Ancient Neotropical origin and recent recolonisation: Phylogeny, biogeography and diversification of the Riodinidae (Lepidoptera: Papilionoidea) ☆

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ABSTRACT

We present the first dated higher-level phylogenetic and biogeographic analysis of the butterfly family Riodinidae. This family is distributed worldwide, but more than 90% of the c. 1500 species are found in the Neotropics, while the c. 120 Old World species are concentrated in the Southeast Asian tropics, with minor Afrotropical and Australasian tropical radiations, and few temperate species. Morphologically based higher classification is partly unresolved, with genera incompletely assigned to tribes. Using 3666 bp from one mitochondrial and four nuclear markers for each of 23 outgroups and 178 riodinid taxa representing all subfamilies, tribes and subtribes, and 98 out of 145 described genera of riodinids, we estimate that Riodinidae split from Lycaenidae about 96 Mya in the mid-Cretaceous and started to diversify about 81 Mya. The Riodinidae are monophyletic and originated in the Neotropics, most likely in lowland proto-Amazonia. Neither the subfamily Euselasiinae nor the Nemeobiinae are monophyletic as currently constituted. The enigmatic, monotypic Neotropical genera *Styx* and *Corrachia* (most recently treated in Euselasiinae: Corrachiini) are highly supported as derived taxa in the Old World Nemeobiinae, with dispersal most likely occurring across the Beringia land bridge during the Oligocene. *Styx* and *Corrachia*, together with all other nemeobiines, are the only exclusively Primulaceae-feeding riodinids. The steadily increasing proliferation of the Neotropical Riodininae subfamily contrasts with the decrease in diversification in the Old World, and may provide insights into factors influencing the diversification rate of this relatively ancient clade of Neotropical insects.

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1. Introduction

The butterfly family Riodinidae is sister to Lycaenidae (the "blues, coppers and hairstreaks"), and the divergence of these two families is estimated to have occurred around 88 Mya in the late Cretaceous (Heikkilä et al., 2012). Riodinidae are commonly known as "metalmarks" due to their spectacular metallic colours in many lineages. In fact, Riodinidae exhibit the greatest variation in wing shape, color and pattern seen in any butterfly family, and mimic members of many other lepidopteran families (e.g. DeVries, 1997). Riodinidae represent over 8% of all butterflies, but about 93% of them are found in the Neotropics compared with only 7% in the Palaeotropics. More precisely, the New World riodinids comprise about 133 genera and over 1300 described species arranged in two subfamilies (Riodininae with 1200 described species and Euselasiinae with 176 described species), whereas the Old World Riodinidae comprise only 13 genera and 110 described species arranged in just one subfamily, the Nemeobiinae. The Nemeobiinae are mostly concentrated in Southeast Asia (around 60 species), with about 15 described species in Africa and Madagascar, 28 in the Australasian region (New Guinea and surrounding islands, one reaching Northern Queensland) and a single representative in Europe (Lamas, 2008). Riodinids constitute a substantial proportion of the butterfly community of Neotropical low and mid-elevation forests (Heppner, 1991; Robbins, 1993), and are known for their fascinating life histories with some species being myrmecophilous and/or aphytophagous in their larval stages (DeVries, 1991a, 1997; Campbell and Pierce, 2003; Hall et al., 2004a).

This prominent diversity, mimicry and variation in morphology and life history was noted early (Bates, 1868) and has caused some confusion for classification. Staudinger (1876), for example, in his description of the species *Styx infernalis* (Fig. 1, endemic to the Peruvian Andes), noted that the taxon was so odd that it had initially been taken for a moth, but then placed it within Pieridae. More recently, what was described as the species *Stiboges lushanica* (Nemeobiinae) by Chou and Yuan (2001) is actually an epicopeiid moth. The relationship between the three currently recognized riodinid subfamilies Riodininae, Euselasiinae and Nemeobiinae has never been clear, and there has been little work on the classification within the subfamily Nemeobiinae, with the exception of the now exclusively Asian genus *Abisara* (Bennett, 1950; Saito and Saito, 2005) and some regional accounts (e.g. Callaghan, 2003, 2009).

Despite similarities in the configuration of male genitalia and egg shape, the monotypic genera *Styx* and *Corrachia* (Fig. 1, the latter endemic to mountains in southern Costa Rica), were treated in monotypic subfamilies (Harvey, 1987a). However, they were subsequently placed together in the tribe Corrachiini, and tentatively placed within Euselasiinae based on biogeographical parsimony rather than morphology by Hall and Harvey (2002a).

Riodininae is currently subdivided into seven tribes (Riodinini, Nymphidiini, Stalachtini, Helicopini, Symmachiini, Mesosemiini and Eurybiini), and an additional *incertae sedis* section with at least a dozen genera. The classification of tribes has traditionally been based on the number of forewing radial veins, with four veins considered to be the apomorphic state found in Symmachiini, Helicopini, Nymphidiini, Stalachtini, Riodinini and the *incertae sedis* taxa (the "Emesini" *sensu* Harvey, 1987a) and five veins being the plesiomorphic state, found in Eurybiini, Mesosemiini, and including the *incertae sedis* taxa of Harvey (1987a), that are now placed in Mesosemiini: Napaeina (Hall, 2003). Using cladistic methods and morphology, Hall (2003) inferred that Eurybiini is sister to the rest of the Riodininae, followed by Mesosemiini, although this conclusion was only supported by a single pupal synapomorphy.

Over the last 20 years, several tribes, sections and species groups of Riodinidae have been revised using morphological characters and cladistic methods. These include, for example, the tribes Mesosemiini (Hall, 2003, 2005), Symmachiini (Hall and Harvey, 2002a; Hall and Willmott, 1996), and the Nymphidiini (Hall, 1999, 2002, in press; Hall and Harvey, 2001, 2002b; Penz and DeVries, 1999). We have assembled all cladograms produced during the last 20 years into a single consensus tree that represents the current state of Riodinidae systematics based on morphological data (supplementary file S1 and S2).

Two attempts have been made to infer a molecular phylogeny of the Riodinidae, but both suffered from low taxon and/or gene sampling. In early work, Campbell (1998, also see Campbell et al., 2000; Campbell and Pierce, 2003) included 28 riodinid taxa, and used the nuclear genes wingless (wg) and Elongation factor 1-alpha (EF-1α) together with the mitochondrial gene Cytochrome Oxidase I (COI) to construct a phylogeny. Saunders (2010) used the same genes, and included 68 riodinid species, but only one (*Hamearis lucina*) from the Old-World subfamily Nemeobiinae. His results indicated that many currently recognized tribes and subtribes were not monophyletic.

To provide a unified phylogenetic history of the Riodinidae, here we present the first well-sampled, dated phylogenetic and biogeographic inference, together with a diversification rates analysis. Although urged previously (DeVries and Poinar, 1997), no large scale dating analysis of riodinids has been attempted thus far. Additionally, the anomaly (for any species rich butterfly clade) of an order of magnitude higher diversity in the New World than the Old World has never been examined comparatively in a phylogenetic context. Here, we infer riodinid phylogeny including all Old

Styx infernalis   *Corrachia leucoplaga*
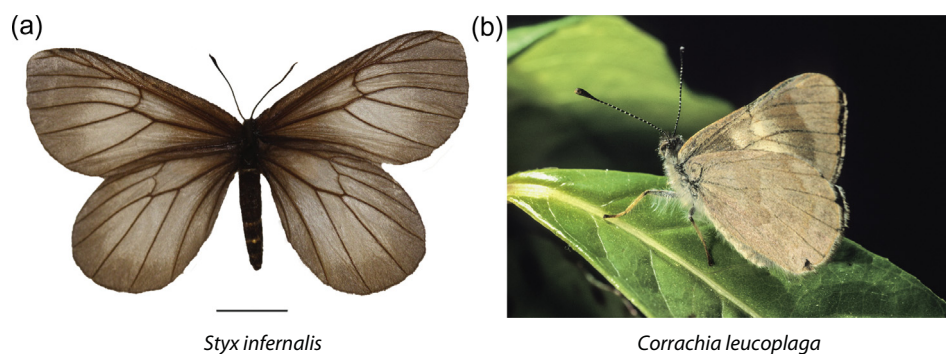
Fig. 1. The morphologically deviant species (a) *Styx infernalis*, endemic to the Peruvian Andes, and (b) *Corrachia leucoplaga*, endemic to the mountains in southern Costa Rica, constituted long standing enigmas in Riodinidae classification and have been tentatively placed together in the tribe Corrachiini, in Euselasiinae. We show that they belong to the otherwise Old World subfamily Nemeobiinae. Scale bar is 1 cm. Photo (a) ©McGuire Center for Lepidoptera and Biodiversity (MGCL), photo (b) ©Phil DeVries.

World riodinid genera, all tribes and subtribes of Neotropical species, and many genera. Our phylogeny is based on up to five loci (one mitochondrial, four nuclear, for a total of 3666 bp, with 19% missing data), 178 riodinid taxa including all subfamilies, tribes and subtribes (98 out of 145 described genera), and 23 outgroups. This is the first time the monotypic genus *Corrachia* and any taxa from the classic Nemeobiinae other than *Hamearis* and *Abisara* have been included in molecular phylogenetic work.

2. Material and methods

2.1. Sampling

Specimens were netted in the field and processed later in the laboratory. Wings are preserved as vouchers in cross-referenced glassine envelopes, and bodies in ⩾ 95% ethanol in a freezer at −80 °C. Taxa included in the analysis are listed in supplementary file S3. Specimens used in this study are deposited in the Pierce DNA and tissues collection of the Museum of Comparative Zoology at Harvard University or in the DNA tissue collection of Yu-Feng Hsu at the Department of Life Science, National Taiwan Normal University, Taipei. Sequences for six specimens were taken from GenBank (see supplementary file S3 for more information).

2.2. DNA extraction, amplification and sequencing

DNA was extracted from one or two legs using the DNeasy blood & tissue kit (Qiagen, Valencia, CA, USA), Puregene DNA Isolation kit (Gentra Systems, Minnesota, USA), or the AutoGen tissue protocol on an AutoGenPrep 965 robot (AutoGen Inc., Holliston, MA, USA). One mitochondrial locus (Cytochrome Oxidase I, COI) and four nuclear loci (Elongation factor 1α, EF-1a; wingless, wg; histone 3, H3; and Carbamoylphosphate synthetase domain protein, CAD) were amplified for 178 riodinid specimens and 23 outgroups using the primers listed in supplementary file S4. These mitochondrial and nuclear genes were selected due to their utility in reconstructing the phylogeny of other insect groups of similar age and diversity (e.g. Wahlberg et al., 2005; Vila et al., 2011; Talavera et al., 2013; Boyle et al., 2015; Kaliszewska et al., 2015). PCRs were prepared in 25 μl reactions using the Omega 2x Taq Mastermix (Omega Bio-tek, Norcross, GA, USA) and carried out according to a touchdown protocol as follows: initial denaturation for 3 min at 94 °C, 20 cycles of 94 °C for 50 s, annealing temperature starting at 49 °C and ramping down 0.5° for every cycle for 40 s, 72 °C for 1 min, another 20 cycles of 94 °C for 50 s, annealing temperature (48–52 °C) for 40 s, and 72° for 1 min, and a final extension of 72 °C for 5 min. PCR products were checked using 1% agarose gels with SYBR® Safe DNA gel stain (Life Technologies, Grand Island, NY, USA) and a Low DNA mass ladder (Life Technologies). Amplified products were purified using 0.6 μl exonuclease I, 1 μl Antarctic phosphatase buffer and 1 μl Antarctic phosphatase (New England Biolabs, Ipswich, MA, USA) per reaction. Sequencing was done using ABI Big Dye Terminator v3.1 chemistry (Applied Biosystems, Carlsbad, CA, USA) followed by ethanol/$MgCl_2$ purification. Labeled fragments were visualized on an ABI 3730 Automatic DNA Sequencer (Applied Biosystems). Nucleotide sequences were manually edited in Geneious 6.1.7 (Biomatters, Auckland, New Zealand).

2.3. Inferring phylogenies and divergence dating

Sequences were aligned using the FFT-NS-i algorithm in MAFFT v. 7.107 (Katoh and Standley, 2013; Katoh et al., 2002). Sequences were uploaded to Genbank and accession numbers are listed in Supplementary file S3.

We jointly selected the best-fitting substitution models and partitioning schemes using the Bayesian Information Criterion in the software Partitionfinder v 1.1.1 (Lanfear et al., 2012). The program was run twice, once with the models available in BEAST v.1.8.1 (Drummond et al., 2012) and once with those in RAxML v. 8.0.0 (Stamatakis, 2006). The inferred partition schemes and models can be found in supplementary file S5.

Phylogenies were inferred using maximum likelihood and Bayesian inference on the concatenated data set of 3666 bp.

Maximum likelihood analyses were run using RAxML v 8.0.0 (Stamatakis, 2006; Stamatakis et al., 2008) using 250 rapid bootstrap (bs) replicates (as determined by the program) followed by 200 thorough maximum likelihood searches with joint branch length optimization.

To infer a dated phylogeny, we used the program BEAST v1.8.1 (Drummond et al., 2012) with an uncorrelated relaxed clock model and the tree prior set to birth–death with incomplete sampling (Stadler, 2009). All other priors were left as default except for ucld.mean, which was set to a diffuse gamma distribution with shape 0.004 and a scale of 1000 to improve convergence. To calibrate nodes, we relied mainly on fossils, using the two certainly known to be Riodinidae, host plant family age and a secondary calibration point from the literature. The first fossil is a larva of the extant genus *Theope* (Nymphidiini) from Dominican amber with a minimum age of 15–20 Mya (DeVries and Poinar, 1997) and we employed this on the stem of *Theope virgilius* and *T. philotes*. The latter was previously placed in the genus *Parnes*, but synonymized with *Theope* by Hall (1999). In his morphological phylogenetic analysis (Hall, 2002), he found *T. philotes* to fall in a clade that is the sister group to the remaining *Theope* spp., and we can therefore be relatively certain that we are not underestimating the age of *Theope* by placing the fossil on the stem of our included species. For this fossil, we applied a lognormal prior with an offset of 15, a mean of 10 and a standard deviation of 1. The second fossil we used is *Voltinia dramba* (Mesosemiini), also from Oligocene–Miocene Dominican amber with an estimated age of 15–25 Mya (Hall et al., 2004b). We applied this on the most recent common ancestor (MRCA) of the clade containing *Voltinia* and its close relative *Napaea* (Hall, 2005) (here paraphyletic with respect to *Voltinia*, and represented with *N. eucharila* and *N.* cf. *mellosa*), and set the prior as for the above. *N. actoris*, previously in the genus *Cremna*, is here shown not to be closely related to the remainder of *Napaea*, and was not seen as part of this genus for dating purposes.

Additionally, we used a secondary calibration point from Heikkilä et al. (2012). They used multiple fossils to calibrate a phylogeny of the Papilionoidea and dated the MRCA of Lycaenidae and Riodinidae to the late Cretaceous, around 88 Mya, with a credible interval of 73.2–102.5 Mya. We set this as a normal prior on the MRCA of Lycaenidae and Riodinidae, with a mean of 88 and a standard deviation of 7.5 Mya, which gave us a range of possible dates approximating the credibility interval given by Heikkilä et al. (2012). Finally, we also used the age of the primuloid host plants used by Nemeobiinae as a calibration point for this family. All known species of Nemeobiinae feed on Primulaceae *sensu lato*. Primulaceae as a whole appear to closely predate the K/T boundary (based on a "primuloid" flower: Friis et al., 2010), while the known hostplant subfamilies Myrsinoideae and Primuloideae may date back at least 45–48 Ma (Yesson et al., 2009). *Maesa*-like pollen (Maesoideae) is known from the Paleocene Lingfeng Formation c. 55–58 Ma (Song et al., 2004) and it is unlikely that the age of Nemeobiinae is much older than the age of their host plants. We applied this fossil information as a normal prior on the MRCA of Nemeobiinae (including *Styx* and *Corrachia*, see below) with a mean of 58, a standard deviation of 10, and truncated to a maximum of 60 Mya to allow for the hostplants to be slightly older than the fossils.

We ran the program three times, each with 50 million generations and sampling every 5000 generations. Convergence was checked in Tracer 1.5 (Rambaut and Drummond, 2007). Thereafter, we used LogCombiner v1.8.1 (Drummond et al., 2012) to remove a burnin of 15% of each run, combine them and resample to arrive at a final sample of approximately 10,000 trees, which were summarized as a 50% credibility consensus tree with median node heights in TreeAnnotator v 1.8.1. (Drummond et al., 2012).

BEAST and RAxML were run on the CIPRES Cluster (Miller et al., 2010).

2.4. Diversification rates and biogeography

To investigate possible diversification rate heterogeneity, we used the Bayesian Analysis of Macroevolutionary Mixtures (BAMM. 2.2.0) approach (Rabosky, 2014). This method uses reversible jump Markov Chain Monte Carlo and assumes that changes in diversification regimes along the branches of a tree follow a compound Poisson process. We accounted for non-random missing data by assigning every riodinid species included in the phylogeny to tribe, subtribe or genus cluster, and providing the proportion of the species sampled in each tribe or subtribe (Supplementary file S6, data updated from Lamas (2008)). Four Markov Chain Monte Carlo (MCMC) simulations were run for 10 million generations each with a burnin of 15%. Convergence of chains was checked in Coda (Plummer et al., 2006), and output was analyzed in the R package BAMMtools 2.0.2 (Rabosky et al., 2014).

Biogeographic inference was carried out using a model testing approach in the R package BioGeoBEARS 0.2.1 (Matzke, 2014a, 2013) which makes it possible to directly test the fit of commonly used biogeographical inference models; Dispersal-Extinction-Cladogenesis model (DEC) (Ree and Smith, 2008); maximum likelihood versions of dispersal-vicariance analysis (Ronquist, 1997) (DIVALIKE), and Bayesian biogeographical inference (BAYAREA-LIKE) (Landis et al., 2013). Our aim was to infer the worldwide biogeographical history of Riodinidae.

The range of Riodinidae was divided into eight large-scale biogeographical regions (Fig. 3). We used a condensed phylogeny only including one member per genus (except for non-monophyletic genera), and ran a simple model with no geographical constraints, followed by a more complex model where dispersal rates were scaled according to area connectivity across three time slices, 0–30 Mya, 30–60 Mya and before 60 Mya, and adjusted connectivity between biogeographical regions across time (supplementary file S7, modified from Buerki et al., 2011) to account for the changes in geography through time. Additionally, we tested whether a model allowing founder effect speciation (+j, jump of a daughter lineage to an area outside the parental distribution, Matzke, 2014b) would improve the likelihood of the model given the data. These four analyses were repeated for all three inference methods (DEC, DIVA, BAYAREA) and AIC scores and weights were used to infer the best model. Additionally, we ran the stratified DEC + j with the root fixed to the Neotropical region. BioGeoBEARS should technically only be applied on species level phylogenies, but since genera in our phylogeny can confidently be assigned to a single area (or in a few cases two areas) the analysis should not be biased towards widespread ancestors. An analysis of the historical biogeography of the New World Riodininae was not attempted since many genera are widely distributed, and in many cases not well delimited.

3. Results and discussion

3.1. Phylogeny and classification

The total 3666 bp matrix contained a total of 19% missing data (see Supplementary file S3 for Genbank accession numbers), but

one or more specimens per genus was covered by at least one mitochondrial (COI) and two nuclear genes (Ef1-a and wg) to minimize effects of missing data. Trees inferred using maximum likelihood and Bayesian inference showed no major well-supported conflicts and only the dated Bayesian tree is showed here (Fig. 2) with ranges of posterior probabilities (pp) presented as colored squares above and bootstrap values below branches (see Fig. 2 legend for explanation). Both the likelihood and Bayesian tree with the numerical support values can be found in the supplementary information (Supplementary file S8 and S9). We consider a clade to be "supported" when it has an ML bootstrap support value of >75% and posterior probabilities equal to or higher than 0.95.

Higher-level patterns in our phylogeny (Fig. 2) to some degree conform to the classification based on morphology with Riodininae being monophyletic (bs: 100, pp: 1), and with a sister group relationship between Nemeobiinae and Euselasiinae (bs: 92, pp: 1). However, the placement of Styx and Corrachia as a subtribe within Euselasiinae (Hall and Harvey, 2002a) was not supported by our analyses. Rather, we found that the heretofore exclusively Old World subfamily Nemeobiinae is monophyletic (bs: 100, pp: 1) as long as Styx and Corrachia are included. These monotypic genera, endemic to the Peruvian Andes and mountains in southern Costa Rica, respectively, are recovered as sister groups (bs: 100, pp: 1) and are again sister to the widely distributed Oriental genus Zemeros (bs: 78, pp: 1), mainly found in secondary and degraded forest from 0 to 2000 m elevations (Callaghan, 2009). Harvey (1987a) mentioned that the male genitalia of Styx infernalis and Corrachia leucoplaga, as well as their eggs, are similar, which support their placement as sister taxa. Additionally, Harvey found that one synapomorphy for his subfamily Hamearinae (now Nemeobiinae), having hindwing veins Rs and M1 stalked, was found outside this subfamily only in Corrachia, sometimes in Styx, and in Stalachtis (Riodininae). He argued that this venation pattern was presumably convergent in all three cases. However, our analysis showed that it is only convergent in Stalachtis, a genus that unequivocally belongs in the Riodininae.

Our placement of Styx also agrees with molecular studies with sparser taxon sampling (Wahlberg et al., 2005; Heikkilä et al., 2012; Saunders, 2010), which consistently placed Styx together with Hamearis, when the latter was the only representative of the traditional Nemeobiinae that was included. Rearing of Styx (Hall et al., unpubl.) also shows that the larvae lack spatulate setae on the tibia that are characteristic for Euselasiinae (Harvey, 1987b). Furthermore, it was recently discovered that larvae of both Styx and Corrachia feed on species of Myrsine in the Primulaceae s. l. (Lamas, 2003; Nishida, 2010), the same family (and in some cases the same genus) used by Old World Nemeobiinae. Thus, Primulaceae feeding is not convergent in Riodinidae, except in one case: even though several Primulaceae genera occur in South and Central America, only the polyphagous Emesis diogenia (Riodininae) is otherwise known to feed on this family in the Neotropics (Diniz and Morais, 1995; Robinson et al., 2010).

Within Nemeobiinae, the current tribal classification is at variance with our results. Our phylogeny indicates that Nemeobiinae consist of two major clades, the first (bs: 97, pp: 100) which includes a polyphyletic Abisara (a clade including the type species A. kausambi being sister to the Afrotropical Afriodinia) together with six other tropical genera (Saribia, Dicallaneura, Laxita, Taxila, Praetaxila, Paralaxita; see below for Archigenes, which is reinstated), and the second (bs: 100, pp: 1) containing the rest of the nemeobiine genera, including Styx, Corrachia, Zemeros, Stiboges, the Abisara fylla group, Dodona, and the more temperate "hamearine" genera Hamearis, Polycaena and Takashia. The name Abisarini Stichel, 1928 should be used for the first clade, and the oldest available name for the second clade would be Nemeobiini Bates, [1868]. We do not have enough information to further subdivide the
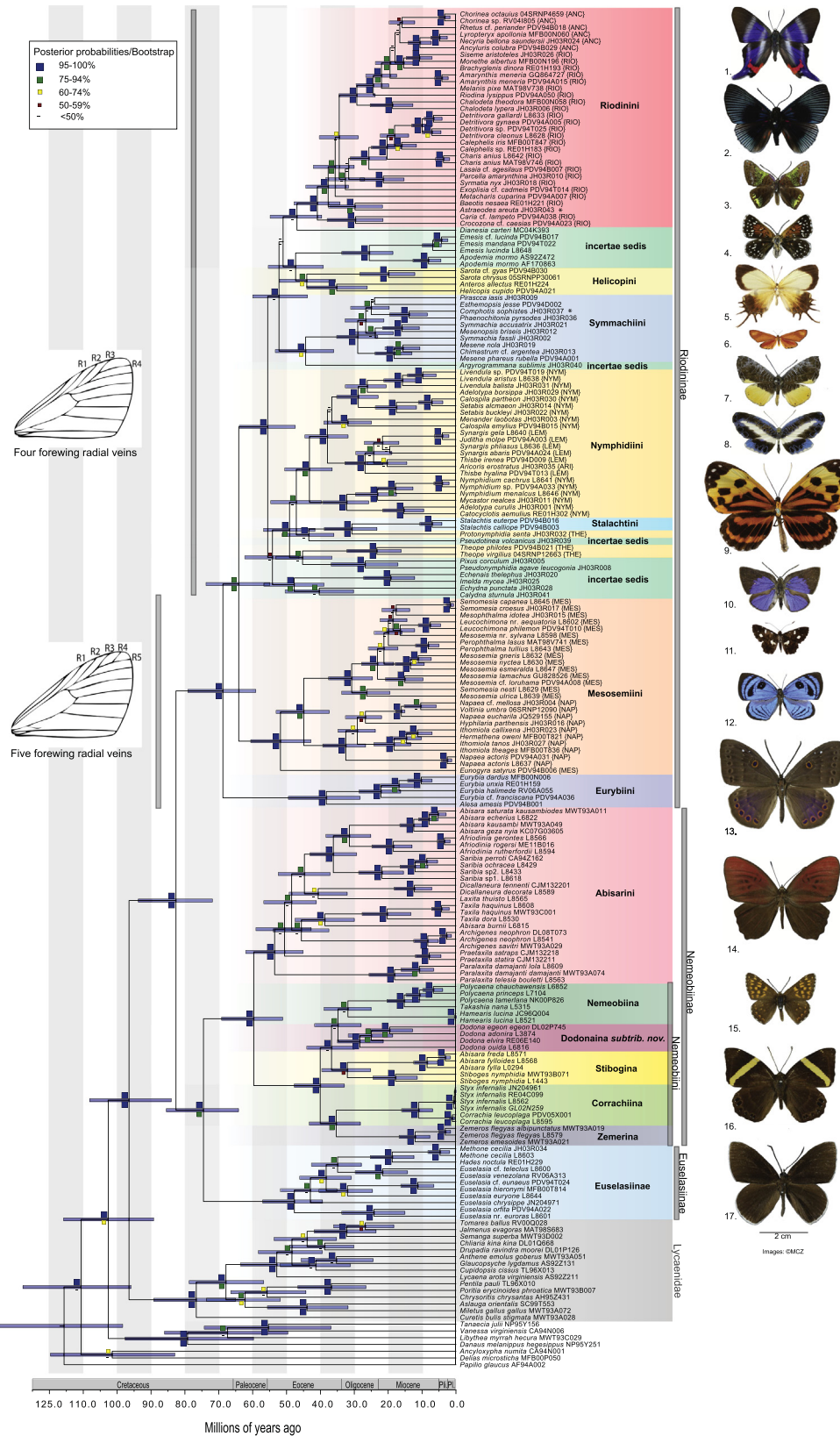
Fig. 2. Dated phylogeny of the Riodinidae with posterior probabilities above branches and bootstrap values below. See the box inset at upper left for explanation. Colors for clades indicate classification prior to this work (shown in Fig. S1). Three letter abbreviations in curly brackets after taxon names imply subtribe or section placement prior to this work. Asterisks denote genera that where placed in the *incertae sedis* group prior to this study. Line drawings of wings on the left show the differences in the number of radial veins between tribes in the Riodininae. Purple bars on nodes denote the 95% credibility interval. ANC = Ancyluris section; RIO = Riodina section; NYM = Nymphidiina; LEM = Lemoniadina; THE = Theopiina; NAP = Napaeina; MES = Mesosemiina. The butterflies pictured are: (1) *Rhetus dysonii*, (2) *Lyropteryx apollonia*, (3) *Caria trochilus*, (4) *Apodemia mormo*, (5) *Helicopis cupido*, (6) *Mesene nola*, (7) *Catocyclotis aemulius*, (8) *Nymphidium mantus*, (9) *Stalachtis calliope*, (10) *Theope theritas*, (11) *Calydna hiria*, (12) *Semomesia croesus*, (13) *Eurybia molochina*, (14) *Paralaxita damajanti*, (15) *Hamearis lucina*, (16) *Abisara fylla*, (17) *Hades noctula*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
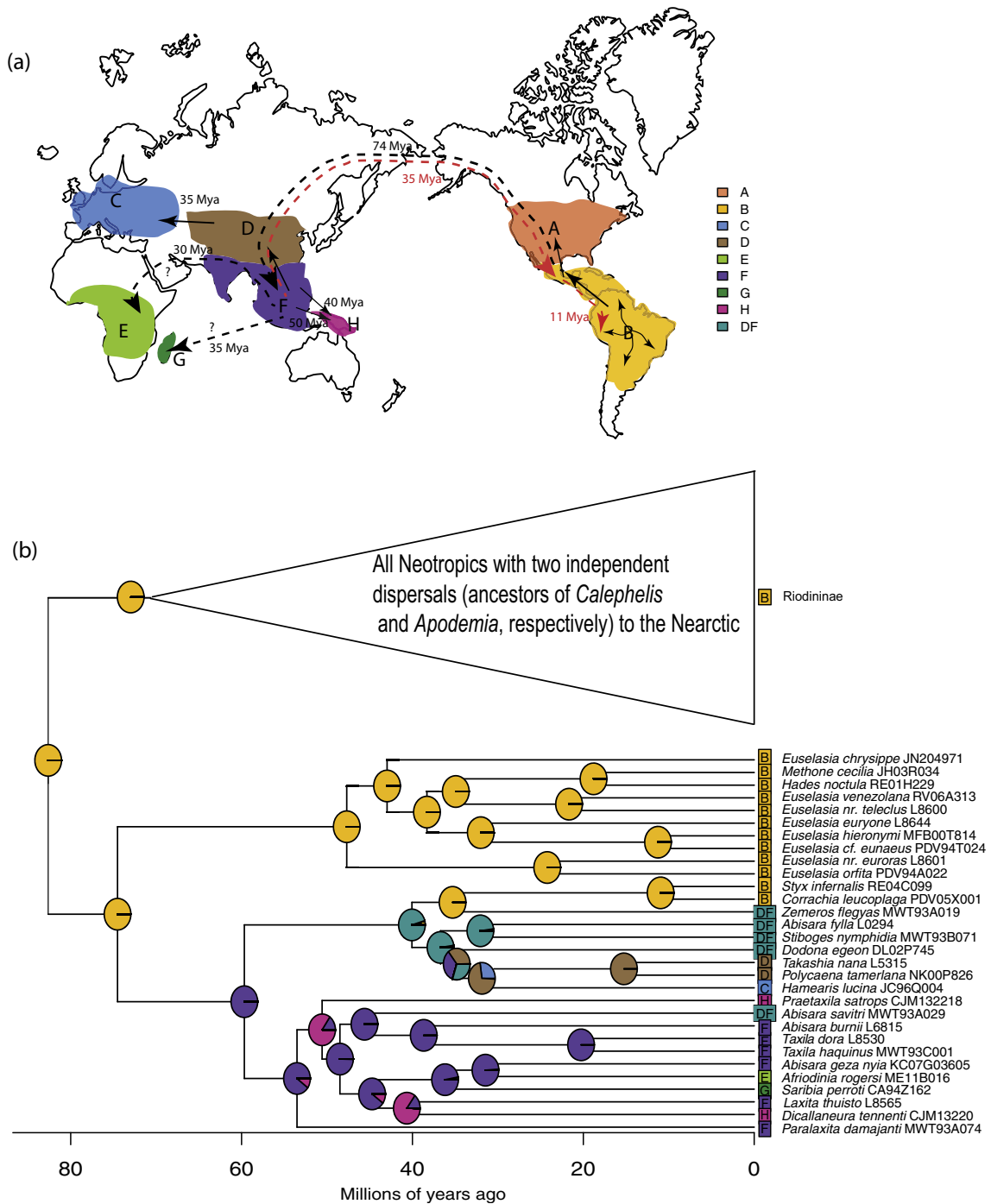
Fig. 3. Biogeographical scenario for Riodinidae using the second best model (stratified BAYAREALIKE + j) inferred from our data by BioGeoBEARS (Matzke, 2014a,b; see discussion in text). (a) Map showing a potential "out of the Neotropics" biogeographical scenario. Black stippled line across Beringia depicts the dispersal of the ancestor of Nemeobiinae to the Old World. Red stippled line shows dispersal of the ancestor of *Styx* and *Corrachia* back into the New World. (b) Condensed phylogeny, with the most likely areas from the stratified BAYAREALIKE + j model presented as pie charts on each node. Only genera found north of far southern Texas are considered as Nearctic in this analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Abisarini into subtribes (although Abisarina would comprise our well supported clade of *Abisara* s.s., *Afriodinia* and *Saribia*; bs: 100, pp: 1), but the Nemeobiini can be subdivided into Nemeobiina (*Hamearis*, *Polycaena*, *Takashia*), Stibogina Stichel, 1928 (*Stiboges* and tentatively the *Abisara fylla* group), Corrachiina Stichel, 1928 (*Corrachia*, *Styx*), Zemerina Stichel, 1928 (*Zemeros* only) and Dodonina Espeland & Hall **subtr. n.** (*Dodona* only, as the type genus) (Fig. 2). Although the subtribe Nemeobiina is not well

supported here (bs: <50, pp: 0.79), features from morphology and biogeography support the recognition of this subtribe. The name *Archigenes* Fruhstorfer, 1914 is available for the *Abisara savitri* group (see Saito and Saito, 2005 for morphological characters delimiting this group) and we propose to reinstate this name for this group (*Archigenes aita* (De Niceville, 1893) **comb. rev.** [type species], *Archigenes neophron* (Guérin, 1843) **comb. rev.**, *Archigenes chela* (Guérin, 1843) **comb. rev.**, *Archigenes attenuata* (Tytler, 1915)

comb. nov., *Archigenes miyazakii* (K. Saito & T. Saito, 2005) comb. nov., *Archigenes atlas* (de Nicéville, 1895) comb. rev, *Archigenes savitri* (Guérin, 1843) comb. rev.).

With the removal of *Styx* and *Corrachia*, Euselasiinae (bs: 100, pp: 1) is again confined to the large widespread genus *Euselasia* and the more range-restricted mono/bitypic genera *Methone* and *Hades*. However, our analysis firmly indicates that the phenotypically distinct *Methone* and *Hades* may be phylogenetically nested within *Euselasia*, although greater taxon and gene sampling will be needed to confirm this unexpected finding and establish the most closely related of the many *Euselasia* species groups.

Within Riodininae, the two five-Forewing-Radial-Veined (FRV) tribes (Eurybiini and Mesosemiini) are found to be basal to the remaining four-FRV tribes (Fig. 2). However, we find that Eurybiini is sister to the rest of the subfamily (bs: 100, pp: 1), followed by Mesosemiini (bs: 79, pp: 0.91). This is at variance to what Hall (2003) found (Mesosemiini being sister to the remainder of Riodininae), although his tentative hypothesis was admittedly based on only a single synapomorphy, the fusion of pupal abdominal segments 9 and 10 that appeared to unite Eurybiini and the four-FRV tribes of Riodininae. Hall (2003) subsumed the five-FRV *incertae sedis* group of Harvey (1987a) within Mesosemiini, placing most genera within the new subtribe Napaeina, but treating *Eunogyra* and *Teratophthalma* in Mesosemiina. This arrangement is largely corroborated here (Fig. 2, subtribe name abbreviations in curly brackets after taxon name), but we find that *Eunogyra* maybe sister to the rest of the Mesosemiini (bs: 94, pp: 1) rather than the rest of the Mesosemiina. However, given the long evolutionary branch lengths inferable from morphological and ecological data between *Eunogyra* and *Teratophthalma*, and to a slightly lesser extant between *Teratophthalma* and the remainder of Mesosemiina (Hall, 2003), the deepest nodes within Mesosemiina will only be definitely resolved with the inclusion of the here-missing *Teratophthalma* in any future analyses.

Symmachiini is defined by the presence of concealed androconial scales on the anterior margins of abdominal tergites 4–7 in males. *Phaenochitonia* has a limited number of these scales, and has consequently been hypothesized to be the most ancestral genus in Symmachini (Harvey, 1987a). *Comphotis* lacks these scales and was placed by Harvey (1987a) in his four-FRV *incertae sedis* section. However, based on wing pattern and genitalia similarities with *Phaenochitonia*, Hall and Willmott (1996) showed that *Comphotis* was clearly associated with Symmachiini, and thus suggested that the genus might be sister to the remainder of the tribe. By contrast, in our analyses, *Comphotis* and *Phaenochitonia*, appear as a derived sister group within Symmachiini (bs: 100, pp: 1), suggesting that the lack of androconial scales is a secondary loss.

Riodinini is found to be monophyletic with the inclusion of *Astraeodes* (currently placed in the four-FRV *incertae sedis* section) (bs: 100, pp: 1). Although this monotypic genus was placed in the polyphyletic four-FRV *incertae sedis* section (see Fig. 2) by Harvey (1987a), it has long been suspected to be a member of Riodinini based on genitalia similarities, the presence of gold markings along the wing margins, and the frequent attraction of males to rotting fish bait (Hall, unpubl.).

With well over 300, often rare, species, Nymphidiini is by far the largest tribe in the family. Our taxon sampling density is thus lower than for the other higher taxa, rendering many findings preliminary. For example there is insufficient data and support to make any meaningful comments on the established subtribe arrangement (Hall, 1999, 2002, in press). However, notable findings include the potential inclusion within Nymphidiini of *Stalachtis* (Stalachtini) see below) and the *incertae sedis* genera *Pseudotinea*, *Pixus* and *Pseudonymphidia* (bs: 80, pp: 100). The last two genera together with *Pachythone*, *Minstrellus*, *Machaya*, *Lamphiotes* and *Roeberella* (not included here) constitute the

Pachythone cluster of genera of the *incertae sedis* section (Hall, 2007). Hall and Harvey (2001) and Hall (2007) suggested that this cluster should be placed in or near Nymphidiini, because they share certain similarities with members of Nymphidiini such as greasy wings. *Pseudotinea* has also been suspected to belong in Nymphidiini, based particularly on possessing long labial palpi and an incomplete vinculum dorsally at the anterior margin of the tegumen (Hall and Callaghan, 2003). Many genera within Nymphidiini are recovered as non-monophyletic and are in need of revision (Hall, in press).

The highly apomorphic genus *Stalachtis* has been placed in its own clade for over 150 years, initially as the subfamily Stalachtinae (Bates, 1861) and subsequently as the tribe Stalachtini (Stichel, 1910–11). We, however, find *Stalachtis* to be nested within the Nymphidiini, thus meriting only subtribal level at most, a result also reported by Saunders (2010). This is a very surprising finding since all established Nymphidiini species with known life histories exhibit multiple early-stage synapomorphies related to ant association, and these are all lacking in *Stalachtis* species. That is, *Stalachtis* lacks the universal larval synapomorphies of the Nymphidiini: a pair of vibratory papillae on the prothorax and a ventrally positioned spiracle on larval abdominal segment one (Harvey, 1987a; Hall, 1999, 2002). Nymphidiine caterpillars also possess pore copula organs (PCO), anterior tentacle organs (ATO) and tentacle nectary organs (TNO), all of which are related to ant association (DeVries, 1988, 1991b; Hall and Harvey, 2002b), and which are not present in *Stalachtis*. Additionally, adults of many nymphidiines have greasy wings, which perhaps makes it easier for them to escape the ants (DeVries, 1991b; Hall, 2007; Hall and Harvey, 2002a, 2002b). None of these traits are found in *Stalachtis* and much denser sampling is needed in and around the Nymphidiini to definitively and more accurately place this enigmatic genus.

New tribes might need to be erected for some of the *incertae sedis* groups that are scattered in the tree in Fig. 2, such as the *Emesis-Apodemia* group, the *Echenais* group, *Argyrogrammana* and *Dianesia*, but higher gene and taxon sampling is needed before this should be attempted, since we have little support at this level of the phylogeny. It is interesting to note, however, that the monotypic genus *Dianesia*, currently the only riodinid in the Antilles (Cuba and the Bahamas) seems to be nearly 50 million years old.

3.2. Biogeography and the Styx and Corrachia enigma

The stratified DEC model with founder effect speciation was found to be the best model by BioGeoBears (AIC = 133.4, Table 1). This model, however, gives a geologically implausible ancestral distribution, with Riodinidae originating in the Oriental (OR), Eastern Palearctic (EP) and Neotropical (NT) regions in the late Cretaceous (Supplementary file S10). This disjunct distribution of the ancestor is unlikely because until the Great American Interchange, there has not been a connection between the Neotropical and Palearctic/Oriental regions since the break up of Pangaea (e.g. Frisch et al., 2011), which occurred long before the assumed origin of Papilionoidea in the early Cretaceous (Heikkilä et al., 2012). Therefore, we instead present the second best model (stratified BAYAREALIKE + j, AIC = 140.6) as a more plausible scenario (Fig. 3, Table 1), where Riodinidae originated in the NT and there was a founder-effect speciation event from the NT to the OR in the ancestor of Nemeobiinae and another in the ancestor of *Zemeros* + *Styx* + *Corrachia*. Additionally, there were independent dispersal events to Africa and Madagascar and twice to NG (New Guinea and surrounding islands) from the OR. It seems likely that the dispersal to Africa from OR could have occurred overland at a time when lush tropical forests were much more extensive as has been documented in the Fayum fossil fauna of Egypt 30–35 Mya (Bown et al., 1982). The timing of the overseas arrival

Table 1
Parameters from biogeographical model testing in BioGeoBEARS. Best model (**) and second best (*) model (shown in Fig. 3) are highlighted in bold.

Model	LnL	# free parameters	AIC	ΔAIC	AIC weight vs. best	AIC weight ratio vs. best	d	e	j
DEC model	−90.06	2	184.1	50.7	9.18E−12	1.05E+11	9.92E−04	1.00E−05	0.00E+00
DEC + j model	−79.97	3	165.9	32.5	8.11E−08	1.19E+07	2.63E−04	1.00E−05	3.58E−03
Stratified DEC model	−70	2	144	10.6	4.73E−03	2.04E+02	2.09E−03	1.00E−05	0.00E+00
**Stratified DEC + j model	−63.68	3	133.4	0	9.67E−01	1.00E+00	1.46E−03	1.00E−05	2.01E−02
DIVALIKE model	−94.5	2	193	59.6	1.08E−13	8.94E+12	1.03E−03	9.55E−04	0.00E+00
DIVALIKE + j model	−90.18	3	186.4	53	2.98E−12	3.24E+11	8.42E−04	1.80E−05	5.86E−04
Stratified DIVALIKE model	−76.62	2	157.2	23.8	6.26E−06	1.54E+05	2.70E−03	1.00E−05	0.00E+00
Stratified DIVALIKE + j model	−71.8	3	149.6	16.2	2.88E−04	3.36E+03	1.79E−03	1.00E−05	2.58E−02
BAYAREALIKE model	−102.18	2	208.4	75	5.00E−17	3.84E−19	9.88E−04	3.18E−03	0.00E+00
BAYAREALIKE + j model	−82.57	3	171.1	37.7	6.06E−09	1.60E+08	1.00E−05	1.52E−03	6.06E−03
Stratified BAYAREALIKE model	−87.78	2	179.6	46.2	8.94E−11	1.08E+10	1.82E−03	3.44E−03	0.00E+00
*Stratified BAYAREALIKE + j model	−67.3	3	140.6	7.2	2.58E−02	3.74E+01	1.10E−03	1.00E−05	3.39E−02
Stratified DEC + j model, root fixed to B	−69.89	3	145.8	12.4	1.93E−03	5.00E+02	1.66E−03	1.00E−05	1.82E−02

LnL = log likelihood, d = dispersal rate per million years along branches, e = extinction rate per million year along branches, j = founder event speciation weighted per speciation event.

Table 2
Most probable area inferred for the root, ancestor of Nemeobiinae + Euselasiinae, ancestor of Nemeobiinae, ancestor of Nemeobiini and ancestor of Styx, Corrachia and Zemeros (ZSC). Best (**) and second best (*) model shown in bold. B = Neotropics, D = E Palearctic, F = Oriental.

Model	Root	Euselasiinae + Nemeobiinae	Nemeobiinae	Nemeobiini	ZSC
DEC model	BDF	BDF	BDF	BDF	BDF
DEC + j model	BDF	BDF	BDF	BDF	BDF
Stratified DEC model	BDF	BDF	BDF	BDF	BDF
**Stratified DEC + j model	BDF	BDF	BDF	BDF	BDF
DIVALIKE model	B	BF	DF	D	BF
DIVALIKE + j model	B	BF	F/E	D	BF
Stratified DIVALIKE model	B	BF	BDF	BDF	BD/BF
Stratified DIVALIKE + j model	B	BF	F	D	BD
BAYAREALIKE model	B	BF	F	DF	BF/B
BAYAREALIKE + j model	B	B	F	DF	DF
Stratified BAYAREALIKE model	BF	BF	F	BDF	BF
*Stratified BAYAREALIKE + j model	B	B	F	EF	B

in Madagascar (leading to the genus *Saribia*) from Asia around 35 Mya, maybe through India, would coincide with the timing of the hypothesized expansion of the Malagasy rainforest biome inferred from three independent tree fern radiations (Janssen et al., 2008). Dispersal events to NG 40–45 Mya presumably benefited from the increasing proximity of the Australian and Asian plates, but in the case of Madagascar dispersal probably still involved traversing some considerable oceanic distances. In the Riodininae, there were two separate dispersals to the Nearctic in the ancestors of *Apodemia* (mainly SW United States, not shown) and *Calephelis* (Central and Eastern US, not shown). A similar scenario was also found when using the stratified DEC + j model while constraining the root to the Neotropics (AIC = 145.8). The NT is the only area consistently found among the areas reconstructed for the root in all analyses (Table 2), and this further supports a Neotropical origin.

A single origin of the Old World taxa (Nemeobiinae) while there already was a New World radiation (Riodininae) in the Neotropics points to dispersal rather than vicariance during Gondwanan times, and the lack of Australian riodinids (with the exception of *Praetaxila segecia* in far northern Queensland, which is clearly of New Guinean origin) precludes a faunal link between Australia and South America (De Jong and van Achterberg, 2007). The Riodininae and Euselasiinae have their center of diversity in lowland forests of the western Amazon, which supports the hypothesis that they, and consequently the entire family, originated in this area. This would further suggest a single migration event to the Old World in the Paleocene or early Cretaceous, presumably through Beringia (although possibly at somewhat lower latitudes via the North Atlantic De Geer route: Brikiatis, 2014) followed by

extinctions in the Nearctic and NE Palearctic as the climate in these areas cooled, a pattern that has been inferred for many organisms. More than 80 genera of plants are, for example, known to have a disjunct Neotropical-Southeast Asian distribution (e.g. tropical 'amphi-Pacific' distribution: Thorne, 1972), as do several animals with limited dispersal power, such as legless lizards (Townsend et al., 2011), freshwater crustaceans (van Damme and Sinev, 2013) and harvestmen (Sharma and Giribet, 2012). Migration via Beringia has been inferred to be the most probable route giving rise to this disjunction for organisms of various ages (e.g. Wang et al., 2004; Townsend et al., 2011; Vila et al., 2011; Li and Wen, 2013; Chin et al., 2014; but see Sharma and Giribet, 2012 for a different explanation). Brikiatis (2014) suggested the De Geer route would have been climatically favorable for biotic exchange between 69 Mya and 65.5 Mya, dates that match the split between Euselasiinae and Nemeobiinae quite well, although this scenario would require large scale extinction in, and subsequent back migration to, the western Palearctic. The only other option would be transoceanic dispersal across the Pacific and/or stepping-stone dispersal across Pacific islands, which is implausible given the vast distances involved and the fact that no riodinids exist on any Pacific islands today.

3.3. Diversification and hostplants

Riodininae started diversifying slightly earlier than Nemeobiinae and Euselasiinae (Fig. 2), but the major diversification in all subfamilies started around 50–55 Mya in the early Eocene. Additionally, the Euselasiinae crown group is younger, but more species-rich than that of Nemeobiinae, so age alone cannot explain
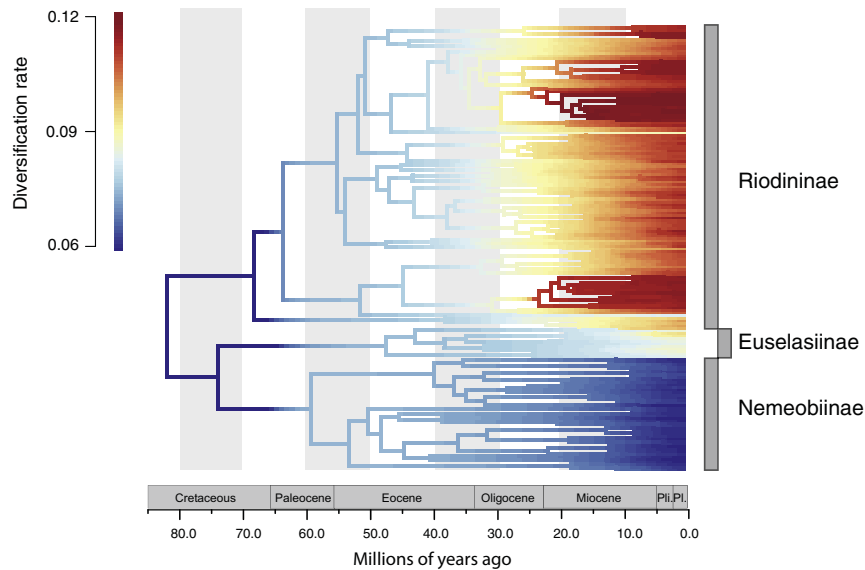
Fig. 4. Mean phylo-rate plot from BAMM (Rabosky, 2014). Red depicts higher diversification rate and blue depicts lower diversification rate. No abrupt shifts in diversification rate on any branches were found, but differences among subfamilies as we define them are apparent. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the great diversity in the New World. The timing of this early diversification coincides with the Paleocene–Eocene Thermal Maximum (PETM, ∼53 Mya: Zachos et al., 2001), and corresponds to the fossil record showing dramatically increased herbivory by insects on angiosperms around this time (Currano et al., 2008), likely including Riodinidae. The angiosperms also diversified significantly during this period (Jaramillo et al., 2010).

We inferred diversification rates (speciation – extinction rate) and possible rate shifts in BAMM. Five shift configurations explained 0.966 of the posterior probability. The best shift configuration had 0 shifts ($p = 0.71$). The second best had 1 shift ($p = 0.19$), an increase in rate at the base of the Nemeobiinae. A phylo-rate plot of model-averaged speciation rates at any point on the phylogeny (Fig. 4) shows that rather than abrupt shifts, there was a gradual increase in diversification rate toward the present in Riodininae, and to a lesser degree also in Euselasiinae, whereas diversification is slowly decreasing over time within Nemeobiinae. The mean speciation rate across the entire riodinid evolutionary history was 0.115 [0.094 (5% quantile)–0.148 (95% quantile)] lineages My^{-1} and mean extinction rate was 0.029 [0.002–0.07] My^{-1}. For Nemeobiinae, mean speciation rate was 0.107 [0.071–0.140] My^{-1} and mean extinction rate was 0.029 [0.002–0.072] My^{-1}, whereas for Euselasiinae, mean speciation rate was 0.113 [0.088–0.153] My^{-1}, and mean extinction rate was 0.027 [0.002–0.071] My^{-1}. Thus Euselasiinae had a lower speciation rate than the more diverse Riodininae (for which mean speciation rate was 0.119 [0.094–0.158] My^{-1} and mean extinction rate was 0.029 [0.003–0.075] My^{-1}). However, this difference is rather small and there is also large variation in estimates across the posterior, as seen by the 5% and 95% quantiles presented in square brackets above. In contrast to what has been observed in Nymphalidae (Wahlberg et al., 2009), diversification does not decrease around the K-T boundary.

Age alone cannot explain the large discrepancy in diversity between subfamilies since Euselasiinae diversified later than Nemeobiinae, but is more diverse, and the megadiverse Riodininae started to diversify only about 10 My earlier than Nemeobiinae. Hostplant breadth correlates with subfamily diversity; Nemeobiinae (110 spp. including *Styx* and *Corrachia*) feeds on three subfamilies within Primulaceae (Myrsinoideae, Primuloideae and Maesoideae), and Euselasiinae (c. 176 spp.) feeds

on at least six plant families (Nishida, 2010), while Riodininae (c. 1200 spp.) feeds on around 70 families (Robinson et al., 2010). Such a relation between diversification and diet breadth was also hypothesized for the Limenitidini (Nymphalidae), where the highly diverse Neotropical genus *Adelpha* feeds on 28 plant families, whereas closely related but less diverse genera are restricted to just a few closely related hostplant species (Mullen et al., 2011). Multiple other traits can, however, correlate with hostplant breadth, such as topography, forest structure, flight height, larval ant association and warning coloration (Pierce and Elgar, 1985; Beccaloni, 1997; DeVries et al., 1999; Elias et al., 2008; Hill, 2010), and the relative importance of these factors needs to be assessed.

Originating in the Cretaceous, Riodinidae is, to our knowledge, likely the oldest butterfly group for which an Amazonian origin has yet been inferred. Most studies on the origin of extant Neotropical biodiversity use either genus crown groups or sister-species comparisons to study potential driving factors of diversification. Consequently, the extant diversity seems mainly to be the result of relatively recent events in the Neogene or Pleistocene (e.g. Hoorn et al., 2010; Rull, 2011; Garzón-Orduña et al., 2014), with older diversification events left unstudied. Riodinids were already diverse in the Neotropics before the start of the climatic fluctuations in the Pleistocene, so other factors must have been important in the initial diversification of this group. The old Neotropical origin of Riodinidae makes the family an excellent system for the study of the ancient diversification in the Neotropics.

4. Conclusions

We provide the first well-sampled higher-level molecular phylogeny of the Riodinidae and examine the temporal and spatial scale of macroevolution. Using 3666 bp from one mitochondrial and four nuclear markers for each of 22 outgroups and 178 taxa representing all Riodinidae subfamilies, tribes, subtribes and 98 out of 145 described genera, we have resolved a number of phylogenetic issues within the Riodinidae, including the placement of the enigmatic genera *Styx* and *Corrachia* within the Old World subfamily Nemeobiinae. An origin in the proto-Amazon followed by a single migration event from the Neotropics to the Old World

through Beringia in the late Cretaceous is recovered as the most plausible single-origin hypothesis. Another migration event in the opposite direction, through Beringia in the Oligocene or early Miocene might then explain the presence of *Styx* and *Corrachia* in the Neotropics. The discrepancy in diversity between the New World and the Old World riodinids seems to be the result of gradually increasing diversification in the Neotropics, concomitant with a gradual slowdown of diversification in the Old World. Our study provides an improved framework to revise the systematics and classification of the Riodinidae, as well as a model system for studying ancient Neotropical diversification, for a detailed understanding of the ecological and biogeographic factors or evolutionary innovations that have produced such rich Neotropical diversity.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2015.08.006.

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