











Phylogeny of the Poritiinae (Lepidoptera: Lycaenidae), butterflies with ant associations and unusual lichenivorous diets

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Abstract

The Poritiinae are a diverse subfamily of lycaenid butterflies with about 700 species divided into two major groups: the Asian endemic tribe Poritiini, and the African endemic tribe Liptenini. Among these, the Liptenini are notable for their lichenivorous diet and the strong but apparently non-mutualistic ant associations of many species. We present the first molecular phylogeny for this subfamily, based on data from 14 gene regions, and including 218 representatives from 177 taxa (approximately 25% of species) in 50 of the 58 (86%) recognized genera. From this analysis, we confirm the division of the

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subfamily into two tribes, and we rearrange the Liptenini tribe into six subtribes, *Durbanina*, *Pentilina*, *Liptenina*, *Iridanina* and *Epitolina*, plus a new tribe, *Cooksoniina* **subtrib. n.**, to fill a gap in the nomenclature revealed by the phylogenetic analysis. We also point to several genera in need of further taxonomic revision. Ancestral range reconstruction could not infer the range of the common ancestor of the *Poritiinae*; however, the common ancestor of the *Poritiini* was likely Asian, while that of the *Liptenini* was likely African, with subsequent narrowing of ranges in several lineages.

KEYWORDS

Lepidoptera, Lipteninae, Lycaenidae, phylogenetics, *Poritiinae*

INTRODUCTION

The *Poritiinae* (sensu Eliot et al., 1992, hereafter referred to as Eliot et al., 1992) is a subfamily of the *Lycaenidae* comprising at least 680 species (D'Abrera, 1986; Williams, 2021), which is further divided into two tribes: *Poritiini* and *Liptenini*. The *Poritiini* comprises about 40 species (Figure 1a, b), mainly found in Southeast Asia west of Wallace's Line, although a few occur as far west as Assam in northeastern India or as far east as the Philippines. The *Liptenini* are endemic to continental Africa (Figure 1c–i), and their nearly 640 species have been recorded to feed almost entirely on lichens and/or cyanobacteria (Williams, 2006).

Although the larval habits of all species are not known, life histories of some species in most genera have been recorded, revealing some general patterns. The most striking feature of the *Poritiinae* is their larval diet. Among the *Poritiini*, only larvae of the genus *Poritia* Moore and *Simiskina* Distant have been described, and these form aggregations for defence and feed on foliage of trees in the families *Combretaceae*, *Dipterocarpaceae* and *Fagaceae* (Eliot et al., 1992; Sáfián & Larsen, 2009; Singh, 2003). In contrast, all species among the *Liptenini* for which life history records are known feed on lichens and/or cyanobacteria (Williams, 2006), save for a handful of dubious records of plant feeding (Fiedler, 1991; Williams, 2006). Bampton (1995) proposed that most *Liptenini* avoid the fungal part of the lichens, consuming only the algae or cyanobacteria symbiont. However, which part of the lichen is fed upon has been carefully examined for only a single species: Williams (2006) found both fungal and algal tissue in the gut of *Alaena amazoula* Boisduval.

Lichen-feeding is an unusual diet that has evolved several times in *Lepidoptera*. While species of *Liptenini* are among the few butterflies which are known to specialize on lichen as larvae (c.f. Karunaratne et al., 2008), several widely distributed moth families also consume lichen, including some species in the *Tineidae*, *Crambidae* and *Hepialidae* (Pierce, 1995; Powell et al., 1998; Wagner et al., 2008), and most species of the *Lithosiini* (*Erebidae*: *Arctiinae*), a tribe that includes more than 3000 species distributed globally (Wagner et al., 2008). The *Lithosiini* are distinctive among lichen feeders for their ability to sequester toxic phenolic compounds for use in defence, and many have aposematic warning colouration (Chialvo et al., 2018). African *Liptenini* such as *Mimacraea* Butler are among the few *Lycaenidae* that are aposematically coloured and involved in mimicry rings (Larsen, 2005). As their names imply, species

in these genera mimic various chemically defended African *Acraea* Fabricius and *Amauris* Hüber species as well as *Danaus chrysippus* (Linnaeus) (Bálint et al., 2018), and it seems likely that they also sequester phenolics from their lichen hosts.

Another unusual characteristic of *poritiines* is their larval relationship with ants. Across the *Lycaenidae* as a whole, the immature stages of as many as 75% of the species associate with ants, with relationships ranging from mutualistic to parasitic, and from obligate to facultative (Fiedler, 2021; Pierce et al., 2002; Pierce & Dankowicz, 2022). While most ant-associated lycaenid larvae produce attractive and manipulative secretions for ants to consume in exchange for defence from predators and parasitoids, larvae of *Poritiinae* are covered in long bristles that do not seem to attract or reward ants. Nonetheless, adults of many *Liptenini* are strongly tied to ants, and caterpillars, while non-trophobiotic and lacking the 'dorsal nectary organ' that produces secretions for attendant ants of many species in other groups of *Lycaenidae*, linger in ants' foraging trails and may even enter nests (Pierce & Dankowicz, 2022; Sáfián, 2015; Sáfián & Collins, 2014; Sáfián & Larsen, 2009). Many forest-dwelling species, especially *epitolines*, associate closely with arboreal ants in the genus *Crematogaster* Lund, or less often with other genera such as *Oecophylla* Smith (Dejean et al., 2017; Pierce & Dankowicz, 2022). While forest-dwelling species in West and Central Africa seem to have obligate associations with ants, *Liptenini* in drier southern Africa are generally facultatively ant-associated (Bampton, 1995). For example, ant associations have never been described for the three 'rock-sitter' genera *Durbanina* Trimen, *Durbaniella* van Son and *Durbaniopsis* van Son, all of which consume rock lichens as larvae and sit on rocks as adults instead of perching on grasses and other vegetation as is typical of other adult *Liptenini* (Williams, 2021). In contrast, little is known about the ant association or lack thereof in *Poritiini*—earlier reports suggest that they are not ant-associated ostensibly because they lack overt mutualistic or parasitic interactions (Fiedler, 1991). However, it remains possible that species of *Poritiini* will prove to be ant-associated in a manner similar to typical *Liptenini* (Pierce & Dankowicz, 2022).

Systematic arrangements of the *Poritiinae* (Table S1) have been based solely on morphological characters, and its classification has varied among authors. In the case of the *Poritiini* (sensu Eliot et al., 1992), Doherty (1886) included the '*Poritiinae*' as a subfamily of the *Lycaenidae*, based on the morphology of the eggs, including members of the genus *Poritia*. More genera related to *Poritia* were subsequently described, and later authors varied in their treatment of this group,

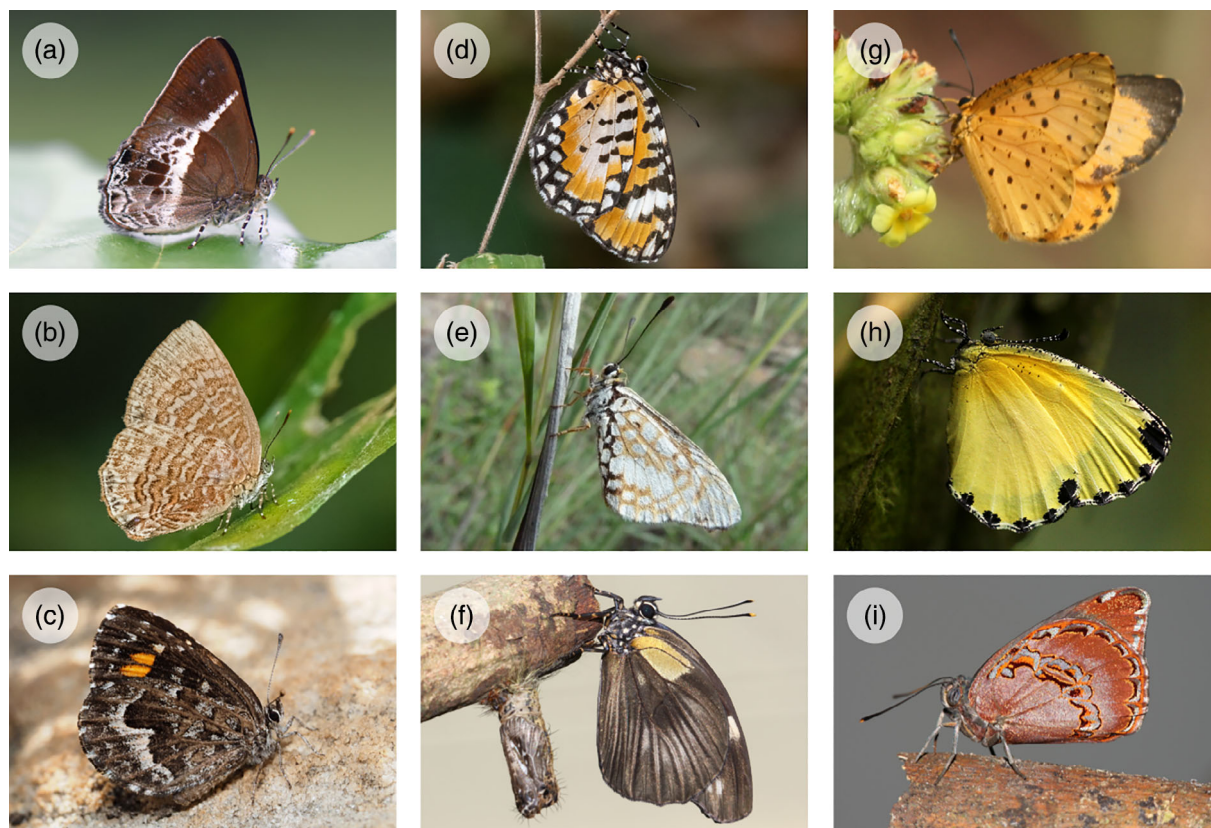


FIGURE 1 Representative adults of Poritiinae. (a and b) are members of the Poritiini. (a): *Simiskina pediada*. (b): *Poritia sumatrae*. (c through i) are members of the Liptenini. (c): *Durbaniopsis saga*. (d): *Telipna acraeoides*. (e): *Alaena ngonga*. (f): *Epitola posthumus* (newly emerged from its pupal casing, left). (g): *Pentila tropicalis*. (h): *Citrinophila terias*. (i): *Iridana kollariki*. Note that each species is shown in its stereotypical perching behaviour, with the Poritiini on the upperside of leaves, members of the Durbaniina subtribe on the upperside of rocks and the remaining Liptenini on the sides of leaves, twigs, rocks, etc. The exception is the genus *Iridana*, members of which settle on leaves or tree trunks. Photos by Yi-kai Tea (a), CheongWeei Gan (b), Stephen Ball (c), Rogério Ferreira (d), Dino Martins (e, g), Szabolcs Sáfián (f, i), Bart Wursten (h).

with some giving these genera subfamily status as the Poritiinae, either within the Lycaenidae (Bingham, 1907; Eliot, 1973) or the Liphyridae (Clench, 1955). Other authors placed these genera in the Lycaenidae, with no subfamily designation (De Nicéville, 1890; Fruhstorfer, 1911; Staudinger & Schatz, 1892), or within the Theclini (Seitz, 1927) or Lycaeninae (Ehrlich, 1958). No authors made any subdivisions within this group of genera.

The much more species-rich Liptenini (sensu Eliot et al., 1992) was first recognized (as a subfamily) by Röber (in Staudinger & Schatz, 1892), along with some taxa now in the Miletinae, based on their wing venation, and later divided into two tribes, the Pentilini and the Liptenini, also based on wing venation, by Aurivillius (in Seitz, 1925). Clench (1955) considered the group to be a single family, Liptenidae, divided into three subfamilies, the Pentilinae, Durbaniinae and Lipteninae. He removed most of the Miletinae to form a separate family, except for the genus *Thestor* Hübner, which he placed as a fourth subfamily within the Liptenidae. Stempffer (1967) removed *Thestor* from the Liptenidae and divided the remainder into four subfamilies, the Lipteninae, Pentilinae, Mimacraeinae and Epitolinae. Eliot's (1973) treatment included most of the genera currently included in Poritiinae, and he recognized it as having subfamily status, with two tribes: Liptenini and Pentilini. However, in a

later work (Eliot et al., 1992), he subsumed the previous two tribes, Liptenini and Pentilini, in a single tribe (the Liptenini), within the subfamily Poritiinae (along with the Poritiini as a second tribe in the subfamily). Larsen (2005) retained the subfamily Lipteninae, and divided it into four tribes, Epitolini, Liptenini, Pentilini and Mimacraeini. Libert (2020) and Williams (2021) assigned these species to three tribes (Epitolini, Liptenini, Pentilini) within the Poritiinae. Recently, several new genera have been proposed, including Libert's (1999) revision of *Epitola* Westwood, which split this large genus into several smaller genera. These major taxonomic arrangements within the Liptenini are summarized in Table S1.

Phylogenetic reconstruction of Poritiinae using molecular characters is yet to be carried out with this group, with the exception of a DNA barcode study by Libert (2020). Wahlberg et al. (2005) and Espeland et al. (2018) provided molecular evidence of the sister relationship between the Poritiini and Liptenini, albeit with only two and four representatives of Poritiini, respectively. Kaliszewska et al. (2015) sampled 11 Poritiinae as part of their outgroup for a phylogeny of the Miletinae, and likewise found the Liptenini and Poritiini to be reciprocally monophyletic. A robust molecular phylogeny permits the evaluation of the competing, morphologically-based taxonomic arrangements, and it will lay the groundwork for future comparative

analyses within the Poritiinae, and between this group and other related lycaenid taxa, including the Aphnaeinae (Boyle et al., 2015) and Miletinae (Kaliszewska et al., 2015). Furthermore, inferring the biogeographic history of this exclusively Old World group can shed light on paleo-environmental factors that may have affected diversification and current distributions. Here, we present the results for the first molecular phylogeny of this subfamily.

MATERIALS AND METHODS

Taxon sampling

We sampled 218 ingroup specimens representing 177 ingroup taxa. This includes four of the five genera of the Poritiini; we were unable to obtain a sample of the monotypic *Poriskina* Druce, which is endemic to Mindanao where it is extremely rare. Among the Lipitenini, 46 of the 53 genera are included. No representatives could be obtained for the monotypic genera *Pseudoneaveia* Stempffer, *Tumerepedes* Bethune-Baker, *Congdonia* Henning & Henning, or the infrequently encountered genera *Eresinopsides* Strand (2 species), *Euthecta* Bennett (2 species), *Parasiomera* Sáfián & Collins (4 species) or *Pseuderesia* Butler (4 species). 13 specimens from different taxa representing other major lycaenid subfamilies were used as outgroups (Figure 2). Of the 231 total specimens, five loci were Sanger sequenced from most (158). 13 loci were obtained from the remainder (75) using an anchored hybrid enrichment approach in order to strengthen the support at deep nodes. Since four loci overlapped between the two data sets, a total of 14 loci are used in this study. Two individuals were sequenced both by Sanger sequencing and anchored hybrid enrichment, hence the specimen total of 231.

Freshly collected butterflies were immediately preserved in 90%–100% ethanol and stored at -20° or -80° C prior to DNA extraction. Wing patterning was used to identify species: wings were removed and stored separately in glassine envelopes. Alternatively, samples were stored in glassine envelopes and dried with silica gel before being transferred to ethanol or an ultracold freezer. The voucher institution of each sample is shown in Table S2.

DNA was extracted from legs or thoracic tissue using either a Qiagen DNEasy Blood and Tissue Kit (qiagen.com) or an AutoGenPrep 965 Tissue DNA Extraction Kit (autogen.com).

Molecular protocols—Sanger sequencing

Fragments were amplified from the mitochondrial gene *cytochrome c oxidase I* (COI), and four nuclear genes, *carbamoyl-phosphate synthetase 2*, *aspartate transcarbamylase and dihydroorotase* (CAD), *elongation factor 1 alpha* (*EF1 α*), *histone 3* (*H3*) and *wingless* (*wg*). Polymerase Chain Reaction amplifications and Sanger sequencing were performed using the primers and reaction conditions described in Boyle et al. (2015), except for the following: The COI

primer Tonya was replaced with TN2126 (Canfield et al., 2008); annealing temperature for COI amplifications was 45° for 60 s. For *EF1 α* , a 766 bp fragment was amplified with the primers EF135 and EF52.6 (Cho et al., 1995). *wg* was amplified with the forward primer Wg1n and the reverse primers Wg2n (Talavera et al., 2013) or Wg2a (Brower & DeSalle, 1998). For CAD, the primer CADFa was replaced by CAD787F (Moulton and Weigmann, 2004).

Molecular protocols—Anchored hybrid enrichment

We used the anchored hybrid enrichment method and BUTTERFLY2.0 probe kit of Kawahara et al. (2018) to capture fragments of 13 genes. These included one mitochondrial locus, COI, and 12 nuclear loci, CAD, *EF1 α* , *wg*, *acetoacetyl-CoA thiolase* (AACT), *catalase* (CAT), *dopa decarboxylase* (DDC), *glyceraldehyde-3-phosphate dehydrogenase* (GAPDH), *hairy cell leukaemia protein 1* (HCL), *isocitrate dehydrogenase* (IDH), *malate dehydrogenase* (MDH), *ribosomal protein S2* (RPS2) and *ribosomal protein S5* (RPS5). The resulting sequence data were then cleaned and assembled using the pipeline of Breinholt et al. (2018) with the modifications described in Kawahara et al. (2018).

Phylogenetic analyses

Sanger sequences were edited in Geneious version 7.1.9. For each of the 14 loci, Sanger and target capture sequences were aligned using MAFFT 7.429 (Katoh & Standley, 2013) using the 'globalpair' algorithm with a gap opening penalty of 1.53, an offset of 0.123 and a maximum of 100 iterations. Both ends of each sequence were then trimmed by removing bases until reaching the first point at which 75% of the individuals in that alignment contained an A, T, C or G.

Alignments for all 14 loci were then concatenated. We partitioned each gene into three, by codon position, then used ModelFinder (Kalyaanamoorthy et al., 2017) as implemented in IQ-TREE 1.6.11 (Chernomor et al., 2016) to choose the appropriate substitution model for each partition separately. We then used those partition models to estimate a maximum-likelihood phylogeny in IQ-TREE using ultrafast bootstrapping with the 'bnni' option and 2000 replicates (Hoang et al., 2018; Nguyen et al., 2015).

Historical biogeography

To estimate ancestral ranges, each ingroup species was coded as residing either in Asia, or in one or more biogeographic zones of Africa (Table S2). We divided Africa into nine biogeographic zones based largely on the seven zones of Linder et al. (2012), with a few modifications where that schema did not correspond with the patterns of diversity of the Liptenini (each of the nine zones is shown on one of the maps marked with a letter code in Figure 3). In particular, we divided Linder et al.'s (2012) Congolian region into three subregions: Congolian, Lower Guinean and Upper Guinean. Species from the

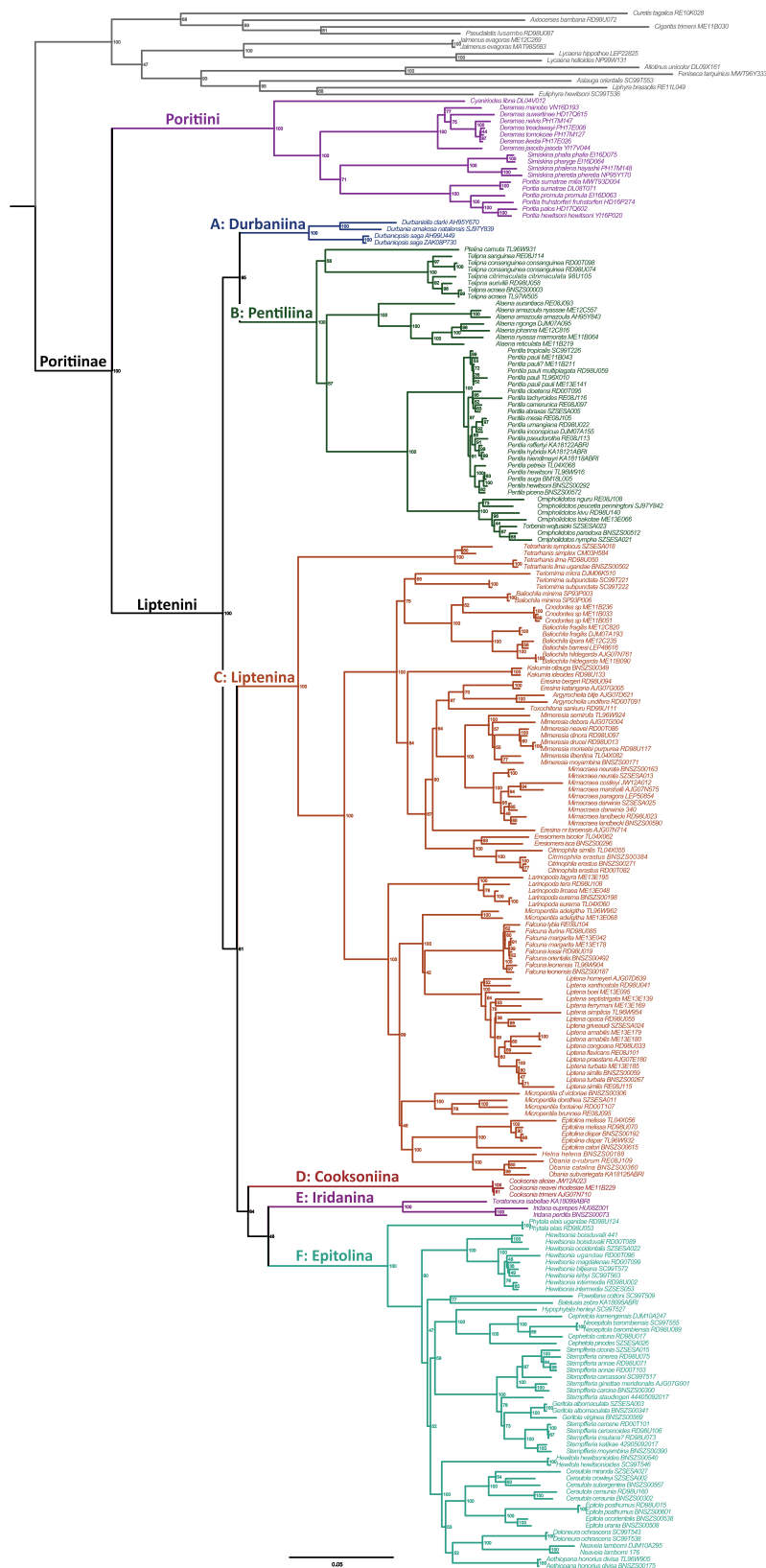


FIGURE 2 Molecular phylogeny of the Poritiinae based on 14 loci and our proposed higher classification of the subfamily. Node labels indicate ultrafast bootstrap support. Tip names are coloured according to their membership: in one of our six proposed subtribes of the Liptenini, in the Poritiini or in the outgroup.

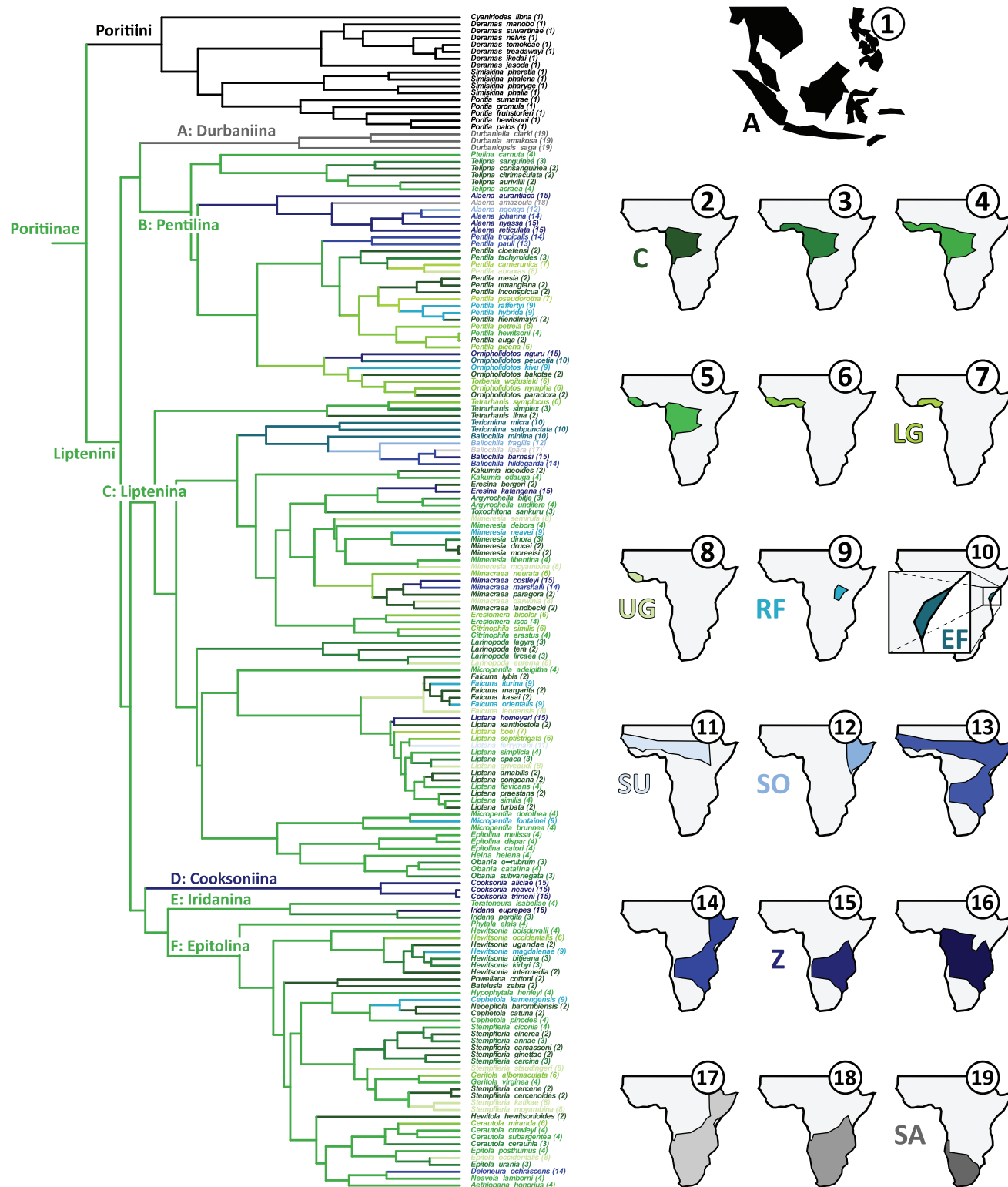


FIGURE 3 Historical biogeography of the Poritinae according to model analyses implemented in BioGeoBEARS. The Poritiini diversified in Southeast Asia, while Liptenini are historically widespread throughout the pan-Congolian region of Africa. Throughout the tree, the most likely range for each ancestral node is indicated by the colour of the three branches that form it. The current range of each taxon is indicated by the colour of each tip as well as a number. Each colour and number corresponds to a particular region or combination of biogeographic regions. The maps to the right show which colour and number is associated with which region or combination thereof. Maps labelled with letters are the individual biogeographic regions; the remaining maps show ranges that consist of combinations of two or more regions. A: Asian. C: Congolian. LG: Lower Guinean. UG: Upper Guinean. RF: East African Rift Forest. EF: East African coastal Forest. SU: Sudanese. SO: Somalian. Z: Zambezian. SA: South African.

forested regions of the Rift Valley were assigned to their own category since this region is not clearly assigned to any biogeographic zone in Linder et al. (2012). The Ethiopian and Somalian regions of Linder et al. (2012) were considered a single region. Finally, the East African Coastal Forest was considered its own region, since this forest is a remnant of an older, pan-equatorial forest joined to the Congolian region (Azeria et al., 2007; Couvreur et al., 2008). The maximum likelihood phylogeny was modified for this analysis using the R package *ape* 5.3 (Paradis & Schliep, 2018). All outgroup taxa were removed from the tree, along with those ingroup taxa for which no range data were available. For species that had multiple representatives in the phylogeny, all but a single individual were removed. The remaining tree was then ultrametricized using the *chronopl* function with a lambda value of 0, and the branch lengths adjusted so that overall age of the tree was 45 million years, the approximate time to the divergence of the Poritiini and Liptenini according to Espeland et al. (2018).

We then performed ancestral range reconstruction, using the resulting phylogeny in the R package BioGeoBEARS 1.1.2 (Matzke, 2013, 2014). Ancestral range evolution was inferred under six different models, representing a variety of possibilities of how daughter species produced during cladogenesis 'inherit' the range of their mother species (see Matzke, 2013 for a visualization of the models). These models represent the range of possibilities implemented in such commonly used ancestral range reconstruction programs as DIVA (Ronquist, 1997), LAGRANGE (Ree & Smith, 2008) and BayArea (Landis et al., 2013).

In the first model, similar to that of BayArea (Landis et al., 2013), daughter species always inherit the range of their parent species. In the second model, similar to that of DIVA (Ronquist, 1997), parent species with a range consisting of a single geographic area pass this range on to their daughter species during cladogenesis. Parent species with a range consisting of multiple geographic areas experience vicariance (the parental range is split into two ranges, with each daughter species inheriting one). The third model, similar to the DEC approach implemented in, for example, LAGRANGE (Ree & Smith, 2008), is like the second model, except that parent species with a range consisting of multiple geographic areas experience either vicariance or subset sympatry (one daughter species inherits the parent's entire range while the other daughter inherits a single geographic area from the parent's range). In addition to these three models, we also ran each model a second time, allowing founder events during cladogenesis; that is, one daughter species may have a range that does not overlap with the parent species'. We calculated Akaike Information Criterion (AIC) values to choose from among the six models.

RESULTS AND DISCUSSION

Phylogenetic hypotheses and systematics

Higher level taxa

Our phylogenetic hypothesis supports the reciprocal monophyly of Poritiini and Liptenini, with 100% bootstrap support of both clades (Figure 2). Within the Liptenini, our phylogenetic hypothesis does not

entirely support any of the previous classifications based on morphology. We recover six well-supported clades, designated A–F on Figure 2, each of which received 100% bootstrap support. Table S1 provides a comparison of our results with previous taxonomic arrangements. A summary of the generic composition is provided below for each of the six major clades.

Clade A comprises *Durbaniopsis*, *Durbania* and *Durbaniella*.

Clade B consists of the genera *Ornipholidotos* Bethune-Baker, *Torbenia* Libert, *Pentila* Westwood, *Alaena* Boisduval, *Telipna* Aurivillius and *Ptelina* Clench. This clade corresponds to the subfamily Pentilinae of Stempffer (1967) and the Pentilini tribe of Eliot (1973).

Clade C includes the genera *Obania* Collins & Larsen, *Helna* Libert, *Liptena* Westwood, *Epitolina* Aurivillius, *Micropentila* Aurivillius, *Falcuna* Stempffer & Bennett, *Larinopoda* Butler, *Citrinophila* Kirby, *Eresiomera* Clench, *Mimacraea*, *Mimeresia* Stempffer, *Toxochitona* Stempffer, *Argyrocheila* Staudinger, *Eresina* Aurivillius, *Kakumia* Collins & Larsen, *Baliocchila* Stempffer & Bennet, *Cnodontes* Stempffer & Bennett, *Teriomima* Kirby and *Tetrarhanis* Karsch. This clade corresponds to Eliot's (1973) *Mimacraea* and *Liptena* sections plus *Epitolina*, which is discussed below.

Clade D consists of the single genus *Cooksonia* Druce.

Clade E comprises the genera *Iridana* Aurivillius and *Teratoneura* Dudgeon, which corresponds to Eliot's (1973) *Iridana* section.

Clade F consists of the genera *Aethiopana* Bethune-Baker, *Cerautola* Libert, *Epitola*, *Geritola* Libert, *Neaveia* Druce, *Deloneura* Trimen, *Stempfferia* Jackson, *Cephetola* Libert, *Neoepitola* Jackson, *Hypophytala* Clench, *Batelusia* Druce, *Powellana* Bethune-Baker, *Hewitsonia* Kirby and *Phytala* Westwood. This clade corresponds to the *Epitola* section of Eliot (1973), except for the absence in our Clade F of the genus *Epitolina* (discussed below).

Monophyly of clades D + E + F has modest support (84% bootstrap support), but relationships among these clades are unclear. Clade C is the likely (81% bootstrap support) sister group to clades D + E + F, while clades A + B are sister to C + D + E + F (85% bootstrap support).

Regarding Eliot's (1973) classification, our molecular phylogenetic analyses support the monophyly of his tribe Pentilini (clade B), although his sections within Pentilini were not supported. Eliot placed *Telipna* and *Ornipholidotos* together in a *Telipna* section, but we found those two genera to be strongly supported sister taxa to *Ptelina* and *Pentila*, respectively. Moreover, his tribe Liptenini is paraphyletic, because his Pentilini (our clade B) is nested within his Liptenini in our phylogeny. Furthermore, his Liptenini section was also not supported, with the *Mimacraea* section nested within the *Liptena* section (*Mimacraea*, *Mimeresia*, and a few other genera nested within the remainder of clade C).

Larsen (2005) included genera in our clades A, B and D in his tribe Pentilini. Our phylogenetic hypothesis lends support for grouping clades A and B, but does not support inclusion of clade D, *Cooksonia*, with the other genera. Genera in Larsen's tribe Epitolini were included in our clades E and F. However, our analysis placed the tribe that he called Mimacraei (*Mimacraea* + *Mimeresia*) within his tribe Liptenini.

The simpler arrangement of Williams (2021) captures the probable sister relationship of clades A and B (in his Pentilini). The

composition of his Liptenini and Epitolini are similar to our clades C and F except for the placement of *Epitolina*, and his inclusion of *Iridana* in Epitolini and *Cooksonia* in Liptenini, respectively. Evidence supporting the placement of these genera was weak, but places both as sister to clade F (the rest of Williams' (2021) Epitolini).

The most striking disagreement between our molecular phylogenetic hypothesis and the previous taxonomic arrangements is the position of the genus *Epitolina*. Previous arrangements placed *Epitolina* with *Epitola*, including the subfamily of Stempffer (1967), the section of Eliot (1973), the tribe of Larsen (2005) or the subtribe of Williams (2021). This was supported by morphological similarities in wing shape, wing colour (an iridescent purplish-blue reflection overlaying the brown ground colour in adult males of most species) and their fast and rather erratic flight, similar to that of the smaller Epitolini (Larsen, 2005). However, we found strong support for placing *Epitolina* squarely within clade C (more-or-less corresponding to Eliot's Liptena, Larsen's Liptenini and William's Liptenina). This arrangement will not be particularly surprising to liptenine taxonomists: Eliot considered *Epitolina* the 'odd man out' of the *Epitola* section and considered placing it in a section of its own (1973) especially based on the shape of the antennae, while Libert's (2020) revision, based on DNA barcode data only, also indicated that this genus does not group with other epitolines.

We recommend maintaining the classification of Eliot et al., (1992) with respect to the two tribes of Poritiini and Liptenini within the subfamily Poritiinae. Within the Liptenini, none of the previous arrangements are entirely satisfactory. Here, we establish six subtribes with five existing names and a new subtribe, corresponding to clades A-F on Figure 1: Durbanina Clench, 1955, Pentilina Aurivillius, 1914, Liptenina Röber, 1892, Cooksoniina **subtrib. n.**, Iridanina Clench, 1965, and Epitolina Jackson, 1962 (Table S1). Although our phylogenetic hypothesis provides some support for the monophyly of the Epitolina+Iridanina+Cooksoniina clade, we nevertheless include these as three distinct subtribes based on their relatively deep divergences in our phylogeny (Figure 2) and their separation from each other in previous taxonomic arrangements (Table S1). A similar rationale supports maintaining separate Durbanina and Pentilina subtribes despite their probable sister-group status.

Description of new subtribe

Tribe: Liptenini.

Cooksoniina Sáfián, Boyle & Pierce **subtrib. nov.**

Type genus: *Cooksonia* Druce, 1905

Transactions of the Entomological Society of London 1905: 256 (251–262).

Type species: *Cooksonia trimeni* Druce, 1905, by monotypy.

Diagnostic characters

All seven members of the sole genus *Cooksonia* Druce, 1905 in the new subtribe are large and conspicuous species with elongate forewings, superficially very different from most Liptenini apart from

some species in the genus *Mimacraea* Butler, [1872]. Their bright colours are highly unusual in the family Lycaenidae. All seven species strikingly resemble the appearance of some aposematic Acraeinae (in the genera *Acraea* and *Telchinia* Hubner) and certain day-flying moths (e.g. *Scopula* = *Aletis* (Schrank)) in the family Geometridae.

The establishment of Cooksoniina **subtrib. n.** is strongly supported also by the phylogenetic analysis and ancestral range reconstruction of the tribe Liptenini on the basis of sequence data from five loci, the mitochondrial gene *cytochrome c oxidase I* (COI), and four nuclear genes, *carbamoyl-phosphate synthetase 2*, *aspartate transcarbamylase and dihydroorotase* (CAD), *elongation factor 1 alpha* (EF1α), *histone 3* (H3), and *wingless* (wg).

Etymology

The name of the subtribe is derived from the sole member genus *Cooksonia* Druce, 1905.

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ZooBank nomenclatural act registration code: <http://zoobank.org/urn:lsid:zoobank.org:act:5D12F331-57F8-4992-9084-1E90F6EE2D51>

Genera

Our phylogenetic analysis provides strong support for most current genus-level divisions of the Poritiinae, but some genera are not monophyletic: *Torbenia* is highly supported as being placed within *Ornipholidotos* from which it was removed by Libert (2000) based on various differences in the genitalia, but especially based on the male foreleg having five clear tarsal segments, as in females, which is not found in any other Liptenini. The wing pattern is, however, similar to standard *Ornipholidotos*, except that the forewing costa is more broadly black (Larsen, 2005). *Eresina* is polyphyletic, with one clade grouping together with *Argyrocheila* and *Toxochitona* with high support, and a sample identified as 'near toroensis' found as the sister group to this clade + *Mimacraea* and *Mimeresia*. *Micropentila* is polyphyletic with *M. adelgitha* (Hewitson) strongly supported as sister to *Falcuna* + *Liptena*, while the remainder of the genus is apparently closer to *Epitolina*, *Obania* and *Helna*, although support for the exact placement is limited. Our findings do not match the three morphological groups listed by Larsen (2005) based on wing patterns, since he placed *M. adelgitha* together with *M. dorothea* Bethune-Baker in his group 1 and here the latter species is placed together with *M. brunnea* (Kirby) found in Larsen's group 2. The other species included here were not included by Larsen (2005) since they do not occur in West Africa. *Cephetola* is only monophyletic if *Neoepitola* is included, which was also indicated by Libert (2020). *Geritola* is included within *Stempfferia*, a result not found by Libert (2020), where a sister relationship was indicated, although not with much support, and only based on DNA barcode data. Reassigning species of the Liptenini to preserve the monophyly of genera is a task for a separate paper since our study

TABLE 1 Models used in multi-model inference of ancestral ranges.

Model	Free parameters	Log-likelihood	AIC
BayArea-like + J	3	−482	970
BayArea-like	2	−548	1100
DEC + J	3	−603	1212
DEC	2	−618	1239
DIVA-like + J	3	−622	1251
DIVA-like	2	−631	1266

TABLE 2 Results of Lagrange analysis for key nodes labelled in Figure 3.

Node	Most likely range ^a	Probability
Poritiinae	C, LG, UG	0.62
Poritiini	A	0.99
Liptenini	C, LG, UG	0.96
A: Durbanina subtribe	SA	0.98
B: Pentilina subtribe	C, LG, UG	0.99
C: Liptenina subtribe	C, LG, UG	0.99
D: Cooksoniina subtribe	Z	0.99
E: Iridanina subtribe	C, LG, UG	0.89
F: Epitolina subtribe	C, LG, UG	0.99

Abbreviations: A, Asian; C, Congolian; LG, Lower Guinean; SA, South African; UG, Upper Guinean; Z, Zambezan.

^aBiogeographic regions.

does not have sufficient taxon sampling to determine the appropriate number of genera or assign most species to a genus with confidence.

Historical biogeography

The model that best fits our data is the BayArea-like model which allows for founder events during cladogenesis (Table 1).

The common ancestor of the Poritiini was most likely Asian, while the common ancestor of the Liptenini was most likely African (Figure 3, Table 2). The provenance of the common ancestor of the Poritiinae as a whole is uncertain, although African ancestry is slightly more likely (0.62 probability of occurrence in the Congolian/Upper and Lower Guinean region; Table 2). Within the Liptenini, the common ancestor appears to be pan-Congolian, including the Congolian, Lower Guinean and Upper Guinean subregions. This is the case for most of the internal nodes of the phylogeny as well, with a few exceptions. The subtribe Durbanina (clade A) appears to have arisen from the Southern Africa region, while the subtribe Cooksoniina most likely arose in the Zambezan region, as did the genus *Alaena*. *Teriomima* + *Baliochila* are reconstructed as having an ancestor in the East African Coastal Forest Zone. It is worth noting in this context that the East African Coast Forest Zone was once contiguous with Congolian forests (Couvreur

et al., 2008). Apart from these, expansions out of the Pan-Congolian region are relatively recent, occurring in the most recent third of the tree, after the common ancestors of the Liptenini genera.

Repeatedly across the tree, ancestral ranges contract from a Pan-Congolian range to a subset of this range. For instance, the ancestors of *Mimacraea* and *Ornipholidotos* are Guinean, while the ancestor of *Telipna* is Lower Guinean + Congolian, and many range contractions are observed within genera.

Inclusion of the *j* parameter evaluating 'jump dispersal' (peripatric speciation) in biogeographic analyses is controversial (Klaus & Matzke, 2020, see their appendix B; Ree & Sanmartín, 2018). We present the results of the single best model according to AIC in Figure 3, but also provide the results of the best model without jump dispersal (BayArea-like) in Figure S1. Disallowing jump dispersal produced similar patterns; the main exceptions were that the deeper lineages were largely Pan-Congolian+Zambezan, with some subsequent range reductions to strictly Pan-Congolian ranges, and the ancestor of the Poritiinae was recovered as Pan-Congolian+Zambezan+Asian.

Ant association

Genera with obligate ant associates belong to subtribes Pentilina, Liptenina, Iridanina and Epitolina. The paucity of available life history data does not allow evolutionary reconstruction of ant association in Poritiinae, but the wide phylogenetic distribution of species obligately associated with *Crematogaster* ants within the tribe Liptenini hints that this might be the ancestral state. Larvae of poritiines' likely sister group, the subfamily Aphnaeinae, are thought to have been ancestrally associated with *Crematogaster* ants (Boyle et al., 2015; Espeland et al., 2018), and all known aphnaeine species are obligately ant-associated (Pierce & Dankowicz, 2022). Liptenini originated in African forests, and numerous clades colonized open habitats secondarily (Figure 3). This scenario is consistent with the hypothesis that the most recent common ancestor of Liptenini were obligately ant-associated. Known obligate Liptenini-ant associations are widespread in forested habitats, while species in open, dry habitats do not generally appear closely ant-associated (Bampton, 1995); however, much more knowledge of the life history of the poritiines is necessary before we can say anything with confidence about the history of ant association in this group.

CONCLUSION

Our study represents the first phylogenetic hypothesis for the Poritiinae based on molecular markers, including about 30% of species and 86% of genera. We confirm the reciprocal monophyly of the Poritiini and Liptenini, and we show that previous classifications of the Liptenini are not monophyletic; thus, we propose a reclassification of six subtribes within the Liptenini. Our work points to several taxa within the Poritiinae in need of further revision: the subtribe Epitolina and the clade including the genera *Liptena*, *Pentila*, *Micropentila* and

Eresina. It also establishes a framework for further comparative studies of the unusual life histories of these fascinating butterflies.

AUTHOR CONTRIBUTIONS

John Boyle: Conceptualization (supporting); data curation (lead); formal analysis (lead); investigation (supporting); methodology (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Marianne Espeland:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); resources (supporting); writing – review and editing (supporting). **Szabolcs Sáfián:** Data curation (supporting); formal analysis (supporting); methodology (supporting); resources (supporting); writing – review and editing (supporting). **Robert Ducarme:** Resources (supporting). **Alan Gardiner:** Resources (supporting). **James Coleman:** Investigation (supporting). **Alan Heath:** Resources (supporting). **Stewart Fisher:** Resources (supporting). **Steve C Collins:** Resources (supporting). **Dino Martins:** Resources (supporting). **Kwaku Aduse-Poku:** Investigation (supporting). **Michel Libert:** Data curation (supporting); writing – review and editing (supporting). **Even Dankowicz:** Writing – original draft (supporting). **Akito Y. Kawahara:** Funding acquisition (lead); resources (lead). **David Lohman:** Data curation (supporting); funding acquisition (lead); writing – review and editing (supporting). **Naomi E Pierce:** Conceptualization (lead); funding acquisition (lead); resources (lead); writing – original draft (lead); writing – review and editing (supporting).

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CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Sequences for each locus used in these analyses are available on GenBank; see Supplementary File S3 for a table of accession numbers. Scripts and the alignment used to run IQ-TREE, the resulting tree and

the scripts necessary to replicate our biogeographic analyses are available on Dryad, (<https://doi.org/10.5061/dryad.3n5tb2rm4>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Comparison between ancestral range reconstructions with and without jump parameters.

Figure S1: Ancestral range reconstruction with the jump parameter. This figure is equivalent to Figure 3 in the main text. Nodes and branch tips are labelled with a series of 4-letter codes indicating the biogeographic region. CNGO: Congolian; EACF: East African Coastal Forest; L_GN: Lower Guinean; RIFT: East African Rift Forest; S_AF: South African; SMLA: Somalian; SUDN: Sudanian; U_GN: Upper Guinean; ZMBZ: Zambezan; ASIA: Asian.

Figure S1.2. Ancestral range reconstruction without the jump parameter. Nodes and branch tips are labelled as in Figure S1.2.

Data S1. Supporting information.

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