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A glide over the Indo-Australian geological maze: repeated transgressions of Lydekker's and Wallace's Lines in archdukes, barons and dukes (Nymphalidae: Limenitidinae: Adoliadini)

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Archdukes, barons, counts, dukes and marquises are forest-dwelling butterflies found in mainland Asia and most islands of the Indo-Australian archipelago west of Wallace's Line, with only a few species occurring as far east as the Bismarck Archipelago. This pattern is unusual among butterfly groups of the region, which often present more widespread geographical ranges bearing little signature of Lydekker's and Wallace's Lines. Using a molecular multimarker matrix, we infer the first dated phylogeny for this clade and estimate its biogeographical history. We recover the Oriental genus *Euthalia* as polyphyletic, although other genera are monophyletic. The clade originated in continental Indomalaya in the late Oligocene ~24 Mya, when the Indo-Australian archipelago was at one of the most dynamic stages of its orogeny. Multiple independent colonization events towards the Lesser Sunda Islands, Moluccas, Australia and New Guinea suggest the relative permeability of Lydekker's and Wallace's Lines to these butterflies. Colonization of Melanesia took place twice, probably before the recent formation of Sulawesi. The study of Indo-Australian Adoliadini provides additional evidence that biogeographical barriers long thought to prevent exchange between the Asian and Australian biotas are, in fact, permeable especially to vagile insect lineages in the region.

ADDITIONAL KEYWORDS: Bayesian relaxed clocks – endemism – historical biogeography – Limenitidinae – Miocene –Wallacea.

INTRODUCTION

The Indo-Australian archipelago (IAA) is a composite geographical area stretching from continental Southeast Asia towards Melanesia, encompassing what Alfred Russel Wallace coined the Malay Archipelago (Wallace, 1869; Lohman *et al.*, 2011). This large tropical archipelago comprises landmasses of very different geological origins and a biota that reflects this complex tectonic history. His work in the Malay Archipelago made it obvious to Wallace (1869) not only how important geological processes were in the formation of faunal mosaics, but how natural history could help to inform geologists. The geological history of the IAA has since been the focus of biological research aiming at reconstructing the evolution and diversification of clades in this archipelagic landscape through space and time at an increasingly finer scale. Our understanding of the IAA geological assembly has never been this precise, in turn allowing biogeographical hypotheses to be tested in an interdisciplinary framework (Hall & Holloway, 1998).

There are clear demarcations in the geographical distributions of clades in the IAA; in fact, some of the most abrupt biotic transitions in the world can be found here, e.g. Wallace's and Lydekker's Lines (the eastern margin of the Asian Sunda Shelf and the western margin of the Australian Sahul Shelf, respectively). Between them lies the Wallacean Archipelago or Wallacea, what is often described as a transition zone

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*Corresponding author. E-mail: emmanuel.toussaint@ville-ge.ch between Oriental and Australian biota (Lohman *et al.*, 2011). Some biogeographers have invoked vicariance, such as biota being moved on microcontinental fragments (Gondwanan material that broke off New Guinea, for example, or drifting Pacific island arcs) from east to west (including Wallace, 1863), to explain extant mosaic distribution patterns in the IAA, in particular in Wallacea. Microcontinents carrying Australian biota would collide with others housing Oriental biota and create larger islands containing clades with very different biogeographical histories. Others took a more dispersionalist view (such as Wallace, 1876) or both (for a detailed review, see Lohman *et al.*, 2011). At present, geological evidence suggests that 'Fragmentation occurred, but has been driven by extension related to subduction, accompanied by complex vertical movements, creating mountains and deep basins influencing biogeography' (Hall, 2017: 343). In short, this presents a framework to test more regional diversification processes empirically over time, rather than invoking long-distance (passive) transport of biota from remote source areas.

Increasing numbers of detailed studies of highly diverse Wallacean arthropods further highlight the role of this geologically complex region as a cradle of diversity. At the same time, it becomes apparent that geographical lineage diversification patterns across Wallacea might also be rather complex, involving multiple crossings of Wallace's and Lydekker's Lines and with different directionality, e.g. with mainland Asian, Sunda or Melanesian source areas (e.g. Condamine et al., 2013, 2015; Toussaint & Balke, 2016; Toussaint *et al.*, 2018; Rowe *et al.*, 2019), even by flightless insects (e.g. Tänzler et al., 2014, 2016; Toussaint *et al.*, 2015). This transition zone consists of three major geographical features, namely Sulawesi, the Moluccas and the lesser Sunda Islands.

Sulawesi is the largest island of Wallacea and is situated right in the heart of the IAA, between Borneo, New Guinea, the Philippines and the lesser Sunda Islands. It features a particularly diverse biota of different geographical origin, predominantly Oriental but also Australian, that has greatly fascinated Wallace (1876) and many naturalists after him (reviewed by Lohman *et al.*, 2011; Stelbrink *et al.*, 2012). In a vicariance scenario, biota would have been transported on microcontinents of the Sula Spur, which is a roughly westward-pointing spur-like extension of the New Guinea region that drifted northwards with the Australian plate (Hall, 2017: fig. 5). Collision of such fragments with West Sulawesi would form the island of Sulawesi, with its central and southern parts being of Australian origin, and explain mosaic biogeographical patterns (see Stelbrink *et al.*, 2012). In fact, summarizing results from different molecular phylogenetic studies, Stelbrink *et al.* (2012) suggested that faunal assembly was driven by both vicariance and dispersal and also suggested that Pliocene fluctuations of sea level might have facilitated faunal exchange. Further back in time, Miocene colonization, possibly also mediated by sea-level changes, from the (Oriental) west and subsequent diversification in a proto-Sulawesi island setting was proposed, e.g. for endemic squirrels (Nannosciurinae; Hawkins *et al.*, 2016). These studies imply that the region featured different islands that would have catalysed initial clade diversification during the Neogene, after collision of the Sula Spur and (north) western parts of Sulawesi (see Stelbrink *et al.*, 2012; Hall, 2017; Nugraha & Hall, 2018). Nugraha & Hall (2018) present the latest tectonic interpretation of Sulawesi and provide new palaeogeographical maps for the postcollisional history at close intervals for the past 20 Myr, including maps considering shifts of the coastline (the configuration of land and sea in the region) caused by changes in sea level. Sulawesi gained its present relief and shape only over the past 5 Myr, for the most part rather recently, from 2 Mya.

In contrast, the much smaller Moluccan islands, including Halmahera, Ambon and Seram, which link Sulawesi with New Guinea, in addition to the lesser Sunda Islands, such as Bali, Lombok, Sumbawa, Flores and Timor, which link Sundaland with the Sahul shelf islands in the east, remain much less studied (Tänzler *et al.*, 2016).

Set against this geological background, we here investigate the evolutionary history of some of the most emblematic arthropods of the region, i.e. nymphalid butterflies in the tribe Adoliadini, namely the archdukes, barons and dukes. The tribe Adoliadini is distributed across the Old World tropics and comprises many genera. A recent study by Dhungel & Wahlberg (2018) allowed the relationships of several genera within Adoliadini to be inferred and recovered five main clades within the tribe. One of these clades, referred to as the Asian *Euthalia* group by Dhungel & Wahlberg (2018), was inferred as sister to the rest of Adoliadini and comprises exclusively Indo-Australian species. This clade (hereafter referred to as the IAA Adoliadini *s.s.*), including six genera, is the focus of this study. Its internal phylogenetic relationships remain little studied to date. A recent study conducted by Dhungel & Wahlberg (2018) inferred the large genus *Euthalia* (referred to as barons and dukes) as paraphyletic, but their limited taxon sampling did not allow additional discussion of the systematics within this clade. The genus *Euthalia* is by far the most species-rich one, with possibly up to ~100 described species, distributed from India to the Moluccas. Few studies have been conducted to investigate the systematics in this group (but see Yago *et al.*, 2011), and it is very likely that this genus might, in fact, represent multiple independent lineages (Dhungel & Wahlberg, 2018). The genera *Lexias* (referred to as archdukes) and *Tanaecia* (referred to as counts and earls) are also relatively diverse and equally widespread in the IAA, and their systematics remain uncertain. The genus *Bassarona* (approximately eight species, referred to as marquises) is distributed from Assam to the Lesser Sunda Islands, while the two monotypic genera *Dophla* and *Euthaliopsis* are respectively widespread in the IAA (from India to Sula) or endemic to the Moluccas and New Guinean region. In their study based on 18 loci, Dhungel & Wahlberg (2018) recovered the genus *Bassarona* as sister to a clade comprising two subclades, the first including the genera *Lexias* and *Euthaliopsis* and the second including the genera *Dophla*, *Euthalia* and *Tanaecia*. These results are in line with a recent and comprehensive phylogeny of butterflies (Chazot *et al.*, 2019). Nevertheless, the relationships among species groups and the monophyly of the different genera within IAA Adoliadini *s.s.* remain elusive.

Using a new molecular phylogenetic dataset, combined with existing data, in the present study we aim at inferring a new and comprehensive phylogeny of IAA Adoliadini *s.s.* and understanding the extent to which the assembly of the IAA impacted the evolution of these butterflies. We also investigate the relevance of the major biogeographical lines for the evolution of the archdukes, barons, counts, dukes, earls and marquises.

MATERIAL AND METHODS

Taxon sampling and molecular biology

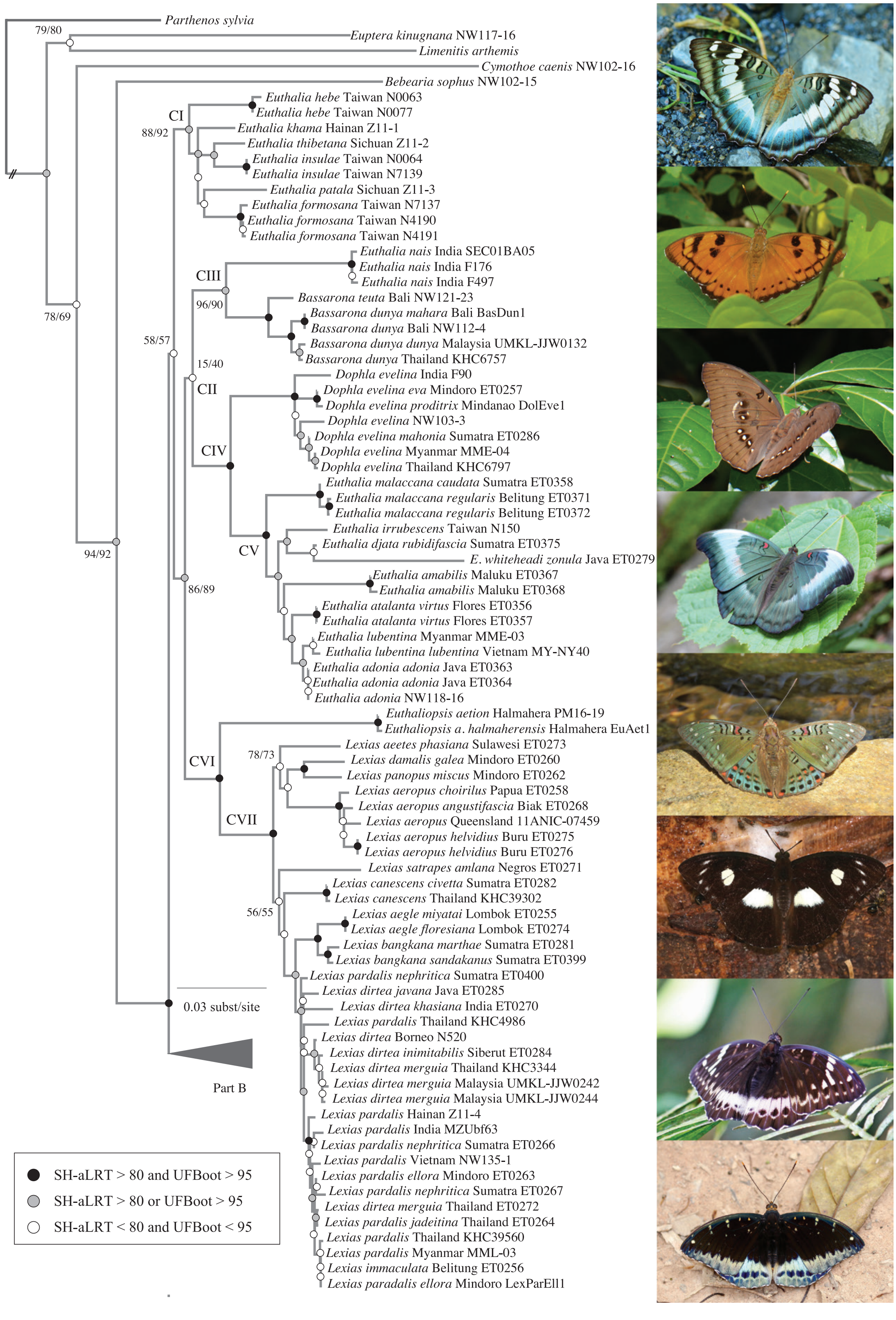
We sampled legs of specimens from dry-pinned collections to assemble a comprehensive taxon sampling of IAA Adoliadini *s.s*. We obtained new genomic DNA for 66 specimens and also included sequence data retrieved from GenBank for 96 additional specimens, representing 60 species out of ~176 described species in the group. The majority of missing species belong to the diverse genus *Euthalia* and are distributed mainly in China and the Indochinese peninsula. Therefore, the aims of our study are unlikely to be impacted by these missing tips in the phylogeny. Total genomic DNA of collection specimens was extracted from leg tissues using a Qiagen DNeasy kit (Hilden, Germany). Using the polymerase chain reaction protocols described by Wahlberg & Wheat (2008), we amplified and sequenced the following loci: cytochrome *c* oxidase subunit 1 (*CO1*, 654 bp), NADH-ubiquinone oxidoreductase chain 5 (*ND5*, 825 bp), elongation factor 1 alpha (*EF1A*, 1194 bp), ribosomal protein S5 (*RPS5*, 639 bp) and *wingless* (414 bp). We selected four outgroups based on the phylogenetic affinities of IAA Adoliadini *s.s.* butterflies as inferred by Espeland *et al.* (2018) and rooted the phylogenies with *Parthenos sylvia* (Espeland *et al.*, 2018). DNA sequences were edited in Geneious R11 (Biomatters, Auckland, New Zealand), aligned using MUSCLE (Edgar, 2004) and with the reading frames checked under Mesquite v.3.5 (http://mesquiteproject.org). All new sequences were deposited in GenBank (accession numbers MN993658 - MN993848).

Phylogenetic analyses

We estimated the best partitioning scheme and best models of nucleotide substitution with ModelFinder (Kalyaanamoorthy *et al.*, 2017). The five protein-coding loci were divided a priori by codon positions for a total of 15 initial partitions. To find the most likely tree, 200 maximum likelihood (ML) independent tree searches were conducted in IQ-TREE v.1.6.6 (Nguyen *et al.*, 2015), with two calculations of nodal support: ultrafast bootstrap (UFBoot) and SH-aLRT tests. We generated 1000 replicates for UFBoot ('-bb' command; Minh *et al.*, 2013; Hoang *et al.*, 2018) and SH-aLRT ('-alrt' command) (Guindon *et al.*, 2010). We took into account recent revisions of the UFBoot calculation and suggestions to avoid overestimation of this metric using a hill-climbing nearest neighbour interchange (NNI) to optimize each bootstrap tree with the command ('-bnni' command; Hoang *et al.*, 2018). When discussing branch support, we refer to 'strong' support as SH-aLRT ≥ 80 and UFBoot ≥ 95.

Divergence time estimation

We estimated species-level phylogenetic relationships and divergence times simultaneously in a Bayesian framework using BEAST v.1.8.4 (Drummond *et al.*, 2012). To do so, we kept only one representative per species; in general, the one with the maximum genetic coverage. The best partitioning scheme and models of substitution were selected in PartitionFinder2 (Lanfear *et al.*, 2017) using the greedy algorithm and the Bayesian information criterion across all models included in BEAST (option models = beast). The dataset was partitioned a priori, similar to the ModelFinder analysis (see previous subsection). The resulting partitioning scheme included six partitions, one for each mitochondrial codon position and one for each nuclear codon position. To take into account the importance of clock partitioning, we implemented: (1) a unique clock (analyses A1 and A2); (2) two clocks, one for the mitochondrial partitions and one for the nuclear partitions (analyses A3 and A4); or (3) a different clock for each partition (analyses A5 and A6). We assigned a Bayesian lognormal relaxed clock model to the different clock partitions. We also tested different tree models by using a Yule (pure


Parthenos sylvia
79/80
Euptera kinugnana NW117-16
Limenitis arthemis
Cymothoe caenis NW102-16
Bebearia sophus NW102-15
Euthalia hebe Taiwan N0063
CI
Euthalia hebe Taiwan N0077
88/92
Euthalia khama Hainan Z11-1
Euthalia thibetana Sichuan Z11-2
Euthalia insulae Taiwan N0064
Euthalia insulae Taiwan N7139
Euthalia patala Sichuan Z11-3
Euthalia formosana Taiwan N7137
Euthalia formosana Taiwan N4190
Euthalia formosana Taiwan N4191
Euthalia nais India SEC01BA05
Euthalia nais India F176
CIII
Euthalia nais India F497
Bassarona teuta Bali NW121-23
96/90
Bassarona dunya mahara Bali BasDun1
78/69
Bassarona dunya Bali NW112-4
58/57
Bassarona dunya dunya Malaysia UMKL-JJW0132
Bassarona dunya Thailand KHC6757
15/40
Dophla evelina India F90
CII
Dophla evelina eva Mindoro ET0257
Dophla evelina proditrix Mindanao DolEve1
Dophla evelina NW103-3
Dophla evelina mahonia Sumatra ET0286
CIV
Dophla evelina Myanmar MME-04
Dophla evelina Thailand KHC6797
Euthalia malaccana caudata Sumatra ET0358
Euthalia malaccana regularis Belitung ET0371
Euthalia malaccana regularis Belitung ET0372
Euthalia irrubescens Taiwan N150
Euthalia djata rubidifascia Sumatra ET0375
94/92
CV
E. whiteheadi zonula Java ET0279
Euthalia amabilis Maluku ET0367
86/89
Euthalia amabilis Maluku ET0368
Euthalia atalanta virtus Flores ET0356
Euthalia atalanta virtus Flores ET0357
Euthalia lubentina Myanmar MME-03
Euthalia lubentina lubentina Vietnam MY-NY40
Euthalia adonia adonia Java ET0363
Euthalia adonia adonia Java ET0364
Euthalia adonia NW118-16
Euthaliopsis aetion Halmahera PM16-19
Euthaliopsis a. halmaherensis Halmahera EuAet1
Lexias aeetes phasiana Sulawesi ET0273
CVI
78/73
Lexias damalis galea Mindoro ET0260
Lexias panopus miscus Mindoro ET0262
Lexias aeropus choirilus Papua ET0258
Lexias aeropus angustifascia Biak ET0268
CVII
Lexias aeropus Queensland 11ANIC-07459
Lexias aeropus helvidius Buru ET0275
Lexias aeropus helvidius Buru ET0276
Lexias satrapes amlana Negros ET0271
Lexias canescens civetta Sumatra ET0282
Lexias canescens Thailand KHC39302
56/55
Lexias aegle miyatai Lombok ET0255
Lexias aegle floresiana Lombok ET0274
Lexias bangkana marthae Sumatra ET0281
Lexias bangkana sandakanus Sumatra ET0399
Lexias pardalis nephritica Sumatra ET0400
Lexias dirtea javana Java ET0285
0.03 subst/site
Lexias dirtea khasiana India ET0270
Lexias pardalis Thailand KHC4986
Lexias dirtea Borneo N520
Lexias dirtea inimitabilis Siberut ET0284
Part B
Lexias dirtea merguia Thailand KHC3344
Lexias dirtea merguia Malaysia UMKL-JJW0242
Lexias dirtea merguia Malaysia UMKL-JJW0244
Lexias pardalis Hainan Z11-4
Lexias pardalis India MZUbf63
Lexias pardalis nephritica Sumatra ET0266
Lexias pardalis Vietnam NW135-1
● SH-aLRT > 80 and UFBoot > 95
Lexias pardalis ellora Mindoro ET0263
Lexias pardalis nephritica Sumatra ET0267
● SH-aLRT > 80 or UFBoot > 95
Lexias dirtea merguia Thailand ET0272
○ SH-aLRT < 80 and UFBoot < 95
Lexias pardalis jadeitina Thailand ET0264
Lexias pardalis Thailand KHC39560
Lexias pardalis Myanmar MML-03
Lexias immaculata Belitung ET0256
Lexias paradalis ellora Mindoro LexParEll1

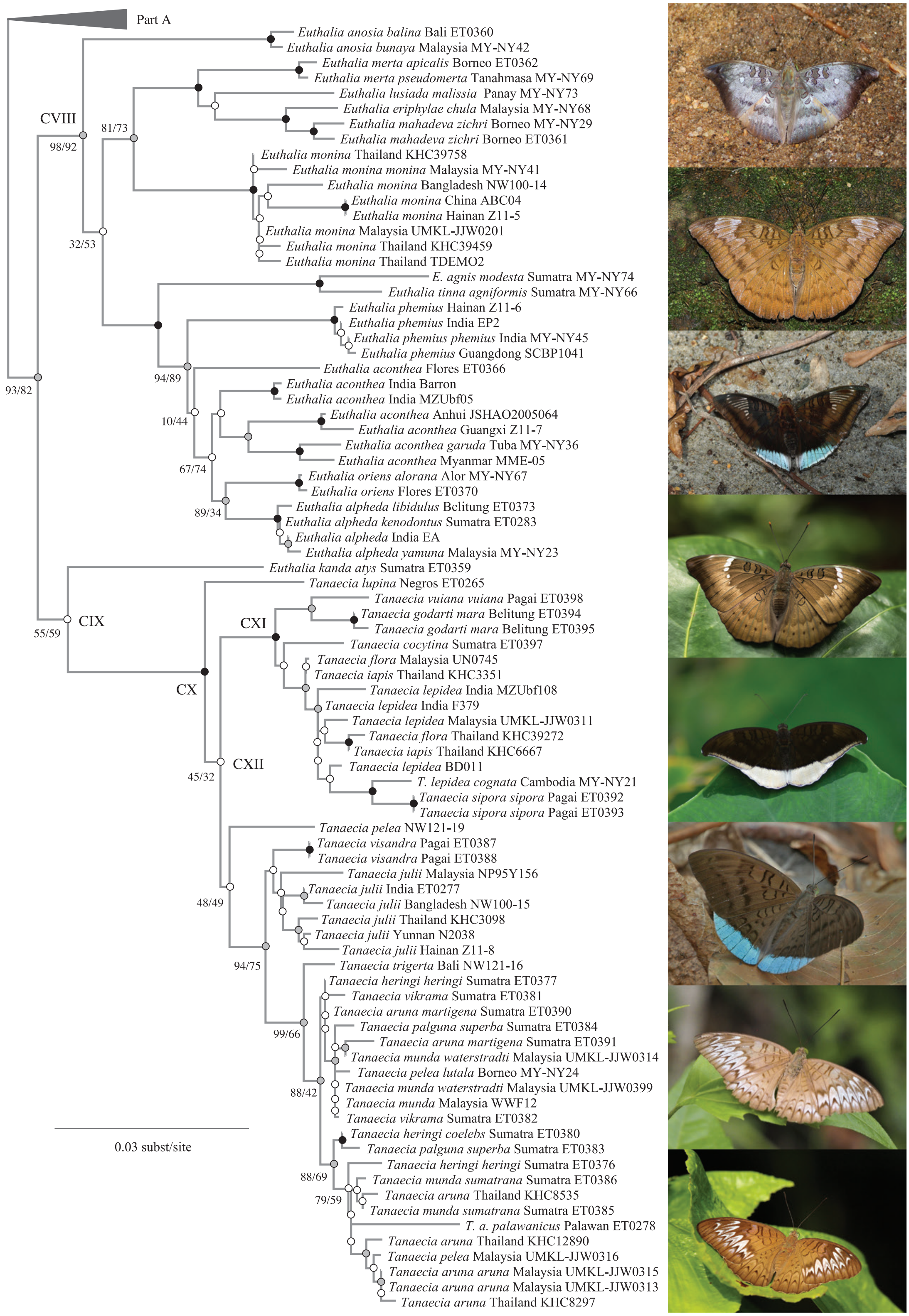


Figure 1. Maximum likelihood phylogenetic relationships of Indo-Australian Adoliadini (IAA) *s.s.* based on a populational taxon sampling. The topology was derived from the best-scoring maximum likelihood tree out of 200 tree searches conducted in IQ-TREE using a multimarker dataset for IAA Adoliadini *s.s.* butterflies. Nodal support, expressed as a combination of

birth, A1, A3 and A5) or a birth–death model (A2, A4 and A6) in different analyses. Clock rates were set with an approximate continuous time Markov chain rate reference prior (Ferreira & Suchard, 2008). All analyses consisted of 20 million generations, with a parameter and tree sampling every 2000 generations. We estimated marginal likelihood estimates (MLEs) for each analysis using path sampling and stepping-stone sampling (Xie *et al.*, 2010; Baele et al., 2012, 2013), with 1000 path steps, and chains running for one million generations, with a log likelihood sampling every 1000 cycles.

We relied on the extensive fossil-based dating frameworks of Espeland *et al.* (2018) for our dating analysis. In this study, the split corresponding to the root of our phylogeny (*Parthenos* sister to the rest of the genera) was recovered with a median age of 44.85 Mya (95% credibility interval = 31.6–63.9 Mya). Therefore, we constrained the root of the tree with a conservative uniform prior encompassing the 95% credibility intervals (31.6–63.9 Mya) estimated for this node by Espeland *et al.* (2018).

ANCESTRAL RANGE ESTIMATION

We used the R package BioGeoBEARS v.1.1 (Matzke, 2018) to estimate ancestral ranges in IAA Adoliadini *s.s*. The analyses were performed only under the dispersal–extinction–cladogenesis (DEC) model (Ree, 2005; Ree & Smith, 2008). Other models included in the package BioGeoBEARS, which included founder-event speciation, were not used, to take into account the ongoing debate regarding the possibility of comparing these models with others not including such parameters (Ree & Sanmartin, 2018). We used the BEAST maximum clade credibility (MCC) tree from the best analysis (see Results and Discussion) with outgroups pruned. We used the following areas in the BioGeoBEARS analyses: continental Indomalaya (I), Philippines (P), Greater Sunda Islands (G), Sulawesi (S), Lesser Sunda Islands (L), Moluccas (M) and Australia and New Guinea (N).

We took into account the dynamic geological history of the IAA by designing five time slices with different dispersal rate scalers following several geological studies focusing on this region and providing palaeo-reconstructions (Hall, 2012, 2013). Time slice 1 (TS1; root age 22.5 Mya) encompasses the period predating the acceleration of orogenies in the Philippines archipelago, Wallacea and New Guinea (Yumul et al., 2008, 2009; Hall, 2013; Toussaint *et al.*, 2014), with deep water separating the Greater Sunda Islands and Sulawesi from Moluccas, Australia and New Guinea, with Indomalaya connected to Greater Sunda Islands by land, some land in west Sulawesi, a volcanic arc in the Philippines with some land northeast of the Greater Sunda Island, and another volcanic arc with some land north of New Guinea, the latter having subaerial landmasses in the Bird's Head. Time slice 2 (TS2; 22.5–12.5 Mya) encompasses the active formation of the IAA, with east and west Sulawesi colliding, the oceanic part of the Philippines rafting from the east to the northwest, and shallow water separating Sunda and Sahul. Time slice 3 (TS3; 12.5–7.5 Mya) encompasses the formation of the Lesser Sunda Islands and enhanced connectivity throughout the IAA and, in particular, in the western side of the archipelago between Sulawesi, Greater Sunda Islands and Continental Indomalaya. Time slice 4 (TS1; 7.5–2.5 Mya) encompasses the period of reduced connectivity between the oceanic Philippine arc and Melanesia, at this time separated by deep water, but also between Sulawesi and the Lesser Sunda Islands, which were also separated by a deep-water corridor. Time slice 5 (TS5; 2.5 Mya to the present) encompasses periods of reduced connectivity between continental Indomalaya and Greater Sunda Islands and between Sulawesi and the Philippines. The dispersal rate scaler values were selected according to terrain and water body positions throughout the time frame of the age of the group. The maximum number of areas per ancestral state was fixed to four. To reduce the computational burden, ancestral states corresponding to unrealistic disjunct areas were removed manually from the list of possible states.

We performed different analyses with the parameter w constrained to zero (M1) or one (M2) or left free (M3), in addition to a null model excluding manually modified dispersal rate scalers and adjacency matrices (M0). The parameter w modifies the user-specified matrix of dispersal rate scalers. If $w = 1$, the best-fitting matrix is the one that was designed manually by the user. However, if $w = 0$ the manually designed

UFBoot and SH-aLRT tests, is presented according to the key in the box. Major clades are labelled. Photographs of live specimens of species distributed across the tree are presented, from top to bottom: *Euthalia formosana* (credit: Hsu Hong Lin), *Euthalia nais* (credit: Dinesh Valke), *Bassarona dunya* (credit: Pavel Kirillov), *Dophla evelina* (credit: A. K. Firos), *Euthalia lubentina* (credit: Vinayaraj), *Euthaliopsis aetion* (credit: Antonio Giudici), *Lexias aeetes* (credit: A. S. Kono), *Lexias pardalis* (credit: Charlie Jackson), *Euthalia anosia* (credit: Subhendukhan), *Euthalia monina* (credit: U. Ajith), *Euthalia phemius* (credit: Atudu), *Euthalia aconthea* (credit: Vineeth Viswanath), *Tanaecia lepidea* (credit: Vinayaraj), *Tanaecia julii* (credit: J. M. Garg), *Tanaecia palguna* (credit: C. W. Gan) and *Tanaecia pelea* (credit: Charles J. Sharp).

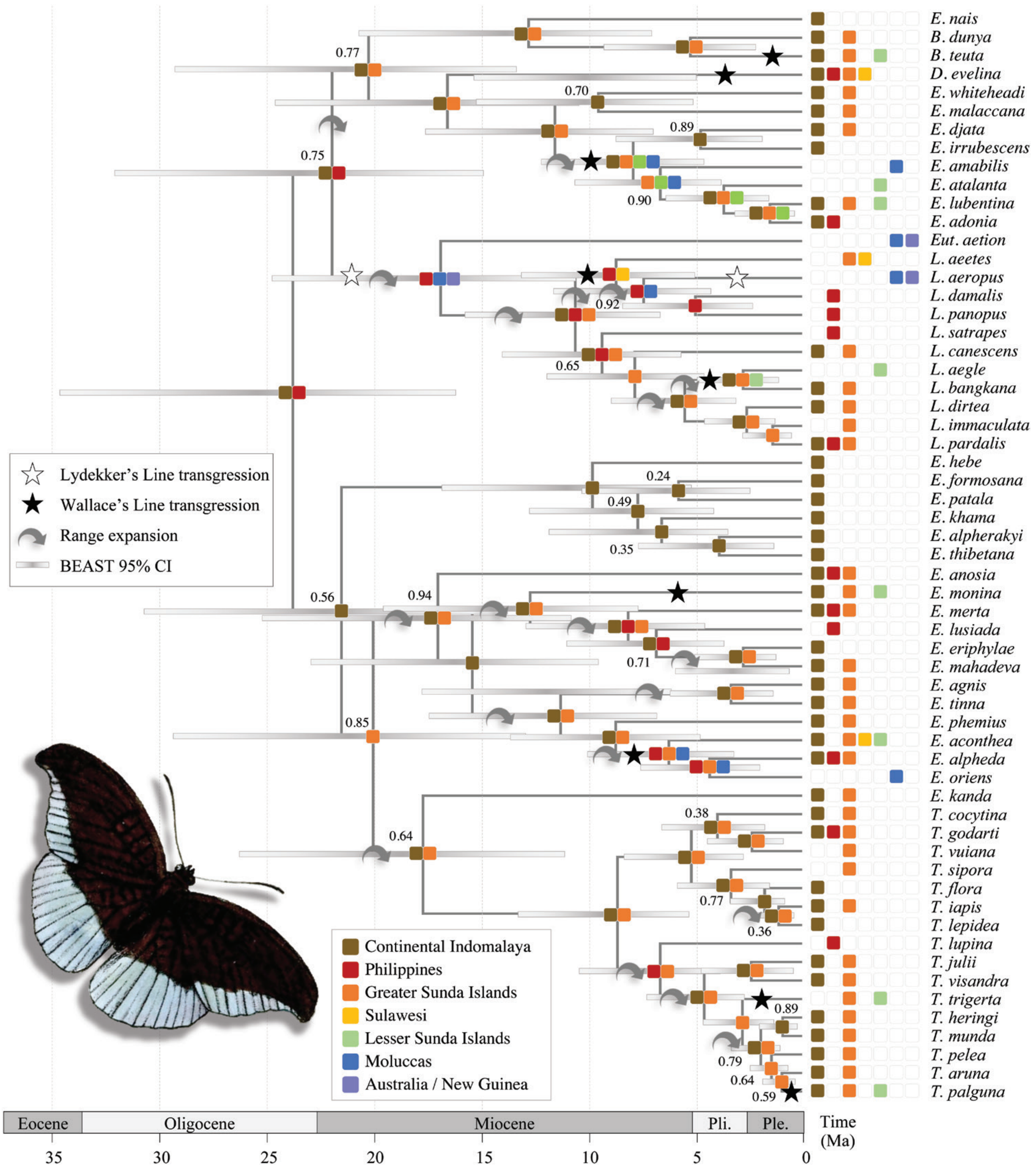


Figure 2. Bayesian divergence time estimates and historical biogeography of Indo-Australian Adoliadini (IAA) *s.s.* The chronogram was derived from the best BEAST analysis using two Bayesian relaxed clocks, a Yule tree model of speciation, a secondary calibration from Espeland *et al.* (2018) and based on the species-level dataset of IAA Adoliadini *s.s.* Posterior probabilities (PP) are given for each node when PP <1.0. The node ages correspond to median estimates from the post-burn-in posterior distribution. The 95% credibility intervals are given for each node. Current geographical distributions of all taxa are given on the right side of the figure and coded according to the coloured key in the box. The result of the BioGeoBEARS ancestral range estimation under the DEC model are presented for each node with the highest relative probability as

matrix of dispersal rate scalers is not the best fit and is discarded. When $w < 1$ or $w > 1$ but $w \neq 0$ or 1, then the impact of the dispersal rate scaler matrix is respectively decreased or increased, and the differences between different dispersal multipliers are decreased or increased. As a result, we performed two null analyses with $w = 0$ and $w = 1$, in addition to an alternative model with w as a free parameter (one additional free parameter). We then compared the different models using the Akaike information criterion (AIC) calculated using the function getAIC in R.

RESULTS AND DISCUSSION

Phylogenetics and taxonomy

Our ML phylogenetic inference, based on the extensive dataset at the population level, recovers a moderately well-supported phylogenetic hypothesis for the group (Fig. 1; Supporting Information, Appendix S1). Branching patterns between major clades are, in some cases, discordant with the species-level phylogeny inferred in BEAST (Fig. 2; Supporting Information, Appendix S2). We recover the IAA Adoliadini *s.s.* as monophyletic in both Bayesian Inference and ML, in line with Dhungel & Wahlberg (2018) and Chazot *et al.* (2019) (Figs 1, 2).

The genus *Euthalia* is recovered as polyphyletic, with five different clades spread across the tree in both BI and ML, although their respective placement differs between BI and ML (Figs 1, 2). The first clade in ML is sister to the rest of IAA Adoliadini *s.s.*, whereas it is recovered in a more derived position in BI (Fig. 2). This clade comprises several *Euthalia* species from China and Taiwan and, based on both reconstructions, should be given a generic status to accommodate the polyphyly of *Euthalia*. We propose the establishment of a monophyletic genus-level classification in a separate taxonomic paper including morphological evidence. The second lineage in *Euthalia* is the single species *Euthalia nais*, recovered as sister to *Bassarona* in both ML and BI. The third lineage, comprising the type species *Euthalia lubentina* and other species, is recovered as the sister group of the monotypic genus *Dophla* (*Dophla evelina*) in both BI and ML (Figs 1, 2). The fourth lineage, broadly corresponding to the concept of the *Euthalia aconthea* group, is recovered as sister of the clade *Tanaecia* + *Euthalia kanda* in both BI and ML (Figs 1, 2). This clade should also be raised to genus status with respect to the divergence between genera in other parts of the tree. Likewise, *Euthalia kanda*, which is recovered as sister to *Tanaecia* in both BI and ML (albeit with moderate to low support), should be raised to genus level to accommodate the polyphyly of *Euthalia*. Again, we propose to address the formal classification of the group in a separate paper. As a similar pattern, in a different part of the tree, the monotypic genus *Euthaliopsis* (*Euthaliopsis aetion*) is recovered as sister to the monophyletic genus *Lexias* in both BI and ML (Figs 1, 2).

Origins and biogeography

Our BEAST analyses all converged well, and divergence time estimates are largely comparable between analyses (Table 1). The best analysis, based on a comparison of marginal likelihood estimates, included two clocks and a Yule pure birth model. The resulting chronogram of this analysis is presented in Figure 2 along with the BioGeoBEARS estimation of ancestral ranges under the DEC model (Table 2; Supporting Information, Appendix S3). We present the results of analysis M3, in which the parameter w was free, because this analysis is statistically a better fit than the other models (Table 2). In this analysis, $w = 4.117$, indicating that dispersal rate scalers are of importance to estimate the evolutionary history of the group. Although the BEAST analysis recovers moderately supported phylogenetic relationships, it is unlikely that our biogeographical patterns are biased, considering the overwhelming distribution of IAA Adoliadini *s.s.* west of Wallace's Line. The timing and directionality of transitions across Lydekker's and Wallace's Lines are also unlikely to be affected, because the relevant nodes are often well supported and relatively derived in the phylogeny (Fig. 2).

The IAA Adoliadini *s.s.* diverged from their sister lineage *Bebearia* in the Oligocene ~29 Mya. Given that IAA Adoliadini *s.s.* butterflies are very likely to be sister to an Afrotropical clade (Dhungel & Wahlberg, 2018; Chazot *et al.*, 2019), they possibly represent yet another example of Old World tropical disjunct distribution that might be linked to late Neogene climatic disruptions (e.g. Aduse-Poku et al., 2009, 2015; Kaliszewska *et al.*, 2015; Sahoo *et al.*, 2018; Toussaint *et al.*, 2019). We estimate an origin of modern IAA Adoliadini *s.s.* between the Philippines and continental Indomalaya ~24 Mya, in line with Chazot *et al.* (2019), who recovered an origin for the clade ~21.4 Mya. This ancestral range estimation is

recovered in BioGeoBEARS. Range expansion and biogeographical barrier transgressions are indicated according to the key in the box on the left. A drawing of *Tanaecia julii* is presented at the bottom left corner of the figure, recovered from the chapter of Arthur Gardiner Butler entitled 'A monographic revision of the Lepidoptera hitherto included in the genus *Adolias*, with descriptions of new genera and species' (*Proceedings of the Zoological Society of London*, vol. 1868, plate XLV).

consistent across analyses except for the null model M0, which recovers an origin in Indomalaya (Table 2; Supporting Information, Appendix S3).

The origin of modern IAA Adoliadini *s.s.* corresponds to a period of time when the Philippines were merely a volcanic arc, with limited terranes connected to continental Indomalaya by shallow-water corridors and small volcanic island chains (Hall, 2013). After this origin, we estimate range-expansion events towards the Greater Sunda Islands in the early Miocene in several parts of the tree (Fig. 2). This might reflect active dispersal from continental Indomalaya or simply vicariance as the Greater Sunda Islands are progressively detaching from the continental landmass starting from the early Miocene (Hall, 2013). We infer an early transgression of both Wallace's and Lydekker's Lines ~17 Mya in the clade comprising *Euthaliopsis* and *Lexias* (Fig. 2). At that time, shallow-water corridors connected the Philippines with north Sulawesi and possibly even New Guinea (Hall, 2013), which might have allowed dispersal via stepping stones north of the IAA rather than through its centre. More recent transgressions of the biogeographical barriers occurred between the late Miocene and the Pleistocene, probably facilitated by the formation of the Wallacea and satellite island chains (Hall, 2013). The overall biogeographical history of the group is very dynamic, with multiple range-expansion events across the tree and throughout the evolution of the clade.

Surprisingly, only a few species are nowadays endemic east of Wallace's or Lydekker's Lines. Species from the IAA Adoliadini *s.s.* distributed in the Lesser Sunda Islands, Moluccas or Melanesia are often widespread, with ranges extending towards the Greater Sunda Islands and/or continental Indomalaya. The reason for this pattern is unclear, but it might be the result of several non-exclusive hypotheses. This pattern might result from competition with other butterfly groups of Australian origin or that settled in the Australian region before the IAA Adoliadini *s.s.* Competition could take the form of host-plant or ecosystem carrying capacities being reached and not allowing a more diverse assemblage of lineages to dwell in the same regions. This pattern might also be the result of the recent colonization of the Australian region, with the present geographical distribution of the clade representing the early stages of a future broader distribution, with additional endemic taxa on remote archipelagoes and island chains, as observed in other IAA butterflies (e.g. Müller & Beheregaray, 2010; Müller *et al.*, 2010; Condamine et al., 2013, 2015; Toussaint & Balke, 2016).

The evolutionary history of IAA Adoliadini *s.s.* butterflies provides additional evidence that biogeographical barriers in the IAA are largely permeable to vagile insects and do not seem to impede the colonization of new regions. In the case of butterflies, it is difficult to understand the potential reasons why

Table 1. Results of the different BEAST runs for Bayesian estimation of divergence times in Adoliadini butterflies

	Clocks	Model	PS MLE	SS MLE	Age of IAA Adoliadini *s.s.*
A1	1	Yule	−19430.914	−19431.107	21.9 (14.1–30.9)
A2	1	BD	−19433.323	−19433.353	21.2 (13.8–30.6)
A3	2	Yule	−19391.036	−19390.995	23.7 (15.9–34.3)
A4	2	BD	−19391.645	−19391.239	23.3 (15.3–34.1)
A5	7	Yule	−19413.910	−19414.497	24.5 (17.2–34.3)
A6	7	BD	−19411.433	−19411.721	23.9 (16.7–33.9)

Abbreviations: BD, birth death; IAA, Indo-Australian archipelago; PS MLE, path sampling marginal likelihood estimate; SS MLE, stepping-stone marginal likelihood estimate.

Table 2. Results of the BioGeoBEARS analyses of ancestral range estimation in Adoliadini butterflies

Model	R. Scalers	Adjacency matrix	Number of parameters	d	e	w	LnL	AIC	Origin of IAA Adoliadini *s.s.*
M0	No	No	2	0.017	0	–	−219.31	442.62	I
M1	Yes*	Yes	2	0.034	0.001	0	−191.56	387.12	IP
M2	Yes	Yes	2	0.059	0.004	1	−180.86	365.12	IP
M3	Yes	Yes	3	0.158	0.005	4.117	−171.93	349.86	IP

Abbreviations: AIC, Akaike information criterion score calculated using the R function getAIC; d, dispersal rate; e, extinction rate; IAA, Indo-Australian archipelago; LnL, log-likelihood; R. Scalers, dispersal rate scaler matrix; Yes*, the rate scaler matrix is present, but because $w = 0$ it is technically not informative in the optimization; w, scaling parameter.

some lineages are less ubiquitous than others in some parts of the IAA. The tight link between butterflies and their host plants is certainly a promising avenue to investigate the mechanisms of range expansion and lineage diversification in the region. Additional work is therefore needed to gather host-plant record data and generate more robust phylogenies to enable proper reconstruction of ancestral host-plant preferences and host-plant biogeographical histories and, in turn, allow the fine-scale estimation of IAA butterfly clade evolution.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Best scoring ML tree of IAA Adoliadini *s.s*.
Appendix S2. BEAST Bayesian chronogram of IAA Adoliadini *s.s*.
Appendix S3. BioGeoBEARS ancestral range estimation results in IAA Adoliadini *s.s*.