Systematic Entomology

*Systematic Entomology* (2020), **45**, 703–722 DOI: 10.1111/syen.12432

# Molecular phylogeny of the tribe Candalidini (Lepidoptera: Lycaenidae): systematics, diversification and evolutionary history

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**Abstract.** The butterfly tribe Candalidini is geographically restricted to Australia and mainland New Guinea and its adjacent islands. With 60 species and subspecies, it represents a large radiation of Papilionoidea in the Australian region. Although the species-level taxonomy is relatively well understood, the number of genera is uncertain, varying from two to eight. We reconstructed the phylogeny of the Candalidini based on a 13-locus hybrid enrichment probe set (12.8 Kbp: COI, Thiolase, CAD, CAT, DDC, EF1-a, GAPDH, HCL, IDH, MDH, RPS2, RPS5, Wingless), including all previously recognized genera and 76% (28/37) of the species-level diversity of the tribe. Maximum likelihood analysis recovered the Candalidini as a strongly supported monophyletic group. In conjunction with morphological characters, the phylogeny provided a robust framework for a revised classification in which we recognize four genera, 37 species and 23 subspecies. The genus *Nesolycaena* Waterhouse & R.E. Turner is considered in synonymy with *Candalides* Hübner, and four other genera are not recognized, namely, *Holochila* C. Felder, *Adaluma* Tindale, *Zetona* Waterhouse and *Microscena* Tite. Of the four valid genera, the *absimilis* group (23 species) is placed in the newly described genus *Eirmocides* Braby, Espeland & Müller **gen. nov.** (type species *Candalides consimilis* Waterhouse). The *erinus* group (six species) is assigned to *Erina* Swainson, which is reinstated. *Chrysophanus cyprotus* Olliff is assigned to *Cyprotides* Tite, which is also reinstated as a monotypic genus. The remaining seven species are placed in *Candalides sensu stricto*. Overall, we propose 47 new nomenclatural changes at the species and subspecies levels, including the synonymy of *Holochila biaka* Tite as *Eirmocides tringa biaka* (Tite) **syn. nov. et comb. nov.** and recognition of *Candalides hyacinthinus gilesi* M.R. Williams & Bollam as a distinct species *Erina gilesi* M.R. Williams & Bollam **stat. rev. et comb. nov.** A dated phylogeny using Bayesian inference in BEAST2 and biogeographical and habitat analyses based on the DEC model in BioGeoBEARS indicated that the ancestor of the Candalidini most likely evolved in rainforest habitats

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of the mesic biome in situ on the Australian plate of Southern Gondwana during the Eocene (c. 43 Ma). A major period of diversification occurred in the Miocene, which coincided with aridification of the Australian continent, followed by a further episode of radiation in montane New Guinea during the Plio-Pleistocene.

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http://zoobank.org/urn:lsid:zoobank.org:pub:47D5CA34-C294-4FBD-84B6-1C2A82B7CADF.

## Introduction

The lycaenid tribe Candalidini is endemic to the Australian region and represents a significant radiation of butterflies in Australia and mainland New Guinea. It occurs from the Lesser Sunda Islands (Sumba and Timor) through mainland New Guinea (Papua New Guinea, Papua and West Papua) and its satellite islands, including Aru, Kai, Tanimbar, the Bismarck Archipelago (New Britain), the D'Entrecasteaux Islands and the Louisiade Archipelago, to Australia, including the island state of Tasmania (Tite, 1963; Parsons, 1998; Braby, 2000; Müller, 2013). It is absent from the Solomon Islands, including Bougainville Island (Tennent, 2002). The butterflies occur in a variety of habitats and are a conspicuous component of the Australian tropical and temperate eucalypt woodlands and open forests and eastern coastal rainforests. The highest species richness occurs in mainland New Guinea and its adjacent islands (total of 23 species), where many species are restricted to lower montane forests (1000–1600 m) and mid-montane forests (1600–2100 m), but others occur widely in lowland forest (<500 m), especially tropical rainforest. In Australia, 14 species are endemic to the continent. Only three species are shared between Australia and New Guinea, *viz: Candalides margarita* (Semper), *C. helenita* (Semper) and *C. erinus* (Fabricius).

The Candalidini currently comprises 37 species (Tite 1963; Tindale, 1965; Common & Waterhouse, 1972; Edwards & Kerr, 1978; Parsons, 1986; d'Apice & Miller, 1992; Braby, 1996, 2008, 2017; Williams & Bollam, 2001; Braby & Douglas, 2004; Tennent, 2005; Müller, 2013, 2014a, 2014b; Müller & Tennent, 2016), but the number of genera remains uncertain (Braby, 2010). Indeed, the taxonomic composition of genera has had a turbulent history over the past half century, varying from as few as two to as many as eight genera (see history of the systematics of the Candalidini below). Phylogenetic relationships of Candalidini remain unknown, and the higher classification of the tribe is in need of systematic revision. Perhaps no other group of butterflies in Australia and New Guinea is beset by such an unstable set of scientific names and poorly resolved classification.

Although the monophyly of the tribe has not yet been confirmed, the Candalidini are characterized by several unique characters (putative synapomorphies). In particular, the male genitalia are distinctive, being flattened and oval-shaped in profile with the uncus lobes well separated and the brachia having a short bifurcation near the tip (Eliot, 1973). The morphology of the pupa is also distinctive and unique among the Lycaenidae, with the anterior end flattened with a median indentation; the thorax with a pair of middorsal projections; the thorax and abdomen with a dorsal ridge; and the abdomen expanded laterally into a pair of flanges, which are upturned at the sides (Common & Waterhouse, 1972, 1981; Braby, 2000). Other morphological features include structure and venation of the wings in which the hind wing termen is without a tail and usually rounded, although in some species, it may be produced towards the tornus; veins Sc and $R_1$ in the fore wing are separated; and in the male, there is the presence of 'dagger-like' androconial scales on the upper side of the fore wing, which may be concentrated into a trident-shaped patch along the basal half of veins $M_3$, $CuA_1$ and $CuA_2$ and sometimes on the adjacent veins beyond the discal cell (Eliot, 1973). Unlike most other butterflies in the Polyommatinae-Theclinae assemblage, these butterflies, when settled with wings closed, never gyrate their hind wings to draw the attention of predators towards the tornal region away from the head. Ant attendance in the larval stage is weakly facultative – the larvae are rarely attended by ants.

Eliot (1973) classified the tribe into the subfamily Polyommatinae; however, a recent comprehensive phylogenomic analysis of the butterflies based on 352 loci (Espeland *et al.*, 2018) revealed that the Candalidini appear to be most closely related to the Australian Ogyrini and Luciini (Theclinae) and evolved in the Eocene (~47 Ma). Moreover, the clade Candalidini + (Ogyrini + Luciini) was nested with the Theclinae and descended from a common ancestor that gave rise to several other lineages endemic to Australia, most notably the genera *Pseudalmenus* H.H. Druce and *Jalmenus* Hübner of the polyphyletic Zesiusini. This phylogenetic placement within the Theclinae is perhaps not surprising

because the males of many Candalidini have androconial scales concentrated in discrete patches on the wings, a trait characteristic of many thecline butterflies but absent among the Polyommatinae.

Our study has three aims: (i) The first is to determine the generic composition of the Candalidini based on a robust phylogenetic framework, integrated with morphological and life history characters. Previous classifications suggest there could be anywhere from 2 to 8 valid genera. (ii) The second is to investigate broad patterns of diversification and evolutionary history of the tribe, particularly their biogeographical history and evolutionary history of habitat associations. The geographical restriction and estimated age of the Candalidini suggest the tribe evolved in situ on the Australian plate in Southern Gondwana when Australia was still connected to Antarctica and South America, but to what extent have the aridification of Australia and concomitant contraction of the Gondwanan rainforests during the Oligocene-Miocene, and the subsequent rise of the New Guinea highlands during the Plio-Pleistocene, shaped the assembly and evolution of this group of butterflies? (iii) The third is to resolve and clarify the species boundaries of problematic taxa, most notably *Candalides biaka* (Tite) and *Candalides hyacinthinus gilesi* M.R. Williams & Bollam, which have been contentious (Parsons, 1998; Williams & Williams, 2006).

## Systematics of the Candalidini

The tribe Candalidini was proposed by Eliot (1973), with *Candalides* Hübner as its type genus. Eliot (1973) considered Candalidini to be composed of seven genera: *Candalides*, *Erina* Swainson, *Nesolycaena* Waterhouse & R.E. Turner, *Adaluma* Tindale, *Zetona* Waterhouse, *Cyprotides* Tite and *Microscena* Tite (Table 1). He considered these taxa to all be closely related based on the morphology of the male genitalia. The arrangement of genera by Eliot (1973) resolved much of the confusion that arose from the earlier classifications proposed by Waterhouse (1903), Clench (1955) and Tite (1963). For example, the genus *Philiris* Röber, previously classified with *Candalides*, was shown to be related to *Hypochrysops* C. & R. Felder and allied genera, and it was placed in the newly erected tribe Luciini (Eliot, 1973; Sands, 1986). However, the higher-level classification and phylogenetic relationships of the Candalidini, particularly the delineation and composition of genera, has been anything but stable (Table 1).

Waterhouse (1903) maintained *Candalides* in the broad sense and resolved much of the nomenclatural confusion that had persisted in the 19th century. He recognized several species groups, namely, *absimilis* group, *erinus* group, *xanthospilos* group, *cyprotus* group and *albosericea* group, based on morphology of the labial palpus and underside pattern and hypothesized that 'I think that three (at least) of the divisions of *Candalides* are as worthy of generic rank' (p. 176). Subsequently, he (Waterhouse & Turner, 1905) introduced the name *Nesolycaena* to accommodate the species *Holochila albosericea* Miskin, although the other species groups were not formally assigned generic status (Waterhouse & Lyell, 1914) (Table 1). Tindale (1922) proposed *Aduluma* for the species *Adaluma urumelia* Tindale. Sands (1971) and Edwards (1980) showed that *Nesolycaena* and *Aduluma* were closely related based on comparative morphology of the immature stages, particularly the pupa. d'Apice and Miller (1992) subsequently synonymized *Adaluma* with *Nesolycaena*. Braby (1996) reached a similar conclusion and provided a diagnosis for *Nesolycaena* to distinguish it from *Candalides*, including relatively short antennae (less than half the length of the costa of the fore wing) and males with bluish-white scales on the upper side of the wings.

The monotypic genus *Zetona* was proposed by Waterhouse (1938) to accommodate the species *Zizera delospila* Waterhouse, which was considered to be related to *Zizeeria*, *Zizina* and allied genera (Waterhouse, 1903; Waterhouse & Lyell, 1914; Clench, 1955). However, Eliot (1973) placed *Zetona* in the Candalidini based on the structure of the male genitalia. This systematic arrangement was supported by the discovery of the immature stages and larval food plant by Braby (1995), which indicated that *Zetona delospila* was most closely related to the *erinus* group of species. Subsequently, Braby (2000) synonymized *Zetona* with *Candalides sensu lato*, pointing out that the distinguishing characters of this genus, including the form of the male genitalia, are present in all members of the *erinus* species group (see Edwards & Kerr, 1978).

Tite (1963) published a systematic revision of *Candalides* and allied genera and divided *Candalides sensu lato* into five genera, namely, *Candalides*, *Erina*, *Holochila* Felder, *Cyprotides* and *Microscena*. Tite (1963) considered an additional two genera, *Philiris* and *Adaluma*, to be closely related to *Candalides sensu lato* (Table 1), but he did not study the genera *Nesolycaena* and *Zetona*. Three of Tite's genera were monotypic (*Candalides*, *Microscena* and *Cyprotides*), and his division was made primarily on the basis of differences in wing shape and venation and on the relative proportions of the segments of the labial palps. Although Tite (1963) studied and illustrated the male genitalia, these components were not considered in his classification.

Tite (1963) used *Holochila* in the narrow sense to accommodate the *absimilis* group of species and followed Waterhouse (1903), who incorrectly designated *Holochila absimilis* C. Felder as the type species for this genus. Although Felder (1862) introduced *Holochila* to accommodate the species *H. absimilis*, it was intended as a replacement name for *Erina*. Thus, *Holochila* is a junior objective synonym of *Erina*, with the same type species (*Papilio erinus* Fabricius), and is therefore invalid for the *absimilis* group of species (Hemming, 1967; Edwards, 1996; Edwards *et al.*, 2001). Hence, if the *absimilis* species group is to be recognized as a distinct genus, a new generic name must be proposed for this group of species, as pointed out by Eliot (1973).

Tindale (1965), D'Abrera (1971) and McCubbin (1971) followed Tite (1963), and all incorrectly used *Holochila* for the *absimilis* species group, with the latter two authors apparently unaware of the earlier remarks of Hemming (1967) on

**Table 1.** Nomenclatural history of genera recognized in the tribe Candalidini Eliot, 1973, over the past 117 years

| Generic name and their type species | Waterhouse (1903) | Waterhouse and Lyell (1914) | Tite (1963) | Common and Waterhouse (1972, 1981) | Eliot (1973) | Braby (2000, 2010) | This work |
|---|---|---|---|---|---|---|---|
| ***Candalides* Hübner, 1819**<br>*Rusticus xanthospilos* Hübner, [1817] | *Candalides* | *Candalides* | *Candalides* | *Candalides* | *Candalides* | *Candalides* | *Candalides* |
| ***Erina* Swainson, 1833**<br>*Papilio erinus* Fabricius, 1775 | *Candalides* | *Candalides* | *Erina* | *Candalides* | *Erina* | *Candalides* | *Erina* |
| ***Holochila* C.** Felder, 1862<br>*Papilio erinus* Fabricius, 1775 | *Candalides* | *Candalides* | *Erina* | *Candalides* | *Erina* | *Candalides* | *Erina* |
| *absimilis* species group (*Holochila* sensu auctt.)<br>*Holochila absimilis* C. Felder, 1862 | *Candalides* | *Candalides* | *Holochila* | *Candalides* | *Candalides* | *Candalides* | *Eirmocides* gen. nov. |
| ***Nesolycaena*** Waterhouse & R.E. Turner, 1905<br>*Holochila albosericea* Miskin, 1891 | *Candalides* | *Nesolycaena* | | *Nesolycaena* | *Nesolycaena* | *Nesolycaena* | *Candalides* |
| ***Adaluma*** Tindale, 1922<br>*Adaluma urumelia* Tindale, 1922 | | | *Adaluma* | *Adaluma* | *Adaluma* | *Nesolycaena* | *Candalides* |
| ***Zetona*** Waterhouse, 1938<br>*Zizera delospila* Waterhouse, 1903 | *Zizera* | *Zizina* | | *Zetona* | *Zetona* | *Candalides* | *Erina* |
| ***Microscena*** Tite, 1963<br>*Lycaena heathi* Cox, 1873 | *Candalides* | *Candalides* | *Microscena* | *Candalides* | *Microscena* | *Candalides* | *Candalides* |
| ***Cyprotides*** Tite, 1963<br>*Chrysophanus cyprotus* Olliff, 1886 | *Candalides* | *Candalides* | *Cyprotides* | *Candalides* | *Cyprotides* | *Candalides* | *Cyprotides* |

A total of eight generic names have been applied to this group of butterflies in the past. The type species are listed for each genus. Note *Holochila* C. Felder is a junior objective synonym of *Erina* Swainson, with the same type species; it was introduced by Felder (1862) for the species *absimilis* C. Felder but was intended as a replacement name for *Erina*. Tite (1963) used *Holochila* in the narrow sense to accommodate the *absimilis* group of species and followed Waterhouse (1903), who incorrectly designated *Holochila absimilis* C. Felder as the type species for this genus (Hemming, 1967; Edwards, 1996; Edwards *et al.*, 2001).

the synonymy of *Holochila*. D'Abrera (1971) and McCubbin (1971) also recognized *Adaluma*, *Nesolycaena* and *Zetona* as valid taxa, and thus, eight generic names were used in their systematic arrangement of species. However, Common and Waterhouse (1972, 1981), as well as Edwards and Kerr (1978) and Fisher (1978), did not follow Tite's arrangement and maintained most Australian taxa under *Candalides sensu lato*, mainly because of the lack of a generic name for the *absimilis* species group but also because of similarities in the morphology of the pupa of *Candalides sensu stricto*, *Microscena* and *Erina*. However, the genera *Adaluma*, *Nesolycaena* and *Zetona* were retained by Common and Waterhouse (1972, 1981) (Table 1). *Candalides cyprotus* appears to be allied to the *absimilis* species group, but its life history and biology are distinctive (Atkins & Heinrich, 1987).

In summary, the Candalidini comprise 37 species, but the number of genera and their evolutionary relationships are uncertain. The most recent classification (Braby, 2000, 2008, 2010; Braby & Douglas, 2004) recognized only two genera – *Candalides* and *Nesolycaena* – with the former divided into three species groups (*absimilis*, *erinus* and *xanthospilos*), but six other generic names have been used to differentiate this group of butterflies (Table 1). Most of these names are still in common usage, such as *Erina* (Grund 2001, 2009), *Zetona* (Johnson & Valentine, 2004), *Cyprotides* (Grund, 2013) and *Holochila* (Müller, 2014b; Müller & Tennent, 2016). Here, we reconstruct the phylogeny of the Candalidini from molecular characters and use this as a robust framework to revise the generic classification of the tribe (Talavera *et al.*, 2013), as well as to investigate patterns of diversification and evolutionary history.

## Materials and methods

### *Taxon sampling and specimens examined*

Our ingroup dataset included 28 species (and 13 subspecies) with a total of 112 samples. Only nine rare species, all in the *absimilis* group from New Guinea, were not included in our study. Thus, our taxon dataset included all previously recognized genera and represented 28 of 37, or 76%, of the species level diversity of the tribe. Specimen vouchers and information for each sample are listed in Table S1.

### *Molecular methods*

DNA was extracted from leg or thorax tissue using the OmniPrepTM DNA extraction kit (G-Biosciences) (Espeland *et al.*, 2018) or the DNeasy Blood & Tissue Kit (Qiagen). Thirteen loci (COI, Thiolase, CAD, CAT, DDC, EF1-a, GAPDH, HCL, IDH, MDH, RPS2, RPS5, Wingless), including the most commonly used markers for butterfly phylogenetics, were captured using the anchored hybrid enrichment probe kit (BUTTERFLY2.0) and methods made available by Kawahara *et al.* (2018). For some additional specimens, cytochrome c oxidase subunit 1 (COI) was amplified using the primer pair LCO1490-JJ and HCO2198-JJ (Astrin & Stüben, 2008). A touchdown thermocycling protocol was applied, reducing the annealing temperature by 1° per cycle during the first 15 cycles, starting at 55°C, with 25 subsequent cycles at an annealing temperature of 50°C and elongation time of 90 s. PCR products were purified using the QIAquick PCR purification kit

(Qiagen), and purified PCR products were sent to Macrogen (Amsterdam, Netherlands) for forward and reverse Sanger sequencing.

### *Data assembly and clean-up*

Hybrid enrichment data were cleaned, assembled and aligned using the pipeline by Breinholt *et al.* (2018) as specified by Kawahara *et al.* (2018). Sanger sequencing data were edited using Geneious R11 (Biomatters). Additional COI sequence data were taken from BOLD (Hebert *et al.* 2013) (Table S2), and all COI sequences were aligned using MAFFT-linsi 7.409 (Katoh & Standley, 2013). The total concatenated dataset included 12 822 base pairs.

### *Phylogenetic analysis and molecular dating*

Ten outgroup taxa representing multiple Theclinae and Polyommatinae tribes were taken from Espeland *et al.* (2018), and *Lycaena hippothoe* (Linnaeus) (Lycaeninae) was used to root the tree. As noted above (see Introduction), the sister group of Candalidini is uncertain. The tribal analysis of the Lycaenidae by Espeland *et al.* (2018) suggests that, within the Theclinae-Polyommatinae assemblage, Candalidini are sister to Ogyrini + Luciini, and this clade is sister to the remainder of the 'subfamily' minus *Pseudalmenus* and *Jalmenus* of the polyphyletic Zesiusini. Because of some uncertainty in deeper-level relationships, we included outgroups representing various tribal taxa within the Theclinae-Polyommatinae assemblage.

Three phylogenetic analyses were undertaken. First, a phylogeny was constructed based on all taxa with 13 loci (67 samples including outgroups) to stabilize the backbone. The concatenated loci were partitioned by locus and codon position, and partition finding and model selection were performed using ModelFinder (Kalyaanamoorthy *et al.*, 2017) in IQ-TREE 1.6.7 (Nguyen *et al.*, 2014). Models and partitions can be found in the File S1. Fifty independent likelihood searches with 1000 ultrafast bootstrap (UFB) replicates were performed, and the one with the highest likelihood was chosen as the best tree. Second, this tree was collapsed to only include nodes with a UFB of 95% or higher and was subsequently used as a constraint tree for the backbone in a set of analyses where COI data generated for this study, and from BOLD, were added. Otherwise, phylogenetic analyses were as given above. Genetic distances were measured for taxa of interest based on COI only, using uncorrected p distances.

Third, a reduced dataset including only one member of each taxon was used to date the phylogeny. This dated tree was then used to derive our revised classification and to analyse patterns of diversification and evolutionary history (see Biogeographical and habitat analyses below). Because no fossils are available for the Lycaenidae, dating was based on secondary calibrations from Espeland *et al.* (2018). In that study, the age of the Theclinae was estimated to be 55.3 Ma with a 95% credibility interval of 68.3–41.7 Ma. This estimate was applied as a normal prior on the Theclinae, with a mean of 55.3 and a sigma of 6.9, which generates 97.5% quantiles that approximate the credibility interval found by Espeland *et al.* (2018). Site and clock models were unlinked, and trees were linked. Model selection was performed within BEAST2.5.2 (Bouckaert *et al.*, 2014) using the bModeltest 1.1 plugin (Bouckaert & Drummond, 2017). The clock model was set to relaxed log normal, the tree prior to the Yule model. Default priors were used with the exception of the ucldMean priors, which were set to the gamma distribution with an alpha of 0.01 and a beta of 1000. BEAST2 was run thrice with 75 million generations and a sampling frequency of 7500. Convergence was checked using Tracer 1.7 (Rambaut *et al.*, 2018). The first 10% were removed as burnin, and the remaining trees were combined and subsampled in LogCombiner 2.5.2, a part of the BEAST2 package, to generate a final posterior distribution of 10 000 trees. A maximum clade credibility tree with common ancestor node heights was finally generated using TreeAnnotator 2.5.2, also part of the BEAST2 package. All BEAST2 analyses were run on the CIPRES cluster (Miller *et al.*, 2010).

### *Biogeographical and habitat analyses*

The dated tree was used as an input tree for biogeographical and habitat analyses. These were performed using the dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008), rather than the DEC + J model for reasons outlined by Ree and Sanmartín (2018), in the R package BioGeoBEARS (Matzke, 2013). In the biogeographical analysis, two areas (Australia and New Guinea) were included, and in the habitat analysis, five habitats (lowland rainforest, lower montane forest, mid-montane forest, open forest, woodland/heathland and sedgeland/grassland) were included. The maximum number of areas occupied by a species was set to two and three. For the biogeographical analysis, Australia refers to mainland Australia and Tasmania, whereas New Guinea refers to mainland Papua New Guinea, Papua and West Papua and their surrounding islands (i.e., Misool, Waigeo, Biak, Yapen, Bismarck Archipelago, D'Entrecasteaux Islands, Louisiade Archipelago, Aru, Kai and Tanimbar). For the habitat analysis, lowland rainforest refers to habitats with a closed canopy (projected foliage cover >70%) below 500 m and includes tropical and subtropical rainforest, monsoon forest and rainforest edge; lower montane forest refers to rainforest habitats with a closed canopy 1000–1600 m; mid-montane forest refers to rainforest habitats with a closed canopy 1600–2100 m; open forest refers to habitats with an open canopy (projected foliage cover <70%) and includes eucalypt tall open forest and open forest; and woodland/heathland refers to habitats with an open canopy (projected foliage cover <30%) and includes eucalypt woodland, low woodland, open woodland, savannah woodland, heathy woodland and heathland. Geographical distribution and habitat data were obtained primarily from Tite (1963), Parsons (1998) and Braby (2000, 2016), as well as from personal experience of the authors.

*Morphological characters*

Morphological characters of the adult stage, including the male genitalia, pupal stage and life history data, were compiled for the type species and, where known, all other species for each genus based primarily on the published literature (Waterhouse, 1942; Tite, 1963; Tindale, 1965; Sands, 1971; Edwards & Kerr, 1978; Edwards, 1980; Atkins & Heinrich, 1987; Braby, 1995, 1996, 2000; Braby & Douglas, 2004), as well as from examination of material in the Australian National Insect Collection, Canberra (ANIC). Characters were divided into binary or multi-states, scored for each taxon, assembled into a matrix and then compared against the molecular phylogeny to determine diagnostic features. A total of 17 morphological characters were assessed.

*Genitalia*

Male and female genitalia in the *Candalides hyacinthinus* complex were examined to inform species delimitation of this group, particularly *C. hyacinthinus gilesi*. Multiple samples of genitalia (mounted on microscope slides in Euparal) were examined for each sex of each subspecies preserved in the ANIC, as follows: *C. hyacinthinus hyacinthinus* ♂: Kuranda, QLD (ANIC M340), Bateman's Bay, NSW (ANIC M308); *C. hyacinthinus hyacinthinus* ♀: Narara, NSW (ANIC M277), Ashton Park, NSW (ANIC M336), Hawkesbury Lookout, NSW (ANIC M338), Katoomba, NSW (ANIC M326); *C. hyacinthinus simplex* ♂: Murray Bridge, SA (ANIC M312), Coonalpyn, SA (ANIC M270); *C. hyacinthinus simplex* ♀: West Wyalong, NSW (ANIC M327); *C. hyacinthinus gilesi* ♂: Margaret River, WA (ANIC M310), Porongurups, WA (ANIC M328); and *C. hyacinthinus gilesi* ♀: Margaret River, WA (ANIC M311), Yalgorup, WA (ANIC MFB105).

## Results

*Phylogenetic relationships*

Phylogenetic analysis of the smaller ingroup taxon set (23 species, 56 samples) that included samples with all 13 loci demonstrated the Candalidini as a strongly supported monophyletic group (Fig. 1). The backbone of this tree was well resolved with three deep basal lineages recovered, corresponding to the *absimilis* species group (clade I), *erinus* species group (*Zetona* + *Erina*) (clade III) and a clade that included eight species (*cyprotus*, *xanthospilos*, *heathi*, *noelkeri*, *albosericea*, *medicea*, *urumelia* and *caesia*) (clade IV). The latter two clades were sisters to each other with strong nodal support (clade II). Within the *absimilis* species group (clade I), there were three subgroups – one comprising three species (clade IA: *Candalides consimilis*, *C. absimilis* and *C. grandissima*); another with three species (clade IB: *C. margarita*, *C. tringa* and *C. biaka*); and the third comprising all the other taxa (clade IC), mainly from New Guinea. Within the *erinus* species group (clade III), *C. delospila* was sister to the four other species but with weak support (77% BS), thus giving little evidence of recognition of *Zetona* as a genus distinct from *Erina*. Clade IV included five genera according to previous classifications, with the following topology: *Cyprotides* + ((*Candalides sensu stricto* + *Microscena*) + (*Nesolycaena* + *Adaluma*)). According to the current classification, which recognizes just two genera (Table 1), *Candalides sensu lato* was paraphyletic with *Nesolycaena* nested within it (Fig. 1). Although *Nesolycaena*, in the broad sense, comprised a well-supported monophyletic group, it was sister to *Candalides xanthospilos* + (*C. heathi* + *C. noelkeri*), and this clade (clade VI) was sister to *C. cyprotus* (clade V).

The larger ingroup taxon set (28 species, 112 samples), through the inclusion of additional samples (56 COI sequences) to the dataset, yielded the same basic topology with three deep lineages in which the *absimilis* species group (clade I) was sister to the *erinus* species group (clade III) plus all other taxa (clade IV) (Fig. 2). Again, there was little support for *Zetona*, and *Nesolycaena* was nested within *Candalides sensu lato*. The key finding from this analysis, however, was that most taxa were monophyletic with 100% bootstrap support. The exceptions to this were *Candalides tringa* and *C. helenita*. *Candalides tringa* was paraphyletic because of the inclusion of *C. biaka*: the four samples sequenced otherwise comprised a well-supported monophyletic group (100% BS). *Candalides helenita* comprised a complex of four lineages: (i) *C. helenita helenita* from the Wet Tropics, QLD; (ii) *C. helenita helenita* from Cape York Peninsula, QLD and southern Papua New Guinea (Western Province); (iii) *C. cupreus* from mainland New Guinea; and (iv) *C. helenita dimorphus* from northern Papua New Guinea (East Sepik Province). For several polytypic species, there was evidence of reciprocal monophyly among the various subspecies, namely, *C. margarita margarita*, *C. margarita gilberti*, *C. hyacinthinus hyacinthinus*, *C. hyacinthinus simplex*, *C. geminus geminus*, *C. geminus gagadju* and *C. heathi alpinus*, but not for taxa within the species *C. consimilis*, *C. absimilis*, *C. erinus* and *C. cyprotus* (Fig. 2). The phylogenetic divergence of *C. hyacinthinus gilesi* from the other subspecies of *C. hyacinthinus* was particularly deep (2.8%, based on the barcode region of COI), suggesting that the lineage may be specifically distinct.

*Revised classification*

Clearly, the current higher classification is untenable because *Candalides sensu lato* is paraphyletic. Moreover, previous classifications are cumbersome due to oversplitting of genera, some of which are poorly differentiated (e.g., *Zetona*, *Microscena*, *Nesolycaena sensu stricto*, *Adaluma* and *Candalides* as a monotypic genus). Three obvious solutions are to: (i) treat the entire tribe as a single genus (i.e., *Candalides sensu lato*), (ii) recognize the two reciprocally monophyletic lineages (clades I and II) as separate genera or (iii) recognize the three major lineages (clades I, III and IV) as three distinct genera. The latter option is adopted in the present study, although clade IV is considered to comprise two genera (corresponding to clades V and VI)

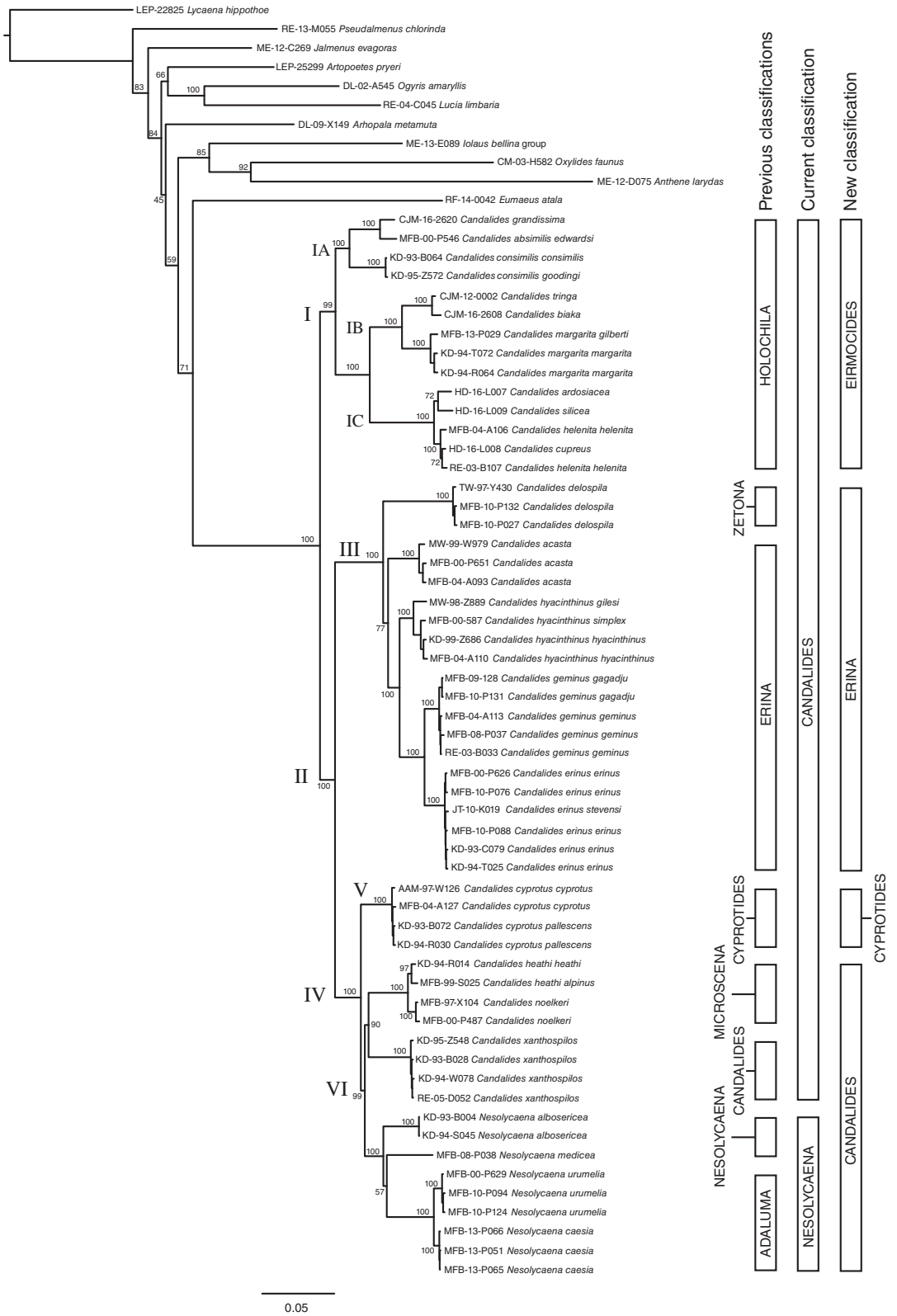



**Fig. 1.** Maximum likelihood tree of the Candalidini based on samples for which 13 loci were sequenced. Previous generic classifications are shown together with the current classification and our new (revised) classification. Major clades are numbered I–VI. Support values are shown as ultrafast bootstrap at nodes.

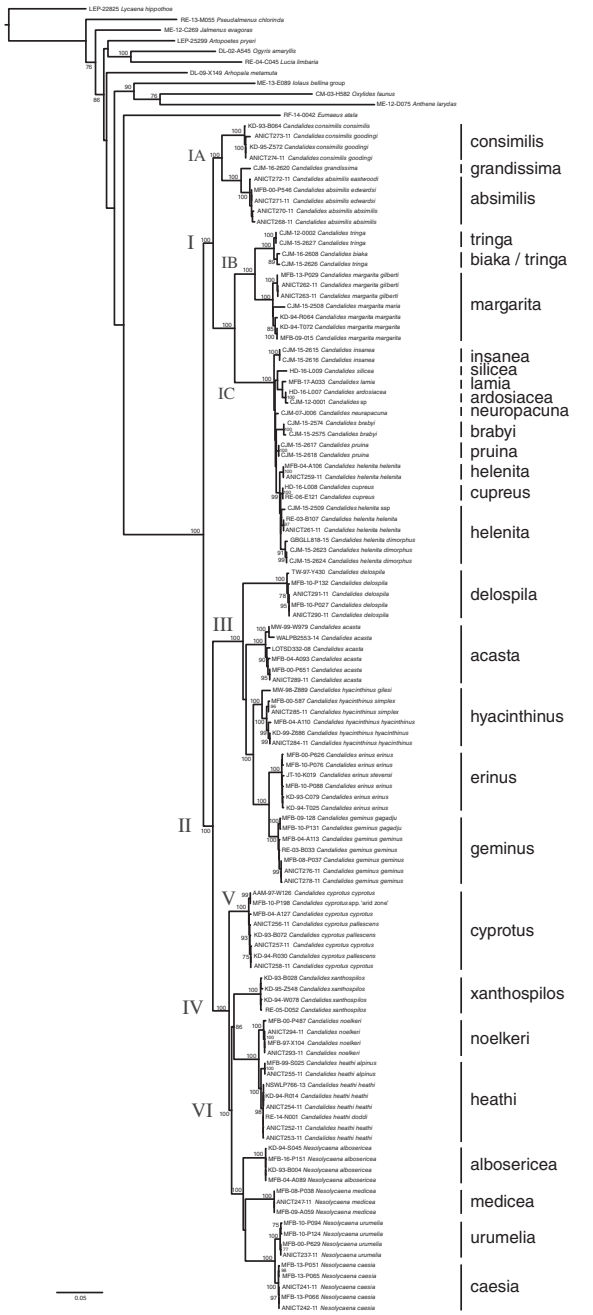



**Fig. 2.** Maximum likelihood tree of the Candalidini based on all samples and molecular data (13 loci plus additional COI sequences from BOLD). Species names are shown to the right of each clade and indicate that most taxa are monophyletic. Major clades are numbered I–VI. Support values are shown as ultrafast bootstrap at nodes.

rather than a single genus because of pronounced morphological divergence (autapomorphies) of the taxon *C. cyprotus* relative to other members of clade IV. Justification for this arrangement is based on the consideration of adult morphology and wing colour pattern, morphology of the male genitalia, morphology of the pupal stage and other life history traits, which collectively provide a set of diagnostic characters for each of the four clades (Table S3).

A summary phylogenetic tree of the Candalidini based on a reduced taxon set comprising at least one exemplar of each of the 28 species and six monophyletic subspecies in the combined dataset (13 loci and COI) is shown in Fig 3. Our new, revised classification of genera is shown to the right of this tree, together with the type species of each genus. In this classification, we recognize four genera. The *absimilis* species group (clade I) is placed in a new genus *Eirmocides* Braby, Espeland & Müller **gen. nov.**; the *erinus* species group (clade III) is assigned to *Erina*, which is reinstated; and the taxon *cyprotus* (clade V) is assigned to *Cyprotides*, which is also reinstated, whereas the remaining seven species (*heathi*, *noelkeri*, *xanthospilos*, *albosericea*, *medicea*, *urumelia* and *caesia*) (clade VI) are placed in *Candalides sensu stricto*. A revised systematic checklist of the Candalidini according to this study is presented in Appendix A. The generic classification is discussed in more detail below (see Systematics).

### *Diversification*

Our dating estimates indicate that the Candalidini evolved during the Eocene [stem-group *c*. 43 (54.5–32.6) Ma], and then, the crown group differentiated at the Oligocene/Miocene boundary [*c*. 22.3 (28.2–16.5) Ma] (Fig. 3). Subsequently, the extant genera all differentiated in the Miocene: *Eirmocides* [crown-group *c*. 18.8 (24.0–13.9) Ma], *Cyprotides* + *Candalides* [crown-group *c*. 13.7 (17.6–10.1) Ma] and then *Erina* [crown-group *c*. 11.7 (15.1–8.6) Ma]. Although *Eirmocides* started to differentiate in the early Miocene, the major radiation did not occur until the Plio-Pleistocene (<5 Ma). In contrast, most of the extant species of *Erina* and *Candalides* differentiated earlier in the late Miocene.

### *Historical biogeography*

Historical biogeographical analysis suggests an origin of the tribe in mainland Australia (Fig. 4). Subsequently, two separate colonizations of New Guinea generated the following: the clade comprising the ancestor of *Eirmocides tringa*–*E. helenita* and *E. grandissima*, followed by two independent dispersals back to Australia: *E. margarita* ssp. and *E. helenita* complex. The two haplotypes of *E. helenita helenita* indicate a single dispersal back to Australia with subsequent diversification; alternatively, if the two haplotypes are in fact separate species, then two dispersal events to northern Australia may have occurred. A third colonization of New Guinea consisted of a simple range expansion by *Erina erina* out of Australia and into mainland New Guinea and its adjacent islands (Louisiade Archipelago) and Indonesia (Maluku, Timor and Sumba). Although mainland New Guinea and its adjacent islands are more species rich, with 22 species, almost all of these species belong to the single genus *Eirmocides*, of

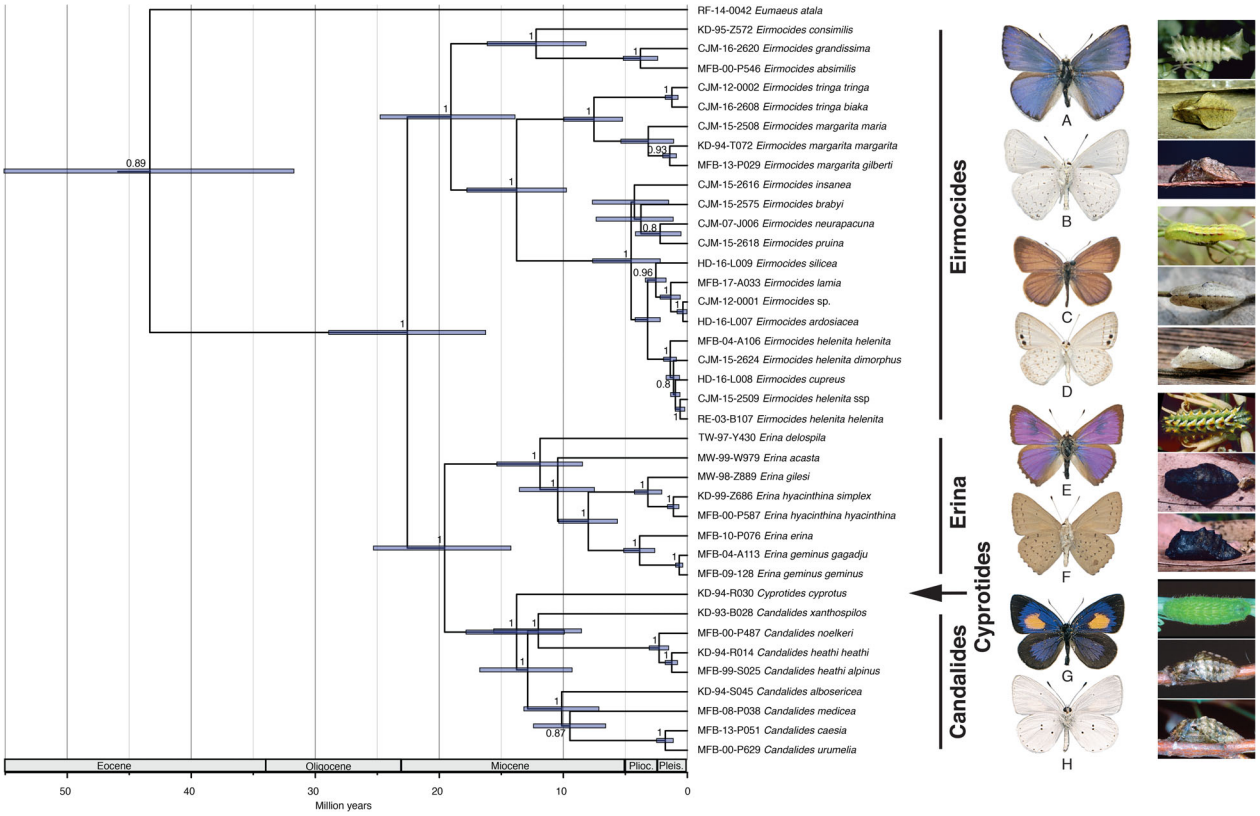



**Fig. 3.** Dated phylogeny of the Candalidini based on a reduced taxon set (one exemplar of each species and each monophyletic subspecies) of the combined dataset (13 loci plus COI sequences from BOLD), estimated using Bayesian inference in BEAST2 with secondary calibration from Espeland *et al.* (2018). Support values are indicated as posterior probabilities, and blue bars indicate 95% highest posterior density age intervals. Most outgroups have been removed for clarity (see File S2 for the full dated nexus tree file). Support values below 0.8 are not shown. Our revised generic classification of the tribe is shown to the right of the tree, with illustrations showing adults (male upper- and underside) of the type species of each genus, as follows: **(A, B)** *Eirmocides consimilis*; **(C, D)** *Erina erina*; **(E, F)** *Cyprotides cyprotus*; and **(G, H)** *Candalides xanthospilos*. Illustrations of the immature stages (final instar larva dorsal view, pupa dorsal view and pupa lateral view) are shown to the right of each of the four representative species (all photos © M.F. Braby). [Colour figure can be viewed at wileyonlinelibrary.com].

which 19 are endemic to New Guinea. In contrast, in Australia four genera embrace 18 species, of which 15 are endemic to the continent.

### *Habitat associations*

The evolution of habitats showed a clear segregation between the two major clades I and II (Fig. 4), with *Eirmocides* occurring mainly in rainforest predominantly in New Guinea, and *Erina* + (*Cyprotides* + *Candalides*) occurring mainly in open forest and woodland in Australia. Within *Eirmocides*, three subspecies (*E. consimilis goodingi*, *E. absimilis edwardsi* and *E. margarita gilberti*) predominantly occur in open forest or woodland habitats, suggesting independent colonizations of these habitats, and within *Erina*, there were two colonizations (putative reversals) into rainforest where two species (*Erina hyacinthina* and *E. erina*) occasionally breed along the edge of rainforest.

## Systematics

*Eirmocides* Braby, Espeland & Müller **gen. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:0045253A-687F-433F-B676-B5F3DBA13BF0.

Type species: *Candalides consimilis* Waterhouse, 1942 (hereby designated).

*Diagnosis. Eirmocides* differs from the other genera in the following characters: the labial palp is comparatively long, but the third (terminal) segment is relatively short, being approximately one-third the length of the second (middle) segment, and is constricted below its centre; the termen of the fore wing is distinctly convex between veins, giving the wing margin a scalloped effect; the tornus of the hind wing is slightly produced (although in some species, it may be strongly produced); the stalk subtending veins $R_3$ and $R_5$ on the fore wing extend to one-third the distance between its origin and the end of vein $R_3$ (in the other genera, it extends to less than half the distance

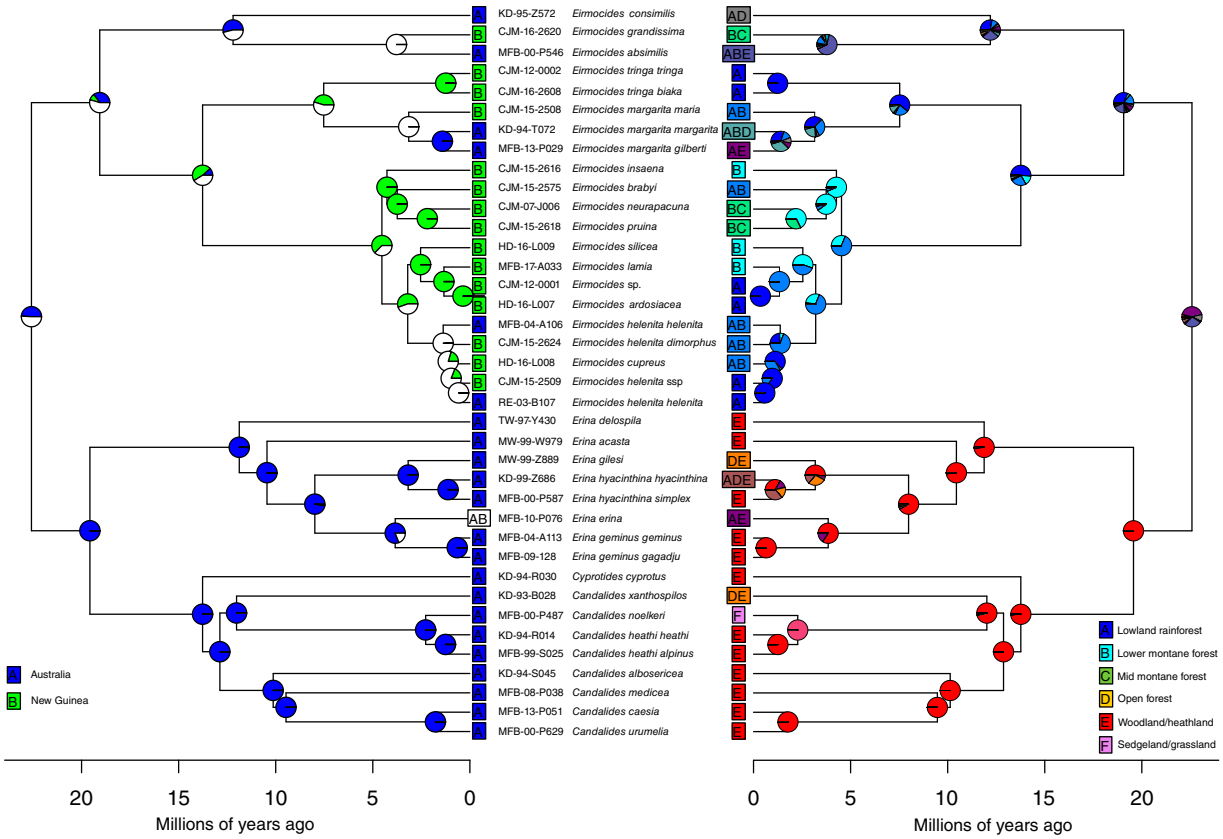



**Fig. 4.** Historical biogeography and evolution of habitats in the Candalidini based on the DEC model in BioGeoBEARS. For each phylogenetic tree, the most likely areas (left) and habitats (right) are shown as pie charts on the nodes. Two broad geographical distributions are optimized: Australia refers to mainland Australia and Tasmania; New Guinea refers to mainland Papua New Guinea, Papua and West Papua and their surrounding islands (i.e., Misool, Waigeo, Biak, Yapen, Bismarck Archipelago, D'Entrecasteaux Islands, Louisiade Archipelago, Aru, Kai and Tanimbar). Note that the Lesser Sunda Islands (Sumba and Timor) are not included for *E. erina*. [Colour figure can be viewed at wileyonlinelibrary.com].

between its origin and the end of vein $R_3$); and in males, the androconial scales are present in the median and sub-median areas of the fore wing where they are concentrated into a diffuse trident patch along the basal half of veins $M_3$, $CuA_1$ and $CuA_2$ and sometimes on the adjacent veins, particularly the base of $M_1$ and $M_2$ and the median area of 1A + 2A.

The sexes are strongly dimorphic: the males are typically blue but very occasionally green or bronze-brown with narrow black margins, whereas the females are frequently black with contrasting white, or rarely blue, patches on the upper side. The underside ground colour is generally white or pale grey, with a series of small black or dark brown markings forming conspicuous lines, and a series of black terminal spots and a larger tornal spot on the hind wing. An exception to this general pattern is *E. grandissima*, in which the underside ground colour has a pinkish hue and the brown markings are exceptionally broad. The males of five species (*E. viriditincta*, *E. nokopo*, *E. neurapacuna*, *E. pruina* and *E. insanea*) are also unusual, having exceptionally broad black margins on the termen of the fore wing. The underside markings are exceptionally pronounced in *E. insanea*.

The male genitalia fall into two groups, which broadly correspond to the major lineages recovered in our phylogeny. In *E. consimilis*, *E. absimilis* (Waterhouse, 1942, figs 1c–1e; Tite, 1963, figs 36, 41; Tindale, 1965, figs 1–4; Braby, 2008, figs 26–28) and *E. grandissima* (Tite, 1963, fig. 39) (clade IA) and in *E. margarita* (Tite, 1963, figs 15, 19–21; Braby, 2008, figs 29–32; Müller & Tennent, 2016, fig. 36a), *E. tringa* and *E. biaka* (Tite, 1963, figs 17, 22, 23; Müller, 2014a, fig. 10) (clade IB), as well as *E. afretta* (Parsons, 1986, fig. 44), the valvae are relatively simple without apical appendages, whereas in all the other species (clade IC), the valvae are more complex, possessing long appendages stemming from near the apex (Tite, 1963; Müller, 2014b). In clade IA, the valvae are generally broader apically and terminate in a series of teeth or sharp projections, whereas in clade IB (which probably includes *E. afretta*), the valvae are narrowly tapered to a point or simple spine at their apex.

The morphology of the pupa differs from the other genera in that the dorsal ridge of the thorax and abdomen and the lateral flanges of the abdomen are far more pronounced (Samson & Wilson, 1995; Braby, 2008; Müller, 2015) (Fig. 3). In some species, the anterior end is deeply divided to form a prominent median indentation.

*Remarks. Eirmocides* is introduced to accommodate the *Candalides absimilis* species group, which previously did not have a generic name, sometimes being incorrectly assigned to *Holochila* (Tite, 1963; Tindale, 1965; D'Abrera, 1971; McCubbin, 1971). This is the largest genus in the tribe, containing 23 described species (Appendix A), with *Holochila biaka* Tite synonymized under *E. tringa* (Grose-Smith) (see below). However, further taxonomic work is needed to determine if the *E. helenita* complex, which is paraphyletic because of the inclusion of *E. cupreus* (Röber), comprises a single species of a lineage that is otherwise well supported (99% BS) or a set of up to four or five largely allopatric species. Röber (1886) originally described *E. cupreus* as a variety (subspecies) of *Plebeius dimorphus* Röber, which was also newly described in the same paper, mainly because of the pronounced differences in dorsal colouration among males: in *cupreus*, the upper side ground colour is uniformly copper-brown, whereas in *dimorphus*, the colour is pale iridescent turquoise-blue with conspicuous black margins. Tite (1963), however, treated *cupreus* as a distinct species, whereas *dimorphus* was synonymized under *helenita* as a subspecies. In our experience, *E. cupreus* and *E. helenita dimorphus* are narrowly sympatric in mainland New Guinea: *E. cupreus* is widespread but rare, where it occurs from sea level to approximately 1600 m, whereas *E. helenita dimorphus* is also widespread but much more common at lower altitudes, from sea level to approximately 1000 m. Our preliminary investigations of the male genitalia and adult morphology (wing colour pattern) indicate differences between *E. cupreus*, *E. helenita dimorphus*, *E. helenita* near *dimorphus* (southern PNG), *E. helenita helenita* (Cape York Peninsula) and *E. helenita helenita* (Wet Tropics). A more detailed appraisal of these taxa, together with a thorough examination of their types, is required before a clear assessment can be made. Röber's types of *cupreus* and *dimorphus* appear to be missing, apparently lost or destroyed during World War II. At least three names are available for the population from Cape York Peninsula: *Holochila helenita* Semper, *Holochila androdus* Miskin and *Holochila subargentea* Grose-Smith & Kirby (Edwards *et al.*, 2001).

*Etymology.* The name *Eirmocides* is derived from the Greek word *eirmos*, which means a series or joined in a row to form a line, and refers to the conspicuous black spots and markings on the underside, particularly of the hind wing, which are joined together to form a series of lines. The gender is masculine.

*Ecology.* Most members occur in mainland New Guinea and surrounding islands and the coastal areas of eastern Australia, where the larvae feed on a wide range of plant families, including Araliaceae, Cunoniaceae, Fabaceae, Flagellariaceae, Lauraceae, Loranthaceae, Malvaceae, Proteaceae, Phyllanthaceae, Rhamnaceae and Sapindaceae growing mainly in lowland tropical forest, lower montane forest and mid-montane forest (Parsons, 1998; Braby, 2000; Müller, 2015). *Eirmocides margarita gilberti* and *E. absimilis edwardsi* and *E. consimilis goodingi* are unusual in that they occur in more open sunlit habitats (tropical savannah woodland and temperate open woodland, eucalypt woodland and open forest) in northern and southeastern Australia, respectively (Braby, 2008).

*Eirmocides tringa biaka* (Tite, 1963*)* **syn. nov., stat. rev. et comb. nov.**

*Holochila biaka* Tite (1963): 205–206, pl 1 figs 120–121, pl 2 figs 131–132.

*Candalides biaka* (Tite). – Parsons (1998): 417; Müller (2014a): 207–208, figs 1–3.

*Type material.* Holotype ♂ 'Type', 'Biak, Schouten Is., North N. Guinea., June 1914., A.C. & F. Pratt.', '*HOLOCHILA biaka* Tite, HOLOTYPE. ♂ BM. Type No. Rh. 16794', 'Gen. 1961-281., G.E.T.', 'biaka ♂', 'biaka, 27A.775, Tite', 'Joicey Bequest., Brit. Mus., 1934-120' (BMNH).

Paratype ♀ labelled similarly to holotype except '*HOLOCHILA biaka* Tite, ALLOTYPE ♀, B.M. Type No Rh. 16795.' (BMNH).

*Diagnosis. Eirmocides tringa biaka* is distinguished from the nominate subspecies by the following five characters: (i) it is smaller in size; (ii) in the male, the apex of the fore wing is more rounded; (iii) in the male, the hind wing is narrower, with the termen straighter and tornus more produced; (iv) in the female, the white patches on the upper side of the fore- and hind wing are absent; and (v) in both sexes, the underside brown markings are more distinct.

*Remarks.* Tite (1963) described *Holochila biaka* Tite as a distinct species; however, Parsons (1998) challenged this hypothesis and suggested that *biaka* may be a synonym (subspecies) of *Candalides tringa* (Grose-Smith). Tite (1963) noted that the structure of the male genitalia of *biaka* and *Holochila tringa* Grose-Smith are more or less indistinguishable. He stated that there are minor differences in the shape of the valva, although his illustrations of the two taxa (figs 22 and 23) are identical. Moreover, comparison of the male genitalia (ventral view) of the holotype of *biaka* (Müller, 2014a, fig. 10) with that of *tringa* (Tite, 1963, fig. 17) are identical with respect to the morphology of the valva, brachia and phallus. Comparison of the males of the two taxa (Parsons, 1998, figs 1779, 1780; Müller, 2014a, figs 1, 2) show negligible differences between them. Both taxa are distinguished from other species of *Eirmocides* by the bright blue upper side, with the colour transitioning from deep blue at the fore wing costa and apex to pale turquoise-blue at the dorsum and throughout the hind wing; the margins of both wings are narrowly black, but the subtornal region of the hind wing is broadly black. The only differences between *biaka* and *tringa* are minor variations in the shape of the fore wing apex and hind wing tornus and clarity of underside markings. However, these characters are well known to be poor diagnostic features for distinguishing species within *Eirmocides*, for example,

*E. absimilis* and *E. margarita* (Braby, 2008), and the most reliable means of species recognition is by the genitalia. Our molecular phylogeny also shows that *Eirmocides biaka* is nested within *E. tringa*, rendering the latter species paraphyletic.

Thus, on the basis of a lack of fundamental differences in genitalia morphology, adult phenotype (wing pattern elements) and phylogenetic relationships according to molecular data, we synonymize *E. biaka* under *E. tringa* and treat it as a subspecies.

*Erina* Swainson, 1833

*Zetona* Waterhouse, 1938.

Type species: *Papilio erinus* Fabricius, 1775 (by original designation).

*Diagnosis. Erina* differs from the other genera by the following characters: the labial palp is comparatively long, with the third (terminal) segment exceptionally long, being more than half the length of the second (middle) segment, and slender and sharply pointed at its apex, and in males, the androconial scales are present on the fore wing where they are scattered over the surface and not concentrated along the veins. Unlike *Eirmocides* and *Cyprotides*, the termen of the fore- and hind wings is rounded, similar to that of *Candalides*.

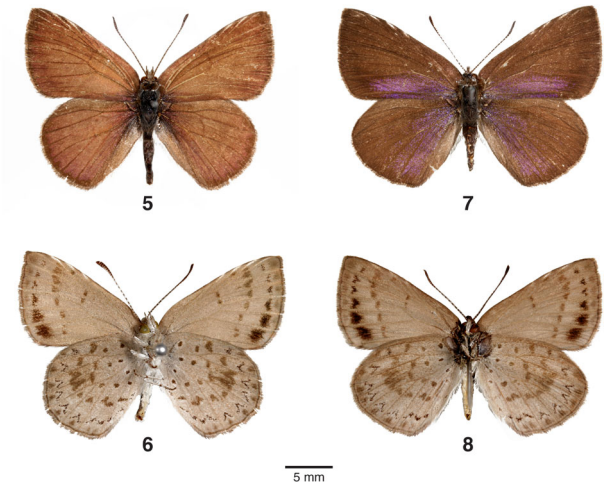
The sexes are weakly dimorphic: the males are typically purple, purplish-bronze or bronze on the upper side, whereas the females are dark brown-black, often with brighter purple basal and central areas. The underside ground colour is generally greyish-white, grey or pale brownish-grey, with a series of small markings similar to *Eirmocides*, but is distinguished by having two or three brown-black subtornal spots or blotches on the underside of the fore wing. The underside markings and spots are particularly well defined in *E. delospila*. The subspecies *Erina hyacinthina simplex* is unusual, with a brilliant iridescent blue upper side.

The male genitalia are distinct in that the valvae are long and taper to a point (Tite, 1963, figs 51–54; Eliot, 1973, fig 72; Edwards & Kerr, 1978, figs 9–12; Braby, 2017, fig. 13).

The pupa is more narrowly elongated compared with the other genera, and the dorsal ridge of the thorax and abdomen and the lateral flanges of the abdomen are far less prominent compared with *Eirmocides* (Fisher, 1978; Edwards, 1980; Braby, 1995, 2017; Field, 2013) (Fig. 3).

*Remarks. Erina* contains six species previously placed in the *Candalides erinus* species group (Edwards & Kerr, 1978; Braby, 1995, 2000) (Appendix A), with the subspecies *C. hyacinthinus gilesi* M.R. Williams & Bollam raised to full species.

*Ecology. Erina* occurs mainly in eucalypt open forest, woodland and heathy woodland where the larvae specialize on *Cassytha* spp. (Lauraceae). The genus occurs mainly in Australia, with one species (*E. erina*) extending to the Lesser Sunda Islands and mainland New Guinea and its adjacent islands. One species (*E. acasta*) also extends to Tasmania.




**Figs 5–8.** *Erina gilesi* **stat. rev. et comb. nov.** adults from Myalup, WA (ANIC), showing: 5, male upper side; 6, male underside; 7, female upper side; and 8, female underside. [Colour figure can be viewed at wileyonlinelibrary.com].

*Erina gilesi* (M.R. Williams & Bollam, 2001) **stat. rev. et comb. nov.**

*Candalides hyacinthinus hyacinthinus* (Semper, 1879) – Edwards & Kerr, (1978): 88; Common & Waterhouse (1981): 537; Hay *et al.* (1994): 57, pl 5 figs. 27–28; Morton (1984): 38; Williams *et al.* (1993): 130; Williams *et al.* (1997): 47.

*Candalides hyacinthinus* (Semper, 1879) 'Local form 2' – Dunn & Dunn (1991): 395.

*Candalides hyacinthinus* (Semper, 1879) 'South-western form' – Braby (2000): 764, pl 55 figs. 1a–1d.

*Candalides hyacinthinus gilesi* M.R. Williams & Bollam, 2001: 49–53, figs. 1–4.

*Candalides hyacinthinus gilesi* M.R. Williams & Bollam. – Williams & Williams (2006): 56; Braby (2004): 262–261; Orr & Kitching (2010): 262; Braby (2010): 14, 72; Braby (2016): 290–291.

*Type material.* Holotype ♂ 'Yalgorup NP, WA, 17 DEC. 1992, M.R. Williams' (WAM).

*Diagnosis. Erina gilesi* (Figs 5–8) differs from *E. hyacinthina* by the following nine phenotypic characters: (i) it is smaller in size; (ii) the apex of the fore wing is more acute and outwardly pointed, with the termen angled at vein $M_1$ (similar to *Cyprotides*); (iii) the termen of the fore wing is more rounded in males; (iv) in males, the upper side ground colour is bronze-brown, sometimes weakly suffused with purple, but

never bright purple or purplish-bronze as in *E. hyacinthina hyacinthina*; (v) the brown-black termen of both wings is consistently narrower in males; (vi) in females, the upper side ground colour is dark brown with the iridescent purple areas duller and narrowly restricted to the dorsum of the fore wing and tornal region of the hind wing, whereas in *E. hyacinthina hyacinthina* the ground colour is darker brown or brown-black with the purple areas richer bluish-purple and more variable in extent but generally far more extensive; (vii) the two large brown-black subtornal spots on the fore wing underside are less distinct, and these, together with the series of subterminal spots, diminish progressively in size from the tornus towards the apex; in *E. hyacinthina*, the subterminal spots are of equal size and less conspicuous, especially in males; (viii) the underside ground colour is pale brown rather than grey or pale brownish-grey; and (ix) the postmedian markings on the hind wing underside are variable and often fuse and spread towards the base rather than forming a clear broken postmedian line as in *E. hyacinthina*.

The immature stages of *E. gilesi* and *E. hyacinthina* are also strikingly different. Although only the egg and early instar larvae of *E. gilesi* have been formally described (Williams & Bollam, 2001), a comparative morphological investigation of the life history of *E. gilesi* (Braby & Eastwood, unpublished data) has identified two character states among the late instar larvae unique to *E. gilesi*: (i) body with dorsolateral line white and conspicuous and (ii) abdominal segments 1 and 6, each with reddish dorsal patches that, when present, are simple and not raised into projections.

In addition, the genitalia differ in at least six characters between the two species (Figs 9–16). In *E. gilesi* males (Fig. 9), the valvae are shorter with the long terminal spine approximately half the overall length of the valva (from base to apex), whereas in *E. hyacinthina* (Figs 10, 11), the terminal spine is approximately three-fifths the overall length; the juxta (located one-third the length of the valva from its base) comprises a short but conspicuous curved sclerotized spine in *E. gilesi*, whereas it is a small, rounded protrusion in *E. hyacinthina*; the brachia in *E. hyacinthina* are conspicuously bifurcated near the tip but much less so in *E. gilesi*; the spicule on the vesica is substantially shorter in *E. gilesi* (Fig. 12), being approximately half the length of that of *E. hyacinthina* (Figs 13, 14); and in *E. hyacinthina*, the apex of the phallus is furnished with a conspicuous dorsal row of small teeth-like spines that are absent in *E. gilesi*. Females of the two species differ principally in the shape of the ostium bursae and sterigma, with that of *E. gilesi* (Fig. 15) comprising a narrow longitudinal opening bordered by a rounded sclerotised plate.

*Remarks.* Edwards & Kerr (1978) first noted that *E. hyacinthina* from the southwestern corner of Western Australia was distinct, but they did not propose a specific or subspecific name for this population. Dunn & Dunn (1991: 395) referred to the population as *E. hyacinthina* 'Local form 2', but remarked that 'it deserves subspecific status rather than recognition as a local form'. Braby (2000) drew further attention to its distinctiveness and referred to it as the 'South-western form'; he also noted how it differed from *E. hyacinthina*. Subsequently, Williams & Bollam (2001) formally described and illustrated the taxon as a subspecies of *E. hyacinthina* and provided a brief diagnosis. However, *E. gilesi* and *E. hyacinthina simplex* are sympatric in the Stirling Range at Mondurup Peak, WA, without any evidence of hybridization between the two taxa (Williams & Williams, 2006). On this basis, Williams & Williams (2006: 56) remarked 'In the light of this finding, the status of *C. h. gilesi* might still warrant further investigation'. The male and female genitalia have not previously been compared and illustrated, although Edwards & Kerr (1978) noted differences in the vesica. Moreover, our molecular phylogeny shows that *E. gilesi* is well differentiated from *E. hyacinthina hyacinthina* + *E. hyacinthina simplex*, the average level of divergence between this split being 2.8% based on COI. This relatively high level of differentiation is larger than the average distance between several pairs of other sister species within the Candalidini, namely, *Candalides urumelia* and *C. caesia* (2.5%), *C. heathi* and *C. noelkeri* (2.4%) and *Erina geminus* and *E. erina* (2.2%).

Thus, on the basis of fundamental differences in genitalia morphology (six characters), adult phenotype (nine characters), immature stages (two characters), phylogenetic pattern according to molecular data and level of pairwise divergence (2.8%) and their narrowly sympatric distributions, we treat *gilesi* as a distinct species sister to *E. hyacinthina*. Presumably, divergence of the two taxa was facilitated by vicariance through the formation of the Great Australian Bight dividing the ancestral lineage into two populations in the Pliocene, in a manner similar to other Lycaenidae (Schmidt *et al.*, 2014), which then speciated allopatrically: *E. hyacinthina* in the east, and *E. gilesi* in the west. *Erina hyacinthina* subsequently differentiated into subspecies, with one adapted to the semi-arid zone (*E. hyacinthinus simplex*), expanding its range back into Western Australia via the Nullarbor Plain.

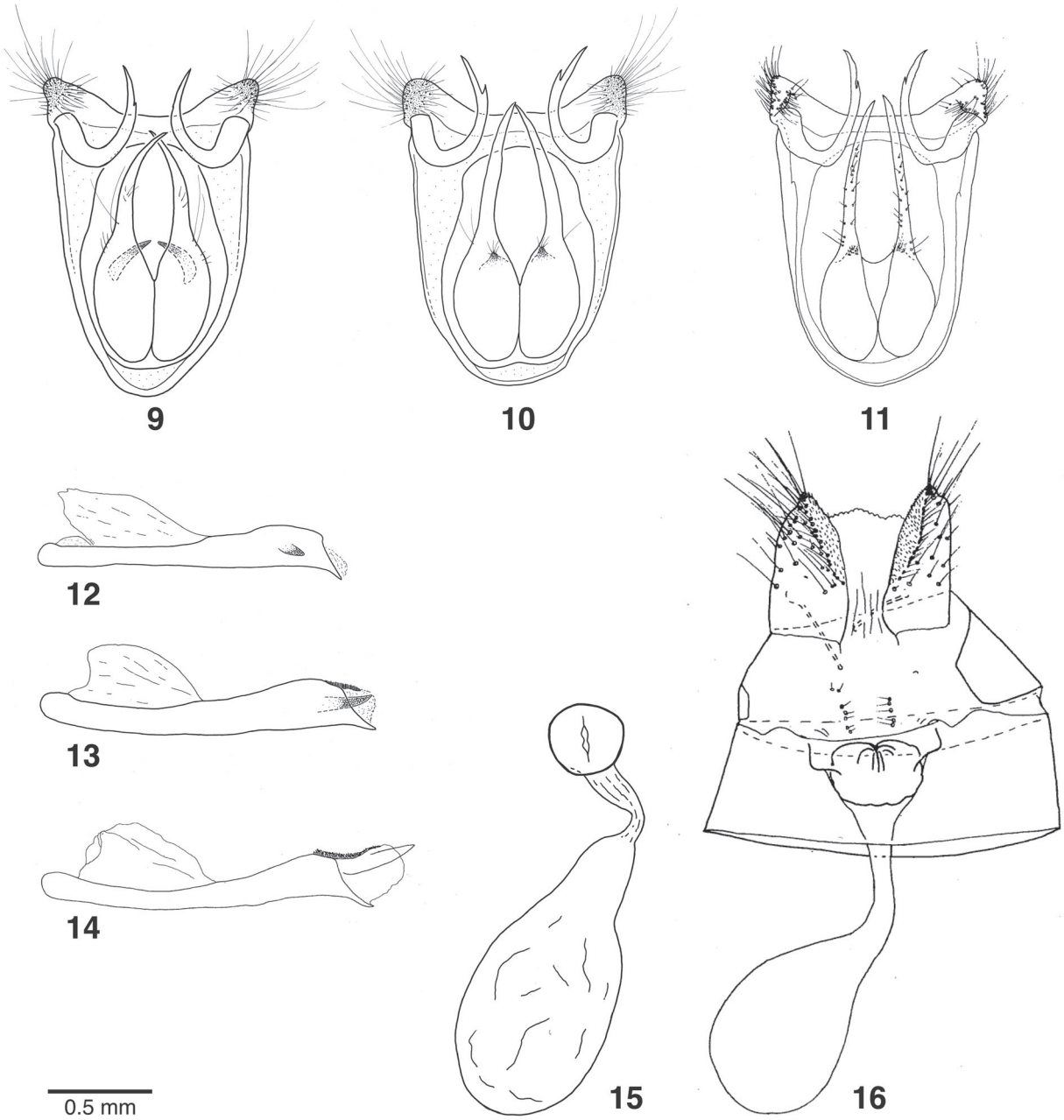
*Ecology and distribution. Erina gilesi* is endemic to southwestern Australia where it is restricted to a limited area from the Porongurups and Stirling Ranges through West Cape Howe to approximately 30 km E of Perth, WA (Edwards & Kerr, 1978; Braby, 2000; Williams & Bollam, 2001). The immature stages have been recorded associated with *Cassytha racemosa* Nees (Lauraceae) (Williams & Bollam, 2001).

*Common name.* We propose Western Dusky-blue as the common name for *E. gilesi*.

*Cyprotides* Tite, 1963

Type species: *Chrysophanus cyprotus* Olliff, 1886 (by monotypy).

*Diagnosis. Cyprotides* is distinguished from the three other genera by the following characters: the labial palp is exceptionally long, with the third (terminal) segment approximately half the length of the second (middle) segment and of even




**Figs 9–16.** Genitalia of *Erina gilesi* **stat. rev. et comb. nov.** and *E. hyacinthina*: 9, *E. gilesi* male genitalia posterior view with phallus removed, Margaret River, WA (ANIC M310); 10, *E. hyacinthina hyacinthina* male genitalia posterior view with phallus removed, Kuranda, QLD (ANIC M340); 11, *E. hyacinthina hyacinthina* male genitalia posterior view with phallus removed, Bateman's Bay, NSW (ANIC M308) (after Edwards & Kerr, 1978); 12, *E. gilesi* phallus lateral view, Porongurups, WA (ANIC M328); 13, *E. hyacinthina simplex* phallus lateral view, Murray Bridge, SA (ANIC M312); 14, *E. hyacinthina hyacinthina* phallus lateral view, Bateman's Bay, NSW (ANIC M308) (after Edwards & Kerr, 1978); 15, *E. gilesi* female genitalia showing ostium bursae, ductus bursae and corpus bursae, Margaret River, WA (ANIC M311); 16, *E. hyacinthina hyacinthina* female genitalia, Hawkesbury Lookout, NSW (ANIC M338) (after Edwards & Kerr, 1978). Figures 9, 10, 12, 13, 15 © M.F. Braby.

width throughout; the termen of the fore wing is distinctly produced towards the apex and slightly angled at vein $M_1$, but not scalloped as in *Eirmocides*; the tornus of the hind wing is strongly produced in the male; and in males, the androconial scales are present in the median and sub-median areas of the fore wing similar to *Eirmocides*, but they are far more conspicuous (and contrasting in colour), being concentrated along the basal half of veins $M_3$, $CuA_1$ and $CuA_2$ (as a diffuse trident patch), as well as along the discocellulars, the base of $M_1$ and $M_2$ and the median area of 1A + 2A.

The adults are sexually dimorphic: the upper side ground colour of males is coppery-brown, variably suffused with pink-purple, whereas that of females varies from purple to purplish-blue. The pattern of the underside markings, which comprise a series of small obscure brown or brown-black spots, is similar to *Eirmocides* and *Erina*, but the ground colour is grey-brown. Unlike *Eirmocides* and *Erina*, prominent subterminal or subtornal spots are absent on the underside of the fore- and hind wings.

The male genitalia are distinct, with the valva broadly oblong but strongly constricted beyond the middle and the apex terminating in a long inwardly curved spine (Tite, 1963, fig. 50). The apical spine is rotated perpendicular to the length of the valva, unlike most species of *Erina* in which it is relatively straight (except in *E. delospila*).

The morphology of the pupa is distinct and differs from the other genera in that the pair of middorsal projections on the thorax are more pronounced, and the dorsal ridge of the abdomen is serrated, comprising a series of prominent projections on segments 1–5 (Atkins & Heinrich, 1987) (Fig. 3). Like *Candalides*, the pupa is rugose, but unlike that genus, the thorax and abdominal segments 1–2 are more humped dorsally, and the overall colour is dull black, resembling a piece of charcoal. The larva is also distinct, bearing a series of conspicuous dorsal and lateral projections, similar to some species of *Eirmocides*.

*Remarks. Cyprotides* is monotypic, containing the single species *Chrysophanus cyprotus* Olliff. The genus was originally proposed by Tite (1963) to accommodate the species *cyprotus* previously placed in the genus *Candalides*.

*Ecology. Cyprotides* is endemic to Australia, where it occurs in the drier temperate open woodlands and heathlands on the tablelands and coastal areas of eastern Australia, and in mallee-heath and mallee shrubland in the semi-arid and arid zones of southern and central Australia. The larvae predominantly feed on Proteaceae and, to a lesser extent, on Fabaceae (Atkins & Heinrich, 1987; Grund, 1997, 2013; Braby, 2000).

*Candalides* Hübner, 1819

*Nesolycaena* Waterhouse & R.E. Turner, 1905.
*Adaluma* Tindale, 1922.
*Microscena* Tite, 1963.
Type species: *Rusticus xanthospilos* Hübner, [1817] (by subsequent designation).

*Diagnosis. Candalides* differs from *Eirmocides*, *Erina* and *Cyprotides* by the following characters: the length and shape of the labial palp is comparatively short, but the third (terminal) segment is relatively long, being more than half the length of the second (middle) segment, and of even width throughout; the shape of the fore- and hind wings in which the termen is broadly rounded, similar to that of *Erina*, but unlike that genus the tornus of the hind wing is much more evenly rounded; and the underside pattern of the hind wing has a series of six black subterminal spots between veins $M_1$ and 3A but otherwise is generally uniform, lacking the prominent markings of zig-zag lines and spots characteristic of the three other genera. In males, the androconial scales are generally scattered on the upper side of the fore wing, similar to *Erina*, but in *C. urumelia*, *C. caesia* and *C. medicea*, they are concentrated to form a central 'patch' along veins $M_3$, $CuA_1$ and $CuA_2$, as well as along the discocellulars and the median area of 1A + 2A and sometimes on $R_{3+5}$, $M_1$ and $M_2$.

The sexes are weakly dimorphic: the females generally have broader dark brown or black margins on the fore wing. *Candalides xanthospilos* is unusual with a prominent yellow central patch on the fore wing. Males of the *C. albosericea* group of species (four taxa formerly assigned to *Nesolycaena*) are peculiar with extensive iridescent white or bluish-white scales on the upper side. The underside ground colour varies from white and grey to brown. The black subterminal spots on the hind wing underside are absent in *C. albosericea* and *C. medicea*. In *C. xanthospilos*, there are three additional black central spots. In the *C. albosericea* species group, the length of antennae is unusually short, being less than half the length of the fore wing costa, and this character appears to be a synapomorphy for the group but not for the genus as a whole. Differences in the morphology of the antenna within *Candalides* are comparable to intrageneric differences in other Australian lycaenids, for example, *Ogyris* in which the *oroetes* species group (*O. oroetes*, *O. olane* and *O. barnardi*) is characterized by the flagellum of the antenna expanding abruptly into a conspicuous club, whereas in the other species groups of *Ogyris*, it expands gradually into a slender club (Braby, 2000).

The male genitalia are variable (Tite, 1963, figs 43–45, 55–59; Sands, 1971, fig. 1; d'Apice & Miller, 1992, figs 9–12; Braby, 1996, figs 9–16; Braby & Douglas, 2004, figs 23–31), but the valvae are generally broad and robust, and with the exceptions of *C. xanthospilo*s and *C. caesia*, the apex tapers to a single point or a deeply bifurcated pair of points.

The morphology of the pupa differs from the other genera in that the median indentation at the anterior end is weakly developed or absent, and the middorsal projections on the thorax are rudimentary (Fig. 3). The pupa is mottled with various shades of brown (or sometimes green) and black and is more compact and rugose than *Eirmocides*, *Erina* and *Cyprotides* (Sands, 1971; Edwards, 1980; Johnson & Valentine, 2001; Braby & Douglas, 2004).

*Remarks. Candalides* contain seven species endemic to Australia (Appendix A) that, until recently, were placed in four separate genera: *Rusticus xanthospilos* Hübner and *Candalides noelkeri* Braby & Douglas in *Candalides*; *Holochila albosericea* Miskin, *Nesolycaena caesia* d'Apice & Miller and *N. medicea* Braby in *Nesolycaena*; *Adaluma urumelia* Tindale in *Adaluma*; and *Lycaena heathi* Cox in *Microscena*.

*Ecology.* The species occur in open habitats (woodland or mixed woodland-heathland, heathland and heathy woodland)

where the larvae feed on Lamiaceae, Plantaginaceae, Scrophulariaceae, Thymelaeaceae and Rutaceae. Larvae of *C. xanthospilos* are associated only with Thymelaeaceae and *C. noelkeri* only with Scrophulariaceae, whereas those of the *C. albosericea* species group specialize on Rutaceae.

## Discussion

*Systematics*

Our revised classification of the Candalidini recognizes four genera, 37 species and 23 subspecies (60 lower taxa) (Appendix A). The nine species missing from our phylogeny all belong in *Eirmocides* and are endemic to New Guinea and its surrounding islands, so their exclusion is unlikely to change the deeper phylogenetic pattern recovered in this study. Our generic classification is based largely on the consideration of available morphological characters (Table S3) in relation to the molecular phylogeny, although further work is needed determine if the diagnostic features for each genus are synapomorphic or pleisiomorphic. Thus, *Nesolycaena* is placed in synonymy under *Candalides*, and four other genera are not recognized, namely: *Holochila*, *Adaluma*, *Zetona* and *Microscena*. Of the four valid genera, the *absimilis* group (23 species) is placed in the newly described genus *Eirmocides*; the *erinus* group (6 species) is assigned to *Erina*, which is reinstated; and the taxon *Chrysophanus cyprotus* is assigned to *Cyprotides*, which is also reinstated; whereas the remaining seven species are placed in *Candalides sensu stricto*. The revision results in 47 new nomenclatural changes at the species and subspecies levels (Appendix A), including the synonymy of *H. biaka* as *E. tringa biaka* and recognition of *C. hyacinthinus gilesi* as a distinct species *Erina gilesi*.

Our phylogenetic analysis recovered seven subspecies to be monophyletic with strong support (i.e., for taxa that had multiple samples), but at least six subspecies (*Eirmocides consimilis goodingi*, *Eirmocides absimilis edwardsi*, *Erina erina erina*, *Cyprotides cyprotus cyprotus*, *Cyprotides cyprotus pallescens* and *Candalides heathi heathi*) were not reciprocally monophyletic in relation to other subspecies sampled within their respective gene trees. Braby *et al.* (2012) argued that reciprocal monophyly is likely to be a property more characteristic of sister species where the divergences are particularly deep than infraspecific categories such as subspecies and should not be a criterion for identifying units below the level of species. They recommended that, under the general lineage species concept, the definition of subspecies be restricted to evolving populations representing partially isolated lineages of a species that are allopatric, phenotypically distinct and have at least one fixed diagnosable character state and that these character differences are (or are assumed to be) correlated with evolutionary independence according to population genetic structure. In other words, under these criteria, allopatric subspecies are distinct evolutionarily significant units within species. Thus, because of their phenotypic divergence, we refrain from synonymizing the non-monophyletic subspecies until additional evidence from population genetics is available.

*Diversification and evolutionary history*

Our dating estimates indicate that the Candalidini evolved during the Eocene (stem-group *c*. 43 Ma) and the crown group differentiated at the Oligocene/Miocene boundary (*c*. 22.3 Ma). Subsequently, the extant genera all differentiated in the Miocene. Although *Eirmocides* started to differentiate in the early Miocene, the major radiation (in New Guinea) did not occur until the Plio-Pleistocene (<5 Ma), coinciding with the recent uplift of the New Guinea highlands (Holloway, 1986; Hall, 1998; Parsons, 1998; Braby & Pierce, 2007; Toussaint *et al.*, 2014). Although mainland New Guinea and its adjacent islands are more species rich, with 22 species, almost all of these species belong in the single genus *Eirmocides*, of which 19 are endemic to New Guinea. In contrast, the four genera found in Australia include 18 species, of which 15 species are endemic to the continent. Differences in species (and generic) richness between the two areas no doubt reflect different evolutionary histories in New Guinea and Australia, with the former comprising a more recent adaptive radiation, most likely in response to the uplift of the central cordillera and formation of adjacent islands leading to allopatric speciation.

The ancestral state analysis for the evolution of habitats was equivocal, but given the age of the stem lineage (Eocene) of the Candalidini and an origin in Australia, the most likely state was rainforest, which covered much of the Australian continent at the time (Barlow, 1981; White, 1994, 1998; Hill *et al.*, 1999; Crisp *et al.*, 2004; Byrne *et al.*, 2011). Interestingly, one taxon in clade II (the genus *Erina*) specializes on plants in the genus *Cassytha* (Lauraceae). Although *Cassytha* is adapted to the drier sclerophyllous habitats, most members of the Lauraceae in Australia occur in rainforest (Floyd, 1989; Le Cussan *et al.*, 2007), and the family has a Gondwanan origin or at least predates isolation of the Australian continent from Antarctica (White, 1994). Host specialization on Lauraceae strongly suggests *Erina* evolved from a rainforest ancestor dating back to at least the early Miocene. Further host plant data for *Eirmocides* are needed to reconstruct the ancestral state of host plant evolution in the Candalidini.

Our phylogeny of the Candalidini supports three hypotheses that have been proposed for the origin and evolution of biota associated with mesic zones of eastern and southwestern Australia (Byrne *et al.*, 2011): (i) the ancestors of Australia's modern biota lived in mesic environments; (ii) rainforest organisms were the ancestors of the present Australian biota; and (iii) rainforest communities suffered extinction and contraction into refugia during the Neogene, whereas sclerophyll lineages expanded. A testable prediction of the first hypothesis is that the mesic biome should be the ancestral state on phylogenies of lineages with mesic and arid representatives. Among the Australian Candalidini, nearly all taxa are restricted to the mesic zone (Braby, 2000); only four recently evolved taxa (*Erina hyacinthina simplex*, *Cyprotides cyprotus cyprotus*, *Candalides heathi heathi* and *C. heathi aeratus*) occur to any extent in the semi-arid/arid zone of Australia, indicating that the mesic biome is ancestral, and the arid biome is derived. The second hypothesis predicts that rainforest habitats should be the ancestral state on

phylogenies of lineages with both rainforest and sclerophyll (open forest) lineages, which appears to be the case, as noted above. The third hypothesis predicts that rainforest lineages should have fewer species than their sister lineages in mesic sclerophyll communities because rainforest lineages are relictual. Again, this prediction is well supported: *Eirmocides* (clade I) in Australia has only four species (of which two comprise recent invasions from New Guinea), whereas its sister lineage (clade II) in open forest/woodland has 14 species (×3.5 more).

In conclusion, combining estimates of divergence times and patterns of diversification with analyses of biogeographical and habitat evolution, the origin and evolutionary history of the Candalidini can be summarized as follows. The ancestor evolved in situ on the Australian plate of southern Gondwana (i.e., Australia–Antarctica–South America) in the mesic biome and almost certainly in rainforest at some point in the Eocene. Following the final rifting of Australia from Antarctica (*c*. 34 Ma) and the concomitant aridification of the continent and contraction of the Eocene Gondwanan rainforests during the Oligocene and Miocene (Hill *et al.*, 1999; Crisp *et al.*, 2004; Hill, 2004; Byrne *et al.*, 2008; Byrne *et al.*, 2011), the ancestor split into two major lineages (clades I and II) during the early Miocene. One of these lineages (clade I: *Eirmocides*) differentiated into two groups, with one group contracting to the rainforests of the mesic biome of eastern Australia [clade IA: *E. consimilis* + (*E. absimilis* + *E. grandissima*)] and subsequently colonizing mainland New Guinea (*E. grandissima*), whereas the ancestor of other group (clades IB + IC) colonized, or followed the spread of rainforest to, New Guinea and its nearby islands where it subsequently radiated during the Pliocene and Pleistocene, particularly in montane areas. A few elements of this latter group later reinvaded northern and northeastern Australia during the Pleistocene (*E. margarita* and *E. helenita*), where they subsequently differentiated at the subspecies level. The second major lineage [clade II: *Erina* + (*Cyprotides* + *Candalides*)] colonized the drier eucalypt sclerophyll open forests, woodlands and heathlands of Australia, which had rapidly expanded during the Oligocene (White, 1994, 1998). This lineage subsequently diversified and radiated during the Miocene, giving rise to three genera largely endemic to the continent – only one species (*Erina erina*) has dispersed out of Australia.

## Supporting Information

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

**File S1.** Dated phylogeny including all outgroups, in nexus format.

**File S2**. Partition file with all partitions and substitution models used for the phylogenetic analyses, as inferred using ModelFinder, in nexus format.

**Table S1.** List of samples used in the study along with their voucher numbers and associated collection data for each species.

**Table S2.** GenBank accession numbers for sequences used in this study.

**Table S3.** List of morphological characters and their states for each of the four genera recognized in this work.

## Acknowledgements

We thank Caroline Storer (Florida Museum of Natural History, University of Florida) for bioinformatics analysis and cleaning raw sequence data; Y. N. Su (ANIC) for preparing digital illustrations of *Erina gilesi*; J. Tennant for photographing the female paratype of *C. biaka* in the BMNH; and K. Beattie, F. Douglas, K. L. Dunn, L. Matthews, A. A. Mignault, A. Moore, J. Tennant, M. R. Williams and T. A. Woodger for providing tissue samples. This work was supported through funding from the Australian Government's Australian Biological Resources Study (ABRS) Bush Blitz Strategic Taxonomy Grants Scheme for a project entitled 'Taxonomic revision of *Candalides* and allied genera in the tribe Candalidini (Lepidoptera: Lycaenidae)' to MFB, National Geographic grant WW-227R-17 to DJL and National Science Foundation grants DEB-1541500 to AYK, DEB-1541557 to DJL and DEB-1541560 to NEP. We declare no conflict of interest. We also confirm that we have no disputes over the ownership of the data presented in the paper, and all contributions have been attributed appropriately, via co-authorship or acknowledgement, as appropriate to the situation.

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Accepted 19 March 2020

## Appendix A.

### Systematic checklist of the Candalidini according to this study

*Eirmocides* Braby, Espeland & Müller **gen. nov.**
- *Eirmocides consimilis* (Waterhouse, 1942) **comb. nov.**
  - *E. consimilis consimilis* (Waterhouse, 1942) **comb. nov.**
  - *E. consimilis goodingi* (Tindale, 1965) **comb. nov.**
  - *E. consimilis toza* (Kerr, 1967) **comb. nov.**
- *Eirmocides absimilis* (C. Felder, 1862) **comb. nov.**
  - *E. absimilis absimilis* (C. Felder, 1862) **comb. nov.**
    - = *persimilis* (Waterhouse, 1942)
  - *E. absimilis eastwoodi* (Braby, 2008) **comb. nov.**
  - *E. absimilis edwardsi* (Braby, 2008) **comb. nov.**
- *Eirmocides afretta* (Parsons, 1986) **comb. nov.**
- *Eirmocides grandissima* (Bethune-Baker, 1908) **comb. nov.**
  - = *morobea* (Wind & Clench, 1947)
- *Eirmocides margarita* (Semper, 1879) **comb. nov.**
  - *E. margarita margarita* (Semper, 1879) **comb. nov.**
  - *E. margarita gilberti* (Waterhouse, 1903) **comb. nov.**
  - *E. margarita maria* (Bethune-Baker, 1908) **comb. nov.**
- *Eirmocides tringa* (Grose-Smith, 1894) **comb. nov.**
  - *E. tringa tringa* (Grose-Smith, 1894) **comb. nov.**
  - *E. tringa biaka* (Tite, 1963) **syn. nov. et comb. nov.**
- *Eirmocides insanea* (Müller, 2013) **comb. nov.**
- *Eirmocides silicea* (Grose-Smith, 1894) **comb. nov.**
- *Eirmocides meforensis* (Tite, 1963) **comb. nov.**
- *Eirmocides lamia* (Grose-Smith, 1897) **comb. nov.**
- *Eirmocides ardosiacea* (Tite, 1963) **comb. nov.**
- *Eirmocides riuensis* (Tite, 1963) **comb. nov.**
- *Eirmocides skotadi* (Müller & Tennent, 2016) **comb. nov.**
- *Eirmocides parsonsi* (Tennent, 2004) **comb. nov.**
- *Eirmocides coeruleus* (Röber, 1886) **comb. nov.**
  - *E. coeruleus coeruleus* (Röber, 1886) **comb. nov.**
  - *E. coeruleus subrosea* (Grose-Smith, 1894) **comb. nov.**
  - *E. coeruleus doreia* (Tite, 1963) **comb. nov.**
- *Eirmocides viriditincta* (Tite, 1963) **comb. nov.**
- *Eirmocides nokopo* (Müller, 2014) **comb. nov.**
- *Eirmocides neurapacuna* (Bethune-Baker, 1908) **comb. nov.**
- *Eirmocides pruina* (Druce, 1904) **comb. nov.**
- *Eirmocides brabyi* (Müller & Tennent, 2016) **comb. nov.**
- *Eirmocides limbata* (Tite, 1963) **comb. nov.**
- *Eirmocides helenita* (Semper, 1879) **comb. nov.**
  - *E. helenita helenita* (Semper, 1879) **comb. nov.**
    - = *androdus* (Miskin, 1890)
    - = *subargentea* (Grose-Smith & Kirby, 1896)
  - *E. helenita dimorphus* (Röber, 1886) **comb. nov.**
- *Eirmocides cupreus* (Röber, 1886) **comb. nov.**

*Erina* Swainson, 1833
- = *Holochila* C. Felder, 1862
- = *Zetona* Waterhouse, 1938
- *Erina delospila* (Waterhouse, 1903) **comb. nov.**
- *Erina acasta* (Cox, 1873)
  - = *anita* (Semper, [1879])
  - = *moerens* (Rosenstock, 1885)
  - = *canescens* (Miskin, 1890)
- *Erina hyacinthina* (Semper, 1879)
  - *E. hyacinthina hyacinthina* (Semper, 1879)
    - = *eugenia* (Waterhouse & Lyell, 1914)
    - = *josephina* (Harris, 1952)
    - = *cassythae* (L.E. Couchman, 1962)
  - *E. hyacinthina simplex* (Tepper, 1882)
    - = *cyanites* (Meyrick, 1888)
- *Erina gilesi* (M.R. Williams & Bollam, 2001) **stat. rev. et comb. nov.**
- *Erina geminus* (E.D. Edwards & Kerr, 1978) **comb. nov.**
  - *E. geminus geminus* (E.D. Edwards & Kerr, 1978) **comb. nov.**
  - *E. geminus gagadju* (Braby, 2017) **comb. nov.**
- *Erina erina* (Fabricius, 1775)
  - *E. erina erina* (Fabricius, 1775)
    - = *subpallidus* (T.P. Lucas, 1889)
  - *E. erina tualensis* (Röber, 1886)
  - *E. erina stevensi* (Wind & Clench, 1947)
  - *E. erina sudesta* Tite, 1963
  - *E. erina sumbensis* Tite, 1963
  - *E. erina taamensis* Tite, 1963
  - *E. erina tenimberensis* Tite, 1963
  - *E. erina timorensis* Tite, 1963

*Cyprotides* Tite, 1963
- *Cyprotides cyprotus* (Olliff, 1886)
  - *C. cyprotus cyprotus* (Olliff, 1886)
    - = *purpurea* (Grose-Smith & Kirby, 1897)
  - *C. cyprotus pallescens* Tite, 1963

*Candalides* Hübner, 1819
- = *Nesolycaena* Waterhouse & R.E. Turner, 1905
- = *Adaluma* Tindale, 1922
- = *Microscena* Tite, 1963
- *Candalides xanthospilos* (Hübner, 1817)
  - = *hubnerii* (Godart, [1824])
  - = *pulchella* (Swainson, 1833)
- *Candalides heathi* (Cox, 1873)
  - *C. heathi heathi* (Cox, 1873)
    - = *paradoxa* (Guest, 1882)
  - *C. heathi aeratus* (Montague, 1914)
  - *C. heathi alpinus* Waterhouse, 1928
  - *C. heathi doddi* Burns, 1948
- *Candalides noelkeri* Braby & Douglas, 2004
- *Candalides albosericea* (Miskin, 1891)
  - = *caeruleolactea* (T.P. Lucas, 1891)
- *Candalides medicea* (Braby, 1996) **comb. nov.**
- *Candalides urumelia* (Tindale, 1922) **comb. nov.**
  - = *wilkinsi* Riley, 1928
- *Candalides caesia* (d'Apice & Miller, 1992) **comb. nov.**