valid	**Unsampled**
Papilio (*Druryia*) *constantinus* Ward, 1871	Valid	Sampled
Papilio (*Druryia*) *cynorta* Fabricius, 1793	Valid	**Unsampled**
Papilio (*Druryia*) *cyproeofila* Butler, 1868	Valid	**Unsampled**
Papilio (*Druryia*) *dardanus* Brown, 1776	Valid	Sampled
Papilio (*Druryia*) *delalandei* Godart, 1823	Valid	Sampled
Papilio (*Druryia*) *echerioides* Trimen, 1868	Valid	**Unsampled**
Papilio (*Druryia*) *fernandus* Fruhstorfer, 1903	Valid	**Unsampled**
Papilio (*Druryia*) *filaprae* Süffert, 1904	Valid	**Unsampled**
Papilio (*Druryia*) *fuelleborni* Karsch, 1900	Valid	**Unsampled**
Papilio (*Druryia*) *gallienus* Distant, 1879	Valid	**Unsampled**
Papilio (*Druryia*) *humbloti* Oberthür, 1888	**stat. rev.** (formerly a subspecies of *dardanus*)	Sampled
Papilio (*Druryia*) *jacksoni* Sharpe, 1891	Valid	**Unsampled**
Papilio (*Druryia*) *leucotaenia* Rothschild, 1908	Valid	**Unsampled**
Papilio (*Druryia*) *lormieri* Distant, 1874	Valid	Sampled
Papilio (*Druryia*) *mangoura* Hewitson, 1875	Valid	**Unsampled**
Papilio (*Druryia*) *mechowi* Dewitz, 1881	Valid	**Unsampled**
Papilio (*Druryia*) *mechowianus* Dewitz, 1885	Valid	**Unsampled**
Papilio (*Druryia*) *menestheus* Drury, [1773]	Valid	**Unsampled**
Papilio (*Druryia*) *meriones* Felder & Felder, 1864	**stat. rev.** (formerly a subspecies of *dardanus*)	Sampled
Papilio (*Druryia*) *nobicea* Suffert, 1904	Valid	**Unsampled**
Papilio (*Druryia*) *ophidicephalus* Oberthür, 1878	Valid	**Unsampled**
Papilio (*Druryia*) *phorcas* Cramer, 1775	Valid	Sampled
Papilio (*Druryia*) *plagiatus* Aurivillius, 1898	Valid	**Unsampled**
Papilio (*Druryia*) *rex* Oberthür, 1886	Valid	Sampled
Papilio (*Druryia*) *sjoestedti* Aurivillius, 1908	Valid	**Unsampled**
Papilio (*Druryia*) *zenobia* Fabricius, 1775	Valid	**Unsampled**

***Eleppone* Hancock, 1979 [2 spp.]: 2 sampled in the current study (=100%)**	**Status**	**In the tree**
Papilio (*Eleppone*) *anactus* Macleay, 1826	Valid	Sampled

Papilio (*Eleppone*) *natewa* Tennent, Chandra & Müller, 2018	Valid	Sampled

***Euchenor* Igarashi, 1979 [2 spp.]: 2 sampled in the current study (=100%)**	**Status**	**In the tree**
Papilio (*Euchenor*) *depilis* Rothschild, 1895	**stat. rev.** (formerly a subspecies of *euchenor*)	Sampled
Papilio (*Euchenor*) *euchenor* Guérin-Méneville, 1830	Valid	Sampled

***Heraclides* Hübner, [1819] [32 spp.]: 32 sampled in the current study (=100%)**	**Status**	**In the tree**
Papilio (*Heraclides*) *anchicayaensis* Constantino, Le Crom & Salazar, 2002	Valid	Sampled
Papilio (*Heraclides*) *anchisiades* Esper, [1788]	Valid	Sampled
Papilio (*Heraclides*) *andraemon* Hübner, [1823]	Valid	Sampled
Papilio (*Heraclides*) *androgeus* Cramer, 1775	Valid	Sampled
Papilio (*Heraclides*) *aristodemus* Esper, 1794	Valid	Sampled
Papilio (*Heraclides*) *aristor* Godart, 1819	Valid	Sampled
Papilio (*Heraclides*) *astyalus* Godart, 1819	Valid	Sampled
Papilio (*Heraclides*) *caiguanabus* Poey, 1852	Valid	Sampled
Papilio (*Heraclides*) *chiansiades* Westwood, 1872	Valid	Sampled
Papilio (*Heraclides*) *cresphontes* Cramer, 1777	Valid	Sampled
Papilio (*Heraclides*) *epenetus* Hewitson, 1861	Valid	Sampled
Papilio (*Heraclides*) *erostratus* Westwood, 1847	Valid	Sampled
Papilio (*Heraclides*) *garleppi* Staudinger, 1892	Valid	Sampled
Papilio (*Heraclides*) *hectorides* Esper, 1794	Valid	Sampled
Papilio (*Heraclides*) *himeros* Hopffer, 1865	Valid	Sampled
Papilio (*Heraclides*) *homothoas* Rothschild & Jordan, 1906	Valid	Sampled
Papilio (*Heraclides*) *hyppason* Cramer, 1775	Valid	Sampled
Papilio (*Heraclides*) *isidorus* Doubleday, 1846	Valid	Sampled
Papilio (*Heraclides*) *lamarchei* Staudinger, 1892	Valid	Sampled
Papilio (*Heraclides*) *machaonides* Esper, 1796	Valid	Sampled
Papilio (*Heraclides*) *melonius* Rothschild & Jordan, 1906	Valid	Sampled
Papilio (*Heraclides*) *ornythion* Boisduval, 1836	Valid	Sampled
Papilio (*Heraclides*) *oviedo* Gundlach, 1866	Valid	Sampled
Papilio (*Heraclides*) *oxynius* (Geyer, 1827)	Valid	Sampled
Papilio (*Heraclides*) *paeon* Boisduval, 1836	Valid	Sampled
Papilio (*Heraclides*) *pallas* Gray, [1853]	Valid	Sampled
Papilio (*Heraclides*) *pelaus* Fabricius, 1775	Valid	Sampled
Papilio (*Heraclides*) *rogeri* Boisduval, 1836	Valid	Sampled
Papilio (*Heraclides*) *rumiko* (Shiraiwa & Grishin, 2014)	Valid	Sampled
Papilio (*Heraclides*) *thersites* Fabricius, 1775	Valid	Sampled
Papilio (*Heraclides*) *thoas* Linnaeus, 1771	Valid	Sampled
Papilio (*Heraclides*) *torquatus* Cramer, 1777	Valid	Sampled

***Menelaides* Hübner, [1819] [54 spp.]: 52 sampled in the current study (=96.5%)**	**Status**	**In the tree**
Papilio (*Menelaides*) *acheron* Grose-Smith, 1887	Valid	Sampled
Papilio (*Menelaides*) *aegeus* Donovan, 1805	Valid	Sampled
Papilio (*Menelaides*) *agenor* Linnaeus, 1758	**stat. rev.** (formerly a subspecies of *memnon*)	Sampled
Papilio (*Menelaides*) *albinus* Wallace, 1865	Valid	Sampled
Papilio (*Menelaides*) *alcmenor* Felder & Felder, 1865	Valid	Sampled
Papilio (*Menelaides*) *alphenor* Cramer, 1776	**stat. rev.** (formerly a subspecies of *polytes*)	Sampled
Papilio (*Menelaides*) *ambrax* Boisduval, 1832	**stat. rev.** (formerly a subspecies of *phestus*)	Sampled

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

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

Papilio (*Pterourus*) *ascolius* Felder & Felder, 1864	Valid	**Unsampled**
Papilio (*Pterourus*) *bachus* Felder & Felder, 1865	Valid	**Unsampled**
Papilio (*Pterourus*) *birchallii* Hewitson, 1863	Valid	Sampled
Papilio (*Pterourus*) *cacicus* Lucas, 1852	Valid	Sampled
Papilio (*Pterourus*) *canadensis* Rothschild & Jordan, 1906	Valid	Sampled
Papilio (*Pterourus*) *elwesi* Leech, 1889	Valid	Sampled
Papilio (*Pterourus*) *esperanza* Beutelspacher, 1975	Valid	Sampled
Papilio (*Pterourus*) *eurymedon* Lucas, 1852	Valid	Sampled
Papilio (*Pterourus*) *euterpinus* Salvin & Godman, 1868	Valid	Sampled
Papilio (*Pterourus*) *garamas* (Geyer, [1829])	Valid	Sampled
Papilio (*Pterourus*) *glaucus* Linnaeus, 1758	Valid	Sampled
Papilio (*Pterourus*) *hellanichus* Hewitson, 1868	Valid	**Unsampled**
Papilio (*Pterourus*) *homerus* Fabricius, 1793	Valid	Sampled
Papilio (*Pterourus*) *maraho* Shiraki & Sonan, 1934	Valid	Sampled
Papilio (*Pterourus*) *menatius* (Hübner, [1819])	Valid	Sampled
Papilio (*Pterourus*) *multicaudata* Kirby, 1884	Valid	Sampled
Papilio (*Pterourus*) *neyi* Niepelt, 1909	Valid	Sampled
Papilio (*Pterourus*) *palamedes* Drury, 1773	Valid	Sampled
Papilio (*Pterourus*) *pilumnus* Boisduval, 1836	Valid	Sampled
Papilio (*Pterourus*) *rutulus* Lucas, 1852	Valid	Sampled
Papilio (*Pterourus*) *scamander* Boisduval, 1836	Valid	Sampled
Papilio (*Pterourus*) *troilus* Linnaeus, 1758	Valid	Sampled
Papilio (*Pterourus*) *victorinus* Doubleday, 1844	**stat. rev.** (formerly a subspecies of *menatius*)	Sampled
Papilio (*Pterourus*) *warscewiczii* Hopffer, 1865	Valid	Sampled
Papilio (*Pterourus*) *xanthopleura* Salvin & Godman, 1868	Valid	**Unsampled**
Papilio (*Pterourus*) *zagreus* Doubleday, 1847	Valid	Sampled
Sinoprinceps **Hancock, 1983 [2 spp.]: 2 sampled in the current study (=100%)**	**Status**	**In the tree**
Papilio (*Sinoprinceps*) *benguetana* Joicey & Talbot, 1923	**stat. rev.** (formerly a subspecies of *xuthus*)	Sampled
Papilio (*Sinoprinceps*) *xuthus* Linnaeus, 1767	Valid	Sampled

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

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

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$_{\text{CAT}}$	**PP$_{\text{PART}}$**	**BS$_{\text{PART}}$**	**UFBS$_{\text{PART}}$**	**Fossil calibrations**	**Secondary calibrations**		
Papilio sensu lato	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: *Heraclides*	1	0.96	75	100	21.22 (13.95 – 33.86)	21.2 (16.07 – 27.48)	CA	Central America
Clade 2: *Papilio sensu lato* excl. *Heraclides*	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
Chilasa + *Pterourus* + *‘Agehana’*	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
Chilasa	1	1	99	100	16.68 (12.49 – 29.71)	18.63 (14.02 – 24.44)	WA	Indonesia
Pterourus + *‘Agehana’*	1	1	79	99	20.38 (13.8 – 32.28)	20.3 (15.3 – 25.92)	EP + WN + CA	Origin centred on Beringia
‘Agehana’	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 *Papilio*	1	0.99	58	85	26.93 (18.62 – 42.62)	26.86 (21.52 – 33.51)	EP	East Palearctic
Old World *Papilio* excl. *Alexanoria*	1	1	86	100	23.74 (16.45 – 37.49)	23.67 (18.96 – 29.58)	WP + EP + AF + WA	Paleotropics
Clade 3a: *Druryia* + *Euchenor*	0.82	0.99	74	99	22.32 (15.3 – 35.23)	22.23 (17.46 – 27.95)	WP + EP + AF + WA	Paleotropics
Euchenor	1	1	100	100	5.49 (2.74 – 9.71)	5.33 (2.84 – 8.42)	AU	Australasia
Druryia	1	1	99	100	17.95 (12.07 – 28.62)	17.88 (13.61 – 22.95)	AF	Afrotropics
Clade 3b: *Eleppone* + *Araminta*	-	0.72	50	93	21.09 (14.82 – 33.9)	20.99 (16.4 – 26.47)	WA	Indonesia
Eleppone	1	1	97	100	9.72 (4.41 – 17.0)	9.54 (4.77 – 15.03)	AU	Australasia
Araminta	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: *Sinoprinceps* + *Papilio sensu stricto*	1	1	97	100	17.39 (11.36 – 27.85)	17.27 (13.1 – 22.34)	EP	East Palearctic
Sinoprinceps	1	1	100	100	1.5 (0.63 – 2.82)	1.44 (0.67 – 2.45)	EP + WA	Asia and Indonesia
Papilio sensu stricto	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: *Nireopapilio*	1	1	76	98	16.1 (10.21 – 25.51)	15.98 (11.78 – 20.65)	AF	Afrotropics
Clade 3e: *Achillides* + *Princeps* + *Menelaides*	-	0.91	54	96	19.52 (13.5 – 30.98)	19.41 (15.57 – 24.39)	WP + EP + AF + WA	Paleotropics
Achillides	1	1	85	99	17.1 (11.45 – 26.88)	17.0 (13.31 – 21.62)	WA + AU	Indonesia and Australasia
Princeps + *Menelaides*	0.93	1	70	99	18.21 (12.6 – 29.05)	18.15 (14.37 – 22.86)	WP + EP + AF + WA	Paleotropics
Princeps	1	1	100	100	11.29 (6.93 – 18.01)	11.21 (8.0 – 14.97)	WP + EP + AF + MD	Paleotropics
Menelaides	1	1	99	100	13.94 (9.4 – 21.98)	13.94 (10.9 – 17.65)	WA	Indonesia

Table 4. Changes to subspecies nomenclature resulting from literature review and this study.

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

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

Supplementary Information

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

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

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

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

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

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

Figure S7. Diversification shifts and diversity dynamics estimated for *Papilio* as estimated by the third best-fitting combination of shifts. A) The phylogeny of *Papilio* with shifts highlighted in colors and best models in parenthesis. Red dots correspond to all tested nodes. B) The evolution of diversification rates through time for the backbone and all subclades that are found as significant shifts. C) Diversity dynamics for the backbone and subclade trees as estimated with the probabilistic approach (dotted line represents the confidence interval of diversity estimates for the backbone). For the sake of clarity, confidence intervals of diversity estimates for subclades are not represented. D) Global diversity dynamics of *Papilio* obtained by summing all the diversity dynamics for the backbone and subclade trees.

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

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

Table S3. Comparisons of diversification models for each subclade. The best models are highlighted in bold. NP=Number of parameters, logL=log(Likelihood), λ=speciation rate (at present if variable), α=dependency parameter of speciation rate, μ=extinction rate, β=dependency parameter of extinction rate.