An illustrated checklist of the genus *Elymnias* Hübner, 1818 (Nymphalidae, Satyrinae)

Chia-Hsuan Wei¹, David J. Lohman²,³,⁴, Djunijanti Peggie⁵, Shen-Horn Yen¹

¹ Department of Biological Sciences, National Sun Yat-Sen University, Kaohsiung, 80424, Taiwan ² Department of Biology, City College of New York, City University of New York, New York, NY, 10031, USA ³ Ph.D. Program in Biology, Graduate Center, City University of New York, New York, NY, 10016, USA ⁴ Entomology Section, National Museum of the Philippines, Manila, 1000, Philippines ⁵ Division of Zoology, Research Centre for Biology-LIPI, Cibinong-Bogor, 16911, Indonesia

Corresponding authors: Shen-Horn Yen (shenhornyen@mail.nsysu.edu.tw); David J. Lohman (dlohman@ccny.cuny.edu)

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Abstract

We review the genus *Elymnias* Hübner, 1818, a morphologically diverse satyrine butterfly clade involved in multifarious Batesian mimicry relationships throughout Asia and Africa. A variety of different model species are mimicked, and many *Elymnias* species are sexually dimorphic mimics, with males and females resembling different model species. We revise species and subspecies delimitations in light of an integrative taxonomic investigation using external morphology, male and female genital morphology, and a multi-locus molecular phylogeny. There is little interspecific genitalic variation among species in this group, and previous taxonomists therefore relied almost entirely on wing patterns. Our molecular phylogenetic analysis reveals several examples of polymorphism or wing pattern divergence within a single species currently classified as two or more different species. We also found examples of wing pattern convergence among disparate lineages that mimic the same widespread model species. Frequently, two or more phenotypically similar species were classified as a single species. This comprehensive checklist reviews all names associated with *Elymnias* to align its taxonomy with the evolutionary history of the group. All available information on nomenclature, type localities, repositories of type specimens, and geographical distributions is summarized, and images of adult specimens and genitalia are provided along with distribution maps of all species and selected subspecies. We identify 2 species *incertae sedis*, establish 15 monophyletic species groups (including 1 species unplaced in any species group), and make 49 taxonomic changes, including 35 new synonyms, 7 new combinations (2 of which have new status), 1 resurrected combination, 1 resurrected subspecies, and 7 status changes.
Keywords
Batesian mimicry, convergent evolution, Elymniiini, polymorphism, sexual dimorphism, Southeast Asia

Introduction

*Elymnias* Hübner, 1818 (Nymphalidae: Satyrinae) is a species-rich and widespread butterfly genus distributed throughout the Old World tropics (Aoki et al. 1982). It derives its name from *Elymnias jynx* Hübner, 1818 (now *Elymnias hypermnestra hypermnestra* (Linnaeus, 1763)) (Frühstorfer 1907). The genus’ widespread range and remarkable wing pattern diversity, together with the economic importance of several species, has attracted the attention of taxonomists and agricultural entomologists for centuries (Merrett 1993; Wallace 1869). However, the entire group has not been examined systematically in over 100 years (Frühstorfer 1907; 1911), and no studies to date have used genetic data to substantiate taxonomic hypotheses. Most species are found in the Indo-Australian Archipelago, a geographically complex and geologically dynamic area with over 20,000 islands that are likely to have contributed to diversification in this taxon (Lohman et al. 2011).

We recognize a single Afrotropical species with two subspecies and 52 Australasian species with 181 subspecies distributed from Nepal to Sri Lanka in the west, throughout tropical and subtropical Asia, and extending east to Taiwan and south to Australia’s Cape York and the Bismark Archipelago of Papua New Guinea. A few species are widespread across several countries or landmasses, but many are restricted to single islands. Several new species have been discovered recently (Monastyrskii 2004; Okubo 2010; Saito and Koshi 2012), highlighting the rarity of many species and their predilection for relatively inaccessible locales, such as high mountains and remote islands.

Species in the genus differ markedly in wing color, pattern, shape, and size, making *Elymnias* one of the most morphologically heterogeneous butterfly genera (Feltwell 1993). This morphological diversity is apparently because most species are Batesian mimics of strikingly different, unpalatable model butterfly species (Corbet 1933; 1943). Many *Elymnias* species are monomorphic; conspecific males and females mimic the same model species (*e.g.*, *E. paradoxa* and *E. vasudeva*). However, some species are sexually dimorphic mimics (Moore 1894; Punnett 1915; Vane-Wright 1976), with males and females mimicking different models and differing markedly in wing color and pattern (*e.g.*, *E. kuenstleri* and *E. harterti*; Corbet et al. 1992; Parsons 2000). A few sexually dimorphic *Elymnias* species mimic a single sexually dimorphic model species, such as *E. casiphone* and *E. saueri*, which both mimic *Euploea mulciber*. A few species exhibit variability in sexual dimorphism: males and females in some populations mimic the same model species and are monomorphic, while the same species is strongly dimorphic in other locales (*e.g.*, *E. hypermnestra* and *E. agondas*).

Larvae of all species with known life histories feed exclusively on palms (Arecaceae) (Bascombe et al. 1999; Ek-Amnuay 2012; Parsons 2000; Robinson et al. 2017), and several species are also agricultural pests on economically important oil palm, *Elaeis guineensis*.
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(Koh and Gan 2007; Merrett 1993). Adults are known to feed on exudates from rotting fruit (Treadaway and Schroeder 2012). Palm-feeding butterflies are not known to sequester noxious secondary compounds from their larval hosts, and naïve avian predators readily consumed adult *E. hypermnestra* in laboratory trials (S.-H. Yen, unpublished results), supporting the hypothesis that *Elymnias* are Batesian and not Müllerian mimics.

After the description of Linnaeus’s *Papilio hypermnestra* (now *Elymnias hypermnestra hypermnestra*) in 1763, the accumulation of new species/subspecies publications was slow and confined to few localities, for instance, *E. nesaea* (Linnaeus, 1764) from Java, *E. panthera* (Fabricius, 1787) from Borneo, and *E. vitellia* (Stoll, [1781]) from Ambon. Most species and subspecies were described during the middle of the 19th century and early 20th century in the following works: Hewitson (1858; 1861; 1867; 1874; South East Asian Islands), Felder and Felder (1860; 1863; 1867; Philippines), Butler (1867; 1871; 1874; 1882; 1883; Asia), Distant (1882a; b; 1883; 1886; Malaysia), Semper (1887; 1892; Philippines), Grose-Smith (1889; 1892; 1894a; b; 1897; South East Asian Islands), Staudinger (1889; 1894a; b; Palawan and New Guinea), de Nicéville (1890; 1893; 1895; 1898; 1900; 1902; Indo-Malaya), Moore (1857; 1875; 1878a; b; 1880; 1886; 1894; Indian subcontinent and Indochina), Fruhstorfer (1894a; b; c; 1895a; b; 1896a; b; c; 1898a; b; c; 1899; 1900; 1902a; b; c; 1904a; b; c; d; Southeast Asia; 1911), Rothschild (1915a; b; c; d; islands surrounding New Guinea), Hemming (1967; global), and Talbot (1929; 1932; Malaysia). Several new taxa have been discovered during the last 40 years, including species described by Jumalon (1975; Philippines), Tsukada and Nishiyama (1979; Southeast Asia), Tateishi (2001; Southeast Asia), Uémura and Kitamura (2001; Philippines), Monastyrskii (2004; the Indochina), Suzuki (2006; the Andaman Islands), Okubo (2010; the Lesser Sunda Islands), and Saito and Koshi (2012; Indochina).

The first checklist of *Elymnias* was compiled by Wallace (1869), followed by Butler (1871); Gaede (1931) enumerated the *Elymnias* species recognized at that time. The most recent comprehensive generic revision was completed by Fruhstorfer (1907; 1911), who recognized over 200 species-level taxa. This most recent study established the genus’ higher classification, infrageneric grouping, geographical distributions, diagnostic characters, and synonyms. He recognized *Elymniopsis* Westwood, [1851] (now a junior synonym of *Elymnias*) as a valid genus and separated *Elymnias* into two subgenera: *Elymnias* and *Mimadelias* Moore, 1894. However, Fruhstorfer’s taxonomic treatment relied entirely on comparisons of wing shape and color pattern; he did not examine genitalia. After this work, a few additional publications provide regional checklists with images of adults, including: Aoki and Uémura (1982), D’Abrera (1985), Pinratana (1988), Corbet et al. (1992), Osada et al. (1999), Chou (2000), Monastyrskii (2005), Ek-Amnuay (2012), Treadaway and Schroeder (2012), and Inayoshi (2017). These works, together with G. Lamas’ catalog of butterfly names established the taxonomic groundwork for the genus. Prior to the present study, ca. 47 species and 190 subspecies were recognized (G. Lamas, pers. comm.).

This checklist enumerates and verifies all current combinations and synonyms, and provides original literature citations, type localities, repositories of type specimens,
photographs of specimens and genitalia, and maps of each subspecies’ geographical range and type locality. Integrative taxonomic practice employing multi-locus molecular phylogenetics in concert with data from wing and genitalic characters has informed taxonomic decisions to retain or revise contentious classification and nomenclature. This checklist is meant to clarify taxonomic problems in the genus and aid biologists interested in studying butterfly biodiversity, but will also serve as a framework for future studies on the phylogeny, biogeography, wing pattern evolution, and speciation of this fascinating radiation of Batesian mimetic butterfly species.

**Material and methods**

**Examination of original literature and type specimens**

The taxonomic changes we propose are based on examinations of hundreds of specimens in dozens of museums, quantification of wing and genitalic characters including over 100 dissections of males and females (Wei et al. in prep.), and a multi-locus molecular phylogenetic analysis based on six genetic markers from over 200 specimens including nearly every species that we recognize (Lohman et al. in prep.).

Verification of type specimens was based on information provided in the original literature as well as critical review of the collection of specific authors, especially Fruhstorfer. All taxonomic treatments proposed in the present study, including the availability of infrasubspecific taxa, follow regulations and suggestions of the latest version of ICZN (1999).

All publications with original descriptions of new taxa or describing new taxonomic acts were consulted to verify the status and collection localities of type material. Geographical information was obtained directly from specimen labels and from literature to provide accurate locality data and minimize misinterpretation of geographical localities caused by misidentified or mislabeled specimens.

All images of specimens photographed in various museum collections are used here with permission from each museum. Except for the photographs provided by KUTH (Department of Entomology, Kasetsart University), David J. Lohman, and the Museum of Comparative Zoology, Harvard University, all the other photographs were taken by Chia-Hsuan Wei and Shen-Horn Yen.

The following abbreviations are used to specify the repository of type material. Specimens, including type specimens, were borrowed and/or photographed from many of these institutions and private collections.

**Abbreviations of specimen repositories**

**DNPFIC**  
Forest Insect Collection, Department of National Parks, Wildlife and Plant Conservation, Thailand
Species concept and integrative taxonomic approach

We ascribe to the Biological Species Concept, which defines species as reproductively isolated groups of populations (Mayr 1940). We have attempted to recognize reproductive isolation between species by identifying coordinated morphological and/or genetic differences among species in several traits. We also expect that species should not be polyphyletic and that species should generally be monophyletic after sufficient
time since divergence from their sister taxon. We regard subspecies as phenotypically
distinctive geographic variants and do not expect them to be monophyletic or repro-
ductively isolated from other subspecies (Braby et al. 2012). However, a subspecies
should be differentiable from other conspecific subspecies using morphology, genetic
data, or other characteristics.

Given the within-species morphological variability known from this and other mi-
metic butterfly taxa (Punnett 1915), we adopted the following procedures for evalu-
ating the validity of prior taxonomic hypotheses: (1) We reconstructed phylogenies
using both morphological (Wei et al. in prep.) and molecular data (Lohman et al. in
prep.), and used these as guides for interpreting relationships among species and taxo-
nomic boundaries within species complexes; (2) In these analyses, we endeavored to
include specimens from the type localities (or the surrounding area—at least the same
island group) of the nominotypical subspecies to substantiate taxonomic boundaries of
geographically widespread species with multiple subspecies (e.g., agondas, casiphone, hy-
permnestra, nesaea, and panthera); (3) We considered the geological history of a species’
range (Hall 2001; Hall and Smyth 2008; Sathiamurthy and Voris 2006), particularly
for taxa that are rare in museum collections and not readily available for morphologi-
cal or molecular study. For example, present-day Sulawesi comprises multiple terranes,
some of which originated in different biogeographical subregions, that collided in the
Miocene (Lohman et al. 2011; Stelbrink et al. 2012). If two or more subspecies of the
same species are described from a large and geologically complex island such as Sulawesi
or New Guinea and we had limited material for phylogenetic study, then we generally
retained the landmass’s different subspecies for lack of evidence to synonymize them;
(4) When genetic and/or ecological data suggested that different names had been ap-
plied to different mimetic forms, sexes, or seasonal forms, we synonymized these taxa.

For convenience, we have divided the genus into 15 monophyletic species groups
(Lohman et al. in prep.) named after each clade’s oldest named species. Because of the
uniformity of genitalia and extreme intraspecific variability in wing patterns, there are
few if any morphological synapomorphies that can be used to discriminate these spe-
cies groups. They have been circumscribed based on relatedness as inferred by a multi-
locus molecular phylogeny.

Distribution maps and type localities

A variety of sources were used to infer the distribution maps that we provide, includ-
ing museum data, taxonomic and other publications (Aoki et al. 1982; Braby 2000;
Ek-Amnuay 2012; Hanafusa 2001; Inayoshi 2017; Monastyrskii 2004; 2005; Okubo
2010; Parsons 2000; Saito and Koshi 2012; Suzuki 2006; Tateishi 2001; Treadaway
and Schroeder 2012; Uémura and Kitamura 2001; Vane-Wright and de Jong 2003).
The majority of Elymnias taxa were described when most of South and Southeast Asia
were colonized by European countries, and many of the type locality names given in
the species descriptions have changed since colonial times. Therefore, in addition to
the original type locality names given in the species description, we have attempted to provide the modern locality names in parentheses. In the text below, we do not attempt to use present knowledge of the taxon’s distribution to infer the precise location where the type was collected. However, when designating type localities on the distribution maps, we have attempted to use knowledge of the taxon’s current distribution and other information to indicate the type locality as precisely as possible. Nonetheless, many type localities are imprecise and cannot be localized because many labels simply list the island where the specimen was found (e.g., New Guinea) rather than a precise locality.

Format of the checklist

This annotated checklist is formatted in the following way:

**valid species name author, year**

Specimens: Figs X, Y, Z; Male genitalia: Figs X, Y, Z; Distribution: Fig: X

**ssp. recognized valid subspecies name, author, year**

Original combination of subspecies, Author, Year. **TL:** Type locality provided in original description (Current name of type locality in a standardized format- Country: Province, locality). **TS:** Depository of type specimen. Original citation.

Junior synonym original combination, Author, Year. **TL:** Type locality provided in original description (Current name of type locality); **TS:** Depository of type specimen. Original citation.

Checklist of Elymnias

**ELYMNIAS Hübner, 1818** (Type species: *Elymnias jynx* Hübner, 1818, = *Papilio hypermnestra* Linnaeus, 1763) *Zuträge Samml. exot. Schmett.* 1:12.

**Didonis** Hübner, [1819] (Type species: *Papilio vitellia* Stoll, 1781) *Verz. bek. Schmett.* 2: 17.

**Dyctis** Boisduval, 1832 (Type species: *Dyctis agondas* Boisduval, 1832) *Voy. Astrolabe.* 1: 138.

**Agrusia** Moore, 1894 (Type species: *Melanitis esaca* Westwood, 1851) *Lepidoptera Indica* 2 (18): 169.

**Bruasa** Moore, 1894 (Type species: *Melanitis penanga* Westwood, 1851) *Lepidoptera Indica* 2 (18): 164–165.

**Melynias** Moore, 1894 (Type species: *Papilio lais* Cramer, [1777]) *Lepidoptera Indica* 2 (18): 156–163.

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The type species of *Didonis* Hübner was erroneously thought to be *Papilio biblis* Fabricius, 1807 in earlier literature. Scudder (1875) subsequently selected *Papilio vitellia* Stoll as the type species, and this designation thereby prevented misusage of the name and confusion with the genus *Biblis* Fabricius, 1807 as stated by Hemming (1967).
Mimadelias Moore, 1894 (Type species: Elymnias vasudeva Moore, 1858)

Elymnias Fruhstorfer, 1907 (Type species: Papilio phegea Fabricius, 1793)

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**bammakoo-group**

**bammakoo (Westwood, 1851)**

Specimens: Fig. 1A–D; Male Genitalia: Fig. 22A; Distribution: Fig. 27

**ssp. bammakoo (Westwood, 1851)**

Papilio phegea Fabricius, 1793. **TL**: Uganda. **TS**: ZMUC. (preoccupied by Papilio phegea Borkhausen, 1788). *Ent. Syst.* 3 (1): 132.

Melanitis bammakoo Westwood, 1851. **TL**: Ashanti (Ghana: Ashanti Region). **TS**: NHM. *Gen. diurn. Lep.* 2: 405, pl. 68, fig. 3.

Elymnias phegea var. intermedia Aurivillius, 1898. **TL**: not indicated. **TS**: NRM. *K. svenska Vetenskakad. Handl.* 31 (5): 45.

Elymnias phegea ab. angustata Bartel, 1905. **TL**: Kamerun, Barombi Station (Cameroon: Southwest Region, Barombi Mbo). **TS**: unknown. *Novit. Zool.* 12: 129.

Elymiopsis bammakoo var. hybrida Niepelt, 1915. **TL**: Kassai River (Democratic Republic of Congo: Kasai River). **TS**: NHM. *Int. Ent. Zs.* 9: 58.

Elymiopsis lise Hemming, 1960. **TL**: Uganda. **TS**: ZMUC. (replaced Papilio phegea Fabricius, 1793). *Annot. lep.* 1: 30.

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**ssp. rattrayi Sharpe, 1902**

Elymnias rattrayi Sharpe, 1902. **TL**: Entebbe (Uganda: Central Uganda, Entebbe). **TS**: NHM. *Entomologist* 35: 41.

Elymnias ugandae Grünberg, 1908. **TL**: Uganda. **TS**: unknown. *Sitzungsber. Ges. Naturf. Freunde. Berlin.* 1908: 51.

Elymiopsis ugandae f. rattrayi Lewis, 1974. **TL**: Uganda. **TS**: unknown. *Butterflies of the World*, p. 266, pl. 115, fig. 15.

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2 Moore (1894) did not include any species when establishing *Mimadelias* in Part 18 of his *Lepidoptera Indica*. The type species *vasudeva* was subsequently designated as the type species in his Part 19 of the same series.

3 *Elymiopsis* has often been regarded as a distinct genus since its establishment in 1907 by Fruhstorfer, and most references of Afrotropical butterflies list it as a genus of its own (e.g., Larsen 2005). Hemming (1943) first synonymized this genus with *Elymnias* and the opinion was followed by Gardiner (2010) and further supported by the phylogenetic studies by Peña et al. (2006). In our molecular phylogenetic study (Lohman et al. in prep.), this taxon is sister to all of the Asian species. However, aside from their wing patterns, which mimic various *Acraea* spp. (Nymphalidae: Heliconiinae), the morphological features of this species are not distinct from other *Elymnias* (Wei et al. in prep.), and we refrain from retaining the monotypic genus *Elymiopsis*.
Elymnias bammakoo rattrayi (Sharpe, 1902). **TL:** Uganda. **TS:** unknown. *Butterflies of West Africa,* p. 283.

**paradoxa-group**

**paradoxa Staudinger, 1894**

Specimens: Fig. 1E–F; Male Genitalia: Fig. 22B; Distribution: Fig. 28

*Elymnias paradoxa* Staudinger, 1894. **TL:** Kubary (Papua New Guinea: Madang Province, Mt. Kubari). **TS:** ZMHB. *Dt. ent. Z. Iris* 7 (1): 116.

*Elymnias erastus* Grose-Smith, 1894. **TL:** Sattelberg (Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg). **TS:** NHM. *Novit. Zool.* 1 (3): 588.

**papua-group**

**papua Wallace, 1869**

Specimens: Fig. 1G–M; Male Genitalia: Fig. 22C; Distribution: Fig. 29

ssp. *papua* Wallace, 18694

*Elymnias papua* Wallace, 1869. **TL:** New Guinea5. **TS:** NHM. *Trans. Ent. Soc. Lond.* 1869 (4): 329.

*Elymnias viridescens* Grose-Smith, 1894. **TL:** Humboldt Bay (Indonesia: Papua, Jayapura, Yos Sudarso Bay). **TS:** NHM. *Novit. Zool.* 1 (2): 365, pl. 12, figs 5–6.

*Dyctis viridescens* var. *kakarona* Hagen, 1897. **TL:** Sattelberg (Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg). **TS:** NHMT. *Jarhb. Nass. Ver. Nat.* 50: 78.

*Elymnias papua bivittata* van Eecke, 1915. *syn. n.* **TL:** Bivakeiland, Kooofbivak, New Guinea (Indonesia: Papua, Asmat Regency, Bivak Island). **TS:** NBC. *Nova Guinea* 13 (1): 65, pl. 3, fig. 5 & 5a.

ssp. *lactentia* Fruhstorfer, 1907

*Elymnias papua lactentia* Fruhstorfer, 1907. **TL:** Waigiu Island (Indonesia: West Papua, Raja Ampat Regency, Waigeo). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 240.

ssp. *cinereomargo* Joicey & Noakes, 1915

*Elymnias viridescens cinereomargo* Joicey & Noakes, 1915. **TL:** Biak Island (Indonesia: Papua, Biak). **TS:** NHM. *Trans. Ent. Soc. Lond.* 1915 (2): 196.

ssp. *climena* Talbot, 1932

*Elymnias climena* Talbot, 1932. **TL:** Mysol Island (Indonesia: West Papua, Raja Ampat Regency, Misool). **TS:** NHM. *Bull. Hill Mus. Witley* 4 (3): 168.

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4 We recognize 5 subspecies of *papua* in the present study and synonymize *bivittata* with *papua* because no significant morphological differences were found. In addition, no apparent barriers to dispersal seem to exist between the geographic ranges of these two taxa.

5 Since Wallace only traveled to the Bird's Head Peninsula on New Guinea, it is likely that the type specimen was collected in what is now the Indonesian province of West Papua.
ssp. euploeoides Talbot, 1932
Elymnias euploeoides Talbot, 1932. TL: Batchian (INDONESIA: North Maluku, Bacan). TS: NHM. Bull. Hill Mus. Witley 4 (3): 167.

esaca-group

esaca (Westwood 1851)
Specimens: Figs 1N–P; 2A–C; Male Genitalia: Fig. 22D–E; Distribution: Fig. 30

ssp. esaca (Westwood, 1851)
Melanitis esaca Westwood, 1851. TL: East Indies. TS: NHM. Gen. diurn. Lep. 2: 405. Elymnias godferyi Distant, 1883. TL: Sungei Ujong (Peninsular MALAYSIA: Negeri Sembilan, Sungei Ujong). TS: NHM. Ann. Mag. nat. Hist. 12 (71): 351. Dyctis esacoides de Nicéville, [1893]. TL: Perak (Peninsular MALAYSIA: Perak), Battak Mountains7 (INDONESIA: North Sumatra). TS: IM. J. Bomb. Nat. Hist. Soc. 7 (3): 323, pl. H, fig. 2.

ssp. egialina (C. & R. Felder, 1863)
Melanitis egialina C. & R. Felder, 1863. TL: Luzon (PHILIPPINES: Luzon). TS: NHMW. Wien. ent. Monats. 7 (4): 121. Melanitis ligya C. & R. Felder, 1863. nom. nud. TL: Luzon (PHILIPPINES: Luzon). TS: NHMW. Wien. ent. Monats. 7 (4): 121. Melanitis pallas C. & R. Felder, 1863. nom. nud. TL: Luzon (PHILIPPINES: Luzon). TS: NHMW. Wien. ent. Monats. 7 (4): 121.

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6 The distinctiveness of esaca and vasudeva has never been doubted and they have been treated as distinct species in all prior studies. The former is distributed throughout most of the Greater Sunda Islands, the Philippines, and the Thai-Malay peninsula, and the range of the latter encompasses northeast India, Myanmar, northern Laos, northern Vietnam and southwest China. The wings of male esaca are shorter and more attenuate than vasudeva, and have black ground coloration with a metallic submarginal band in some specimens. The male of vasudeva is not dramatically different from the female in wing shape or color pattern. However, our molecular phylogenetic analysis (Lohman et al. in prep.) reveals that both specimens of vasudeva (from China and India) are nested within a clade of three esaca specimens from Java, Mindanao, and peninsular Malaysia. This paraphyletic relationship suggests that the two species should be synonymized. However, we regard both species as valid because: 1) wing color and pattern are strongly dimorphic in esaca, but more or less monomorphic in vasudeva; 2) the wing shape of esaca males differs from females, and this is not true of vasudeva; and 3) the two taxa are parapatric.

7 “Battak Mountains” is the type locality for many butterfly and other animal taxa, but the name appears on no recent map of Sumatra. It seems to refer to the mountainous region historically inhabited by the Batak ethnic groups in northeast Sumatra. From the description in de Nicéville and Martin (1895), “Battak Mountains” seems to refer to the portion of the Barisan Mountain Range running along the western edge of North Sumatra Province, including the peaks surrounding Lake Toba.
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ssp. borneensis Wallace, 1869
Elymnias borneensis Wallace, 1869. **TL**: Sarawak (East Malaysia: Sarawak). **TS**: NHM. *Trans. ent. Soc. Lond.* 1869 (4): 324.

Elymnias (Mimadelias) esaca taeniola Fruhstorfer, 1907. **syn. n. TL**: southeast Borneo. **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 250.

ssp. andersonii (Moore, 1886)
*Dyctis andersonii* Moore, 1886. **TL**: Mergui (Myanmar: Thanintharyi, Mergui Archipelago). **TS**: NHM. *J. Linn. Soc. Lond.* 21 (1): 33, pl. 3, fig. 5.

Elymnias (Mimadelias) oberthuri Fruhstorfer, 1902. **syn. n. TL**: Renong, Siam (Thailand: Ranong). **TS**: NHM. *Soc. Ent.* 17 (11): 82.

ssp. mabeswara Fruhstorfer, 1894
Elymnias (Dyctis) mabeswara Fruhstorfer, 1894. **TL**: Gede Vulcan (Indonesia: West Java, Mt. Gede). **TS**: NHM. *Ent. Nachr.* 20 (2): 21.

ssp. leontina Fruhstorfer, 1898
Elymnias esaca leontina Fruhstorfer, 1898. **TL**: Nias (Indonesia: North Sumatra, Nias). **TS**: NHM. *Ent. Zs.* 12 (14): 99.

ssp. pseudodelias Fruhstorfer, 1907
Elymnias (Mimadelias) esaca pseudodelias Fruhstorfer, 1907. **TL**: Sumatra (Indonesia: Sumatra). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 250.

ssp. georgi Fruhstorfer, 1907
Elymnias (Mimadelias) esaca georgi Fruhstorfer, 1907. **TL**: Mindanao (Philippines: Mindanao). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 251.

ssp. saifuli Hanafusa, 1993
Elymnias esaca saifuli Hanafusa, 1993. **TL**: Siberut Island (Indonesia: West Sumatra, Mentawai Islands, Siberut). **TS**: HPC. *Futao* (11): 3.

ssp. popularis Hanafusa, 1994
Elymnias esaca popularis Hanafusa, 1994. **TL**: Tanahmasa Island (Indonesia: North Sumatra, South Nias Regency, Batu Islands, Tanahmasa). **TS**: HPC. *Futao* (17): 19.

ssp. splendidida Tateishi, 2001
Elymnias esaca splendidida Tateishi, 2001. **TL**: Singkep Island (Indonesia: Riau Islands, Lingga Archipelago, Singkep Island). **TS**: FMNH. *Futao* (39): 13.

ssp. lingga Tateishi, 2001
Elymnias esaca lingga Tateishi, 2001. **TL**: Lingga Island (Indonesia: Riau Islands, Lingga Archipelago, Lingga Island). **TS**: FMNH. *Futao* (39): 14.

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8 The subspecies *esaca taeniola* is synonymized with *esaca borneensis* because there are no consistent morphological differences between them and no obvious biogeographical barriers within the island Borneo that would restrict gene flow and maintain subspecific differences.

9 *oberthuri* was originally described as a species by Fruhstorfer (1902b) and subsequently downgraded to be a subspecies of *vasudeva* (Fruhstorfer 1907). We synonymize it with *esaca andersonii* because these two names seem to represent opposite sexes of the same subspecies confined to the Thai-Malay Peninsula.
**ssp. nigricans** Tateishi, 2001
_Elymnias esaca nigricans_ Tateishi, 2001. **TL:** Enggano Island (**Indonesia:** Bengkulu, Enggano Island). **TS:** FMNH. _Futao_ (39): 14.

**ssp. andrewi** Schröder & Treadaway, 2003
_Elymnias esaca andrewi_ Schröder & Treadaway, 2003. **TL:** PHILIPPINES: Oriental Mindoro, Mt. Halcon. **TS:** SMFD. _Nachr. ent. Ver. Apollo_ 23 (4): 193, pl. 1, figs 3–4.

**ssp. leytensis** Schröder & Treadaway, 2003
_Elymnias esaca leytensis_ Schröder & Treadaway, 2003. **TL:** PHILIPPINES: Southern Leyte, Saint Bernard, Hinabian. **TS:** SMFD. _Nachr. ent. Ver. Apollo_ 23 (4): 194, pl. 1, figs 7–8.

**ssp. tateishii** Lamas, 2010
_Elymnias esaca tateishii_ Lamas, 2010. _SHILAP_ 38 (150): 198. (replacement name of _Elymnias esaca lautensis_ Tateishi, 2001).

_Elymnias esaca lautensis_ Tateishi, 2001. **TL:** Laut Island (**Indonesia:** South Kalimantan, Kota Baru, Laut Island). **TS:** FMNH. _Futao_ (39): 13. (preoccupied by _Elymnias harterti lautensis_ Medicielo & Hanafusa, 1994).

**vasudeva** Moore, 1857
Specimens: Fig. 2D–K; Male Genitalia: Fig. 22F; Distribution: Fig. 31

**ssp. vasudeva** Moore, 1857
_Elymnias_ (Mimadelias) _vasudeva vasudeva_ Moore, 1857. **TL:** Darjeeling (**India:** West Bengal, Darjeeling). **TS:** NHM. _Cat. lep. Ins. Mus. East India Coy._ 1: 238.

_Elymnias rhycana_ Wallace, 1869. **syn. n. TL:** INDIA. **TS:** NHM. _Trans. ent. Soc. Lond._ 1869 (4): 323. (8)

_Mimadelias deva_ Moore, 1894. **syn. n. TL:** Khasia Hills, Assam (**India:** Meghalaya, Khasi Hills). **TS:** NHM. _Lepid. Ind._ 2 (19): 167, pl. 142, fig. 2a.

_Mimadelias burmensis_ Moore, 1893. **syn. n. TL:** Tenasserim (**Myanmar:** Tanintharyi, Tenasserim). **TS:** NHM. _Lepid. Ind._ 2 (19): 168, pl. 143, fig. 1a–e.

_Elymnias vacudera_ [sic] _sinensis_ Chou, Zhang & Xie, 2000. **syn. n. TL:** Yunnan (China: Yunnan). **TS:** NWSUAF. _Entomotaxonomia_ 22 (3): 224, figs 7–8.

**dara-group**

**dara** Distant & Pryer, 1887
Specimens: Fig. 3A–D; Male Genitalia: Fig. 22G–I; Distribution: Fig. 32

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10 Having examined all the type specimens and a long series of other material ranging from northeast India to southwest China, we failed to detect any consistent differences among the subspecies described by (Moore 1857; 1894), Wallace (1869), and Chou (2000). We consider all _vasudeva_ subspecies to be indistinguishable from one another; the variable wing patterns lack diagnostic differences and are not reliable for delimiting subspecies.
ssp. dara Distant & Pryer, 1887
_Elymnias dara_ Distant & Pryer, 1887. **TL:** north Borneo. **TS:** NHM. *Ann. Mag. nat. Hist.* (5) 19 (109): 50.

ssp. albofasciata Staudinger, 1889
_Elymnias albofasciata_ Staudinger, 1889. **TL:** Philippines: Palawan. **TS:** ZMH
_Dt. ent. Z. Iris_ 2 (1): 39,11

ssp. deminuta Staudinger, 1889
_Elymnias albofasciata_ var. _deminuta_ Staudinger, 1889. **TL:** Lawang (Indonesia: East Java, Malang, Lawang). **TS:** ZMH. _Dt. ent. Z. Iris_ 2 (1): 40.

ssp. bengena Fruhstorfer, 1907
_Elymnias dara bengena_ Fruhstorfer, 1907. **TL:** Palabuan (Indonesia: West Java, Sukabumi, Pelabuhan Ratu). **TS:** NHM. _Dt. ent. Z. Iris_ 20 (3): 216.

ssp. darina Fruhstorfer, 1907
_Elymnias dara darina_ Fruhstorfer, 1907. **TL:** Battak Mountains (Indonesia: North Sumatra). **TS:** NHM. _Dt. ent. Z. Iris_ 20 (3): 215.

ssp. daedalion (de Nicéville, 1890)
_Dyctis daedalion_ de Nicéville, 1890. **TL:** Myittha (Myanmar: Mandalay, Kyaukse, Myittha). **TS:** IM. _J. Bomb. nat. Hist. Soc._ 5 (3): 202, pl. D, fig. 4.

**patna-group**

**patna** (Westwood, 1851)12
Specimens: Fig. 3E–I; Male Genitalia: Fig. 22J; Distribution: Fig. 33

11 Staudinger (1889) described _albofasciata_ based on specimens from Palawan. However, the locality of a “type specimen” deposited in ZMH is labeled as “Tanyong Malim, Malacca”. We consider the type to be either mislabeled or simply not a type of this subspecies. Staudinger (1889) indicated that he compared specimens of _dara_ from Malacca (specimen provided by Künstler) and Palawan. The mistake in labeling is probably caused by historical confusion of the type locality since its publication.

12 Moore (1894) described _patnoides_ as a distinct species, but Fruhstorfer (1907) downgraded it to be a form of _patna patna_. In the same publication, Fruhstorfer (1907) described _patna stictica_ from Vietnamese specimens. Having examined long series from India, Myanmar, northern Thailand, northern Laos, Vietnam and Hainan (China), we find no consistent differences in wing pattern and wing shape among populations in this region. We therefore synonymize both _patnoides_ and _stictica_ with _patna_. The subspecies _hanitschi_ from the Malay Peninsula has slightly different metallic blue sheen from the nominotypical subspecies, and molecular phylogenetic analysis reveals that the _patna_ from India and _patna_ from Malay Peninsula form distinct sister lineages. We therefore retain the subspecies status of _hanitschi_ in the present study. Ek-Amnuay et al. (2007) described _inayoshii_ based on specimens collected in Ranong and Trang Provinces in peninsular Thailand. The name, however, is not available under the Code. Additionally, the taxonomic status of the peninsular Thai populations is questionable, as we find that the wing shape and coloration of _inayoshii_ are markedly different from _patna patna_ and _patna hanitschi_. Since we have no material for DNA sequencing, we cannot determine whether the peninsular Thai populations should be treated as a subspecies of _patna_ or a different species altogether. The nomenclatural problem of _inayoshii_ requires confirmation of the taxon’s species identity.
**ssp. patna (Westwood, 1851)**
*Melanitis patna* Westwood, 1851. **TL:** East India. **TS:** NHM. *Gen. diurn. Lep.* 2: 405, pl. 68, fig. 2.

*Elymnias patna bercovitzi* Joicey & Talbot, 1921. **TL:** Five Finger Mountains (China: Hainan, Wuzhi Mountain). **TS:** NHM. *Bull. Hill Mus. Witsley* 1 (1): 173.

*Melanitis patnoides* Moore, 1893. **syn. n. TL:** Burma, Karen Hills, East Pegu (Myanmar: Bago). **TS:** NHM. *Lepid. Ind.* 2 (19): 163, pl. 141, fig. 2 & 2a.

*Elymnias patna stictica* Fruhstorfer, 1902. **syn. n. TL:** Than-Moi, Nordtonkin (Vietnam: Lang Son, Than Moi). **TS:** NHM. *Dt. ent. Z. Iris* 14 (2): 271.

**ssp. hanitschi** Martin, 1909
*Elymnias patna hanitschi* Martin, 1909. **TL:** Malayische Halbinsel (Thai-Malay Peninsula). **TS:** NHMT. *Dt. ent. Z. Iris* 22 (1): 52.

**peali** Wood-Mason, 1883
Specimens: Fig. 3J–K; Male Genitalia: Fig. 22K; Distribution: Fig. 34

*Elymnias peali* Wood-Mason, 1883. **TL:** Aideo, Sibsagar district, Assam (India: Assam, Sivasagar). **TS:** NHM. *Ann. Mag. nat. Hist.* (5) 11: 62, pl. 2, fig. A & B.

**ceryx-group**

**ceryx** (Boisduval, 1836)
Specimens: Fig. 3L–M; Male Genitalia: Fig. 22L; Distribution: Fig. 35

*Melanitis ceryx* Boisduval, 1836. **TL:** West Java (Indonesia: West Java). **TS:** NHM. *Hist. Nat. Ins., Spec. Gén. Lépid.* 1: pl. 9, fig. 8.

*Elymnias hestinia* Fruhstorfer, 1911. **TL:** Java (Indonesia: Java). **TS:** NHM. *Gross-Schmett. Erde* 9: 383.

**kuenstleri** Honrath, [1885]
Specimens: Fig. 4A–C; Male Genitalia: Fig. 22M; Distribution: Fig. 36

**ssp. kuenstleri** Honrath, [1885]
*Elymnias künstleri (=kuenstleri)* Honrath, [1885]. **TL:** Perak and Malacca (Peninsular Malaysia: Perak and Malacca). **TS:** NHM. *Berl. ent. Z.* 29 (2): 276, pl. 8, fig. 3.

**ssp. gauroides** Fruhstorfer, 1894
*Elymnias gauroides* Fruhstorfer, 1894. **TL:** Tjisewu, West Java (Indonesia: West Java, Cisewu). **TS:** NHM. *Ent. Nachr.* 20 (3): 43.

**ssp. rileyi** Corbet, 1933
*Elymnias kuentleri rileyi* Corbet, 1933. **TL:** Borneo. **TS:** NHM. *Stylops* 2: 132.

*Elymnias borneensis* Riley, 1923. **TL:** Borneo. **TS:** unknown. *Entomologist* 56 (717): 36.

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13 Westwood (1851) was possibly unaware of the true collection locality of the type specimen of *ceryx*. Having examined the description, we confirm that the type locality of the type specimen should be Java, not Mexico.
ssp. dohrnii de Nicéville, 1895

_Elymnias_ (Melynias) dohrnii _de Nicéville, 1895. **TL:** Bohorok, East Sumatra (Indonesia: North Sumatra, Langkat Regency, Bohorok). **TS:** IM. _J. Bomb. nat. Hist. Soc._ 10 (1): 21, pl. S, fig. 12.

_Elymnias kuenstleri mariae_ Toxopeus, 1936. **syn. n. TL:** Bekoelen (Indonesia: South Sumatra, Bengkulu). **TS:** NBC. _Ent. Med. Ned. Ind._ 2: 46, fig. 1.

ceryxoides _de Nicéville, 1895. stat. rev._**

Specimens: Fig. 3N–O; Distribution: Fig. 37

_Elymnias_ (Melynias) _ceryxoides_ _de Nicéville, 1895. **TL:** Battak Mountains (Indonesia: North Sumatra). **TS:** IM. _J. Bomb. nat. Hist. Soc._ 10 (1): 22, pl. S, fig. 13.

_Elymnias ceryx ceryxoides _f. nigrita_ Fruhstorfer, 1907. **TL:** Vulkan Singalang (Indonesia: West Sumatra, Agam Regency, Mt. Singgalang). **TS:** NHM. _Dt. ent. Z. Iris _20 (3): 213.

pellucida _Fruhstorfer, 1895_

Specimens: Fig. 4D–E; Male Genitalia: Fig. 22N; Distribution: Fig. 38

_Elymnias pellucida_ Fruhstorfer, 1895. **TL:** Kinabalu (East Malaysia: Sabah, Mt. Kinabalu). **TS:** NHM. _Ent. Nachr._ 21 (11): 168.

_Elymnias annea_ Pryer & Cator, 1894. **TL:** Borneo. **TS:** NHM. _Br. N. Borneo Herald _12 (9): 234.

_Elymnias aroa_ Shelford, 1902. **TL:** Mount Penrissen, Sarawak (East Malaysia: Sarawak, Mt. Penrissen). **TS:** SMK. _Proc. Zool. Soc. Lond._ 1902 (2): 272.

penanga-group

penanga _(Westwood, 1851)_**

Specimens: Fig. 4F–L; Male Genitalia: Fig. 22O; Distribution: Fig. 39

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14 Toxopeus’s _mariae_ was described from Sumatra, from which _de Nicéville’s dohrnii_ was also collected. Since there are no remarkable or consistent morphological differences between the subspecies and because no biogeographic or climatic barriers to dispersal seem to exist on Sumatra, we consider _mariae_ to be a junior synonym of _dohrnii_. _de Nicéville’s dohrnii_ was once placed as a subspecies either of _pellucida_ (Fruhstorfer 1907) or of _patna_ (D’Abrera 1985), here we can confirm it should be associated with _kuenstleri_ after having examined the specimens from Sumatra.

15 The taxonomic status of _De Nicéville’s ceryxoides_ has been inconsistent. It was originally proposed as a subspecies of _ceryx_, and the treatment was followed by Fruhstorfer (1907). Aoki et al. (1982) suggested upgrading _ceryxoides_ as an independent species without giving explanation, but this taxon was again downgraded as a subspecies of _ceryx_ by D’Abrera in 1985. Having examined both morphology and genetic data, we conclude that _ceryxoides_ should be regarded as a full species endemic to Sumatra.

16 _Elymnias penanga_ is one of the few _Elymnias_ species with polymorphic female color patterns. However, the female forms are not diagnostically different among subspecies. The diagnostic characters that distinguish subspecies are the size, forewing shape, and metallic sheen of the male.
ssp. penanga (Westwood, 1851)
Melanitis penanga Westwood, 1851. TL: Penang (Peninsular MALAYSIA: Penang). TS: NHM. Gen. diurn. Lep. (2): 405.
Melanitis mehida Hewitson, 1863. TL: Singapore. TS: NHM. Ill. exot. Butts. [4] (Melanitis): [69], pl. [36], figs 2–3.
Elymnias abris Distant, 1886. TL: Province Wellesley (Peninsular MALAYSIA: Penang, Seberang Perai). TS: NHM. Ann. Mag. nat. Hist. 17 (102): 531.
Elymnias penanga penanga f. hislopi (♀) Eliot, 1967. TL: Langkawi (Peninsular MALAYSIA: Kedah, Langkawi). TS: NHM(?). Entomologist 100 (1244): 3.
Elymnias penanga f. immaculata Martin, 1909. TL: INDONESIA: Sumatra. TS: NHMT.Dt. ent. Z. Iris 22 (1): 55.
Elymnias penanga penanga f. johnsoni Talbot, 1929. TL: Penang (Peninsular MALAYSIA: Penang). TS: NHM. Bull. Hill Mus. Witley 3 (1): 80.

ssp. sumatrana Wallace, 1869
Elymnias sumatrana Wallace, 1869. TL: Sumatra (INDONESIA: Sumatra). TS: NHM. Trans. ent. Soc. Lond. 1869 (4): 325.

ssp. konga Grose-Smith, 1889
Elymnias konga Grose-Smith, 1889. TL: Kina Balu Mountain, (East MALAYSIA: Sabah, Mt. Kinabalu). TS: NHM. Ann. Mag. nat. Hist. (6) 3 (16): 317.
Elymnias borneensis Grose-Smith, 1892. TL: Northeast Borneo. TS: NHM. Ann. Mag. nat. Hist. (6) 10 (60): 428. (preoccupied by Elymnias borneensis Wallace 1869).
Elymnias penanga trepchtroides Shelford, 1904. TL: North Borneo. TS: NHM. J. Straits Asiat. Soc. (41): 103. (replacement name for Elymnias borneensis Grose-Smith, 1892).
Elymnias penanga konga f. mehidina, Fruhstorfer, 1907. TL: Borneo. TS: NHM. Dt. ent. Z. Iris 20 (3): 226.
Elymnias penanga konga f. ptychandrina, Fruhstorfer, 1907. TL: North Borneo. TS: NHM. Dt. ent. Z. Iris 20 (3): 227.

ssp. chelensis de Nicéville, 1890
Elymnias chelensis de Nicéville, 1890. TL: Khasi Hills (INDIA: Meghalaya, Khasi Hills). TS: IM. J. Bomb. nat. Hist. Soc. 5 (3): 200, pl. D, fig. 3.

hypermnestra-group

hypermnestra (Linnaeus, 1763)
Specimens: Figs 5A–N, 6A–P, 7A–O, 8A–H; Male Genitalia: Fig. 23A–K; Distribution: Fig. 40

ssp. hypermnestra (Linnaeus, 1763)17

17 Elymnias hypermnestra is one of the few satyrine species that is regarded as a minor pest of several species of palms. The name has been used numerous times in the taxonomic, ecological, and agricultural literature (Corbet 1943; Koh and Gan 2007; Merrett 1993; Shang-Wen 1998; Yong et al. 2012). However, Lamas (2010) raised concern regarding the validity of this name. This species was originally
Papilio hypermnestra Linnaeus, 1763. TL: Java (Indonesia: Java). TS: LSL. Amoenitates Acad. 6: 407.
Papilio protogenia Cramer, 1779. TL: Java (Indonesia: Java). TS: NBC. Uitl. Kapellen. 2 (16): 141, pl. 189, fig. F–G.
Hamadryas jynx Hübner, 1808. TL: not indicated. TS: unknown. Erste Zutr. Samml. exot. Schmett. p. 4.
Elymnias jynx Hübner, 1818. TL: East Indies. TS: unknown. Zuträge Samml. exot. Schmett. 1: 12.
Elymnias hypermnestra hypermnestra f. perpusilla Fruhstorfer, 1907. TL: Java (Indonesia: Java). TS: NHM. Dt. ent. Z. Iris 20 (3): 181.
Elymnias hypermnestra f. atrata Roepke, 1942. TL: Java (Indonesia: Java). TS: NBC. Rhop. Javan. (4): 422.\(^{18}\)

placed in Papilio by Linnaeus (1763), which made it a junior primary homonym of Papilio hypermnestra Scopoli, 1763 (now a synonym of Zerynthia polyxena ([Schiffermüller], 1775) (Papilionidae). Papilio hypermnestra Linnaeus was published after 23 June 1763, whereas Papilio hypermnestra Scopoli was published before that date. Therefore, according to the ICZN Article 57.2, both names are primary homonyms and the junior primary homonym (in this case, hypermnestra Linnaeus) is permanently invalid (see also Article 23.9.5). Given this set of circumstances, Linnaeus’ hypermnestra can only be regarded as valid under one of three conditions according to the code:

57.2.1. its use as a valid name (nomen protectum) is maintained under the conditions specified in Article 23.9, or
57.2.2. it is conserved by the Commission under Article 81, or
57.2.3. it, but not its senior homonym, is included in a relevant adopted Part of the List of Available Names in Zoology."

However, as already stated by Lamas (2010), hypermnestra Linnaeus does not fulfill any of the three conditions specified above, because: 1) hypermnestra Linnaeus has not been maintained as a nomen protectum and does not fulfill the conditions specified in Article 23.9; 2) hypermnestra Linnaeus has not been conserved by the Commission under Article 81; and 3) no part of the List of Available Names in Zoology has been adopted yet for Lepidoptera.

Meanwhile, hypermnestra Scopoli has been used numerous times as a valid name after 1899 [see Article 23.9.1.1], and therefore does not qualify as a nomen oblitum. Consequently, if use of the younger homonym [hypermnestra Linnaeus] is to be maintained, the case needs to be submitted to the International Commission for Zoological Nomenclature for a ruling under the plenary power (Article 81). In addition, if Linnaeus’s hypermnestra is eventually considered invalid by the Commission, the other earliest available name for this species is Papilio undularis Drury, 1773, which is now used to represent the subspecies of northeast India, and the valid subspecific name for the population of Java would be protogenia Cramer, 1779.

\(^{18}\)Roepke’s atrata has rarely been mentioned in previous literature, and, having examined the original description, we regard it as a junior synonym of the nominotypical subspecies, which is also from Java.
ssp. *undularis* (Drury, 1773)<sup>19</sup>

*Papilio undularis* Drury, 1773. **TL**: East Indies. **TS**: NHM. *Ill. Nat. Hist. Exot. Insects* 2: 17, pl. 10, f. 1–2.

*Biblis undularis* Westwood, 1837. **TL**: East Indies, Java (Indonesia: Java). **TS**: NHM. *Ill. Exo. Ent.* 2: 18, pl. X, figs 1–2.

*Melanitis undularis* Westwood, 1851. **TL**: East India, Java (Indonesia: Java). **TS**: NHM. *Gen. diurn. Lep.* 2: 404.

ssp. *fraterna* Butler, 1871

*Elymnias fraterna* Butler, 1871. **TL**: Ceylon (Sri Lanka). **TS**: NHM. *Proc. Zool. Soc. Lond.* 1871: 520, pl. 42, fig. 3.

ssp. *nigrescens* Butler, 1871

*Elymnias nigrescens* Butler, 1871. **TL**: Sarawak (East Malaysia: Sarawak). **TS**: NHM. *Proc. Zool. Soc. Lond.* 1871: 520, pl. 42, fig. 1.

*Elymnias hecate* Butler, 1871. **TL**: Labuan, Borneo (East Malaysia: Labuan). **TS**: NHM. *Proc. Zool. Soc. Lond.* 1871 (2): 520, pl. 42, f. 2.

*Elymnias nigrescens nigrescens* f. *pseudagina* Fruhstorfer, 1907. **TL**: Sarawak, Borneo (East Malaysia: Sarawak). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 191.

*Elymnias nigrescens nigrescens* f. *edela* Fruhstorfer, 1907. **TL**: Pontianak (Indonesia: West Kalimantan, Pontianak). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 191.

*Elymnias nigrescens nigrescens* f. *virilis* Fruhstorfer, 1907. **TL**: Lawas (East Malaysia: Lawas). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 191.

*Elymnias nigrescens nigrescens* f. *hecate* Fruhstorfer, 1907. **TL**: Labuan (East Malaysia: Labuan). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 191.

ssp. *cottonis* (Hewitson, 1874). **comb. n.**<sup>20</sup>

*Melanitis cottonis* Hewitson, 1874. **TL**: Andaman Islands (India: Andaman Islands). **TS**: NHM. *Ann. Mag. nat. Hist.* 14 (83): 358.

*Elymnias cottonis cottonis* Fruhstorfer, 1907. **TL**: Andaman Islands (India: Andaman Islands). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 183.

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<sup>19</sup> Interpretation of the type locality of Drury’s *undularis* has been problematic. Drury did not clearly indicate the origin of the specimen he saw but labeled the locality as “East Indies”. During the late 18th century, the phrase “East Indies” referred to a wide range of possible localities from India to Indonesia. However, authors working after Drury, without clear reason, interpreted *undularis* as a taxon distributed in northeast India rather than Indonesia. We examined many specimens from north India to Java at different museums and also compared the original drawings of *hypermnestra* (and its junior synonyms) and *undularis* in the literature (e.g., Cramer 1779; Drury 1773), but failed to detect any differences between them. We therefore retain the current concept of *undularis* until more evidence becomes available.

<sup>20</sup> Hewitson’s *cottonis* was described as a full species due to the lack of metallic sheen or any other notable markings on the upper side of both the fore- and hindwings; its conspecificity with *hypermnestra* has not previously been suggested. Our unpublished data (Wei et al. in prep.) demonstrates that *cottonis* and *hypermnestra* cannot be distinguished using morphological characters unrelated to possible mimicry, and the molecular phylogeny reveals that cottonis is nested within *hypermnestra* with strong support (Lohman et al. in prep.). We therefore combine *cottonis* (including subspecies *jennifferae* from Little Andaman) with *hypermnestra*, retaining the names *cottonis* and *jennifferae* as distinct subspecies.
An illustrated checklist of the genus Elymnias Hübner, 1818 (Nymphalidae, Satyrinae) 65

ssp. tinctoria Moore, [1879]21
Elymnias tinctoria Moore, [1879]. **TL:** Meetan, Moolai (MYANMAR: Tanintharyi) **TS:** NHM. *Proc. Zool. Soc. Lond.* 1878 (4): 826.

Elymnias hypermnestra tinctoria f. paraleuca Fruhstorfer, 1907. **TL:** Mergui-Archiel, Tenasserim (MYANMAR: Thanintharyi, Mergui Archipelago). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 177.

ssp. hainana Moore, 187822
Elymnias hainana Moore, 1878. **TL:** Hainan (CHINA: Hainan). **TS:** NHM. *Proc. zool. Soc. Lond.* 1878 (3): 696.

Elymnias nigrescens formosana Fruhstorfer, 1903. **TL:** Takau (TAIWAN: Kaohsiung). **TS:** NHM. *Dt. ent. Z. Iris* 16 (1): 17.

Elymnias nigrescens tonkiniana Fruhstorfer, 1902. **syn. n. TL:** Tonkin, Haiphong (VIETNAM: Haiphong). **TS:** NHM. *Dt. ent. Z. Iris* 14 (2): 271.

Elymnias hypermnestra nigrescens f. depicta Fruhstorfer, 1907. **syn. n. TL:** Tonkin (northern VIETNAM). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 188.

Elymnias hypermnestra septentrionalis Chou & Huang, 1994. **syn. n. TL:** Nanning (China: Guangxi, Nanning). **TS:** NWSUAF. *Monographia Rhopalocerum Sinensium* 1: 375, fig. 27.

ssp. discrepans Distant, 188223
Elymnias discrepans Distant, 1882. **TL:** Penang, Province Wellesley (Peninsular MALAYSIA: Penang, Seberang Perai). **TS:** NHM or NHMT. *Ann. Mag. nat. Hist.* (5) 9 (53): 397.

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21 Besides undularis from northeast India, there are three other subspecies with orange, Danaus-mimicking females distributed in Myanmar, Thailand, and Vietnam. The differences between females of the subspecies tinctoria, violetta, and meridionalis, are subtle. Besides the female form mimicking Danaus chrysippus (or D. gemuta), there is another female form with whitish hindwings (the forms obfuscata and paraleuca) that possibly mimics either D. melanippus or D. affinis in Thailand and Vietnam. Since the current subspecies classification has been adopted by local guidebooks and other publications for so long (Corbet et al. 1992; Ek-Amnuay 2012; Monastyrskii 2005; Pinratana 1988), we do not propose any nomenclatural change prior to a thorough phylogenetic/population genetics study based dense sampling of the entire region is completed.

22 Moore’s hainana was described from specimens from Hainan Island, China, and the name has been applied to the Taiwanese population since the late 19th century. Since Hainan is between China’s Guangxi Province and northern Vietnam, where septentrionalis and tonkiniana were described, respectively, and because examination of dozens of specimens evince no consistent morphological differences among these subspecies, we synonymize these three names and regard hainana as the valid name.

23 Penang is a small island in the Andaman Sea lying just off the western coast of peninsular Malaysia. The strait that separates this small island (293 km²) from the peninsula is only 2–8 km wide, yet seems to form a dispersal barrier between the peninsular population (commonly known as agina, but herein changed to beatrice, see discussion below) and insular discrepans. The female type specimen of discrepans seems to be a morphologically intermediate form between orange, Danaus-mimicking tinctoria and dark, Euploea-mimicking phenotypes. This phenotype has not been documented from the mainland. We therefore retain the name discrepans because of the taxon’s distinctive female wing patterns; further studies will ascertain whether this subspecies is genetically distinct from other hypermnestra subspecies.
ssp. orientalis Röber, 1891
Elymnias orientalis Röber, 1891. TL: Flores (INDONESIA: East Nusa Tenggara, Flores). TS: unknown. Tijdschr. Ent. 34: 311.

Elymnias nigrescens dohertyi Fruhstorfer, 1902. TL: Ende Island (INDONESIA: East Nusa Tenggara, Flores, Ende Island). TS: NHM. Dt. ent. Z. Iris 14 (2): 273.

ssp. baliensis Fruhstorfer, 1896
Elymnias protegenia baliensis Fruhstorfer, 1896. TL: Bali (INDONESIA: Bali). TS: NHM. Soc. Ent. 11 (18): 147.

Elymnias nigrescens bulelenga Rothschild, 1915. TL: Buleleng (INDONESIA: Bali, Buleleng Regency). TS: NHM. Novit. Zool. 22 (1): 124.

ssp. violetta Fruhstorfer, 1902
Elymnias undularis violetta Fruhstorfer, 1902. TL: Muok-Lek (THAILAND: Saraburi, Muak Lek). TS: NHM. Soc. Ent. Soc. Ent. 16 (22): 169.

Elymnias hypermnestra violetta f. epixantha Fruhstorfer, 1907. TL: Bangkok (THAILAND: Bangkok). TS: NHM. Dt. ent. Z. Iris 20 (3): 178.

Elymnias hypermnestra violetta f. obfuscata Riley, 1932. TL: Siam (THAILAND). TS: NHM. J. Siam. Soc. 8 (4, Suppl.): 249.

ssp. meridionalis Fruhstorfer, 1902
Elymnias undularis meridionalis Fruhstorfer, 1902. TL: south Annam (southern VIETNAM). TS: NHM. Soc. Ent. 16 (22): 169.

Elymnias meridionalis f. orphnia, Fruhstorfer, 1907. TL: south Annam (southern VIETNAM). TS: NHM. Dt. ent. Z. Iris 20 (3): 179.

ssp. beatrice Fruhstorfer, 1902. comb. n.24

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24 The taxonomic status and the names applied to the populations of Elymnias hypermnestra from Malay Peninsula, Singapore, Borneo, and Sumatra have been historically confusing and chaotic. In 1882, Distant reported and described nigrescens from the Malay Peninsula, Malacca, Billiton (Belitung), and Borneo. Since Butler (1871) already stated that the type locality of the “real nigrescens” is Sarawak (Borneo), and the female wing patterns of the populations in Borneo and Malay Peninsula are slightly different, it is not appropriate to apply the name nigrescens to the peninsular population. Fruhstorfer (1902) noticed that “nigrescens sensu Distant was different from the Bornean one, so he proposed a nomen novum, beatrice, to refer to “nigrescens sensu Distant”. The concept of Fruhstorfer’s beatrice, however, is probably not monophyletic as he listed Perak, Lingga (Riau), Deli (North Sumatra), and Sumatra in the geographical range of beatrice, but our morphological study does not support lumping the Sumatran population with the peninsular Malaysian one. In the same publication, Fruhstorfer (1902a) described an aberration of nigrescens, namely agina, for populations in Singapore, Sumatra, and Perak. The name agina has been used much more frequently than beatrice to represent the population in the Malay Peninsula including Singapore (Corbet 1943; Lamas 2010; Pinratana 1988). However, Article 45.6.2 of the Code, agina was not an available name when Fruhstorfer first proposed it as an aberrant form of nigrescens (now a valid subspecies of hypermnestra). This name might have subsequently become available by Corbet (1943) when he discussed the taxonomy of the Elymnias hypermnestra of Malay Peninsula, and first used agina to represent the populations in Johor and Singapore. According to the Code (Article 45.5.1), Corbet would be the first author to make agina available so in the present study, we correct the authorship and year of agina to be “Corbet, 1943”. Both beatrice and agina are available for the populations in Malay Peninsula, Singapore, Borneo, and Sumatra.
Elymnias nigrescens, Distant, 1882. Rhopalocera Malayana: 61.

Elymnias nigrescens beatrice Fruhstorfer, 1902. nomen n. for Distant’s nigrescens.

**TL:** Singapore, Perak (Peninsular Malaysia: Perak), Lingga (Indonesia: Riau Islands, Lingga Archipelago, Lingga Island), Deli, (Indonesia: North Sumatra Province, Deli Serdang Regency), Sumatra (Indonesia: Sumatra), Wellesley Province (Peninsular Malaysia: Penang, Seberang Perai), Billiton (Indonesia: Bangka-Belitung Province, Belitung). **TS:** NHM. *Dt. ent. Z. Iris* 14 (2): 272.

Elymnias nigrescens ab. agina Fruhstorfer, 1902. unavailable name. **TL:** Singapore, Sumatra (Indonesia: Sumatra), Perak (Peninsular Malaysia: Perak). **TS:** NHM. *Dt. ent. Z. Iris* 14 (2): 272.22

Elymnias nigrescens beatrice f. ornamenta Fruhstorfer, 1907. unavailable name. **TL:** Malay (Peninsular Malaysia). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 190.22

Elymnias hypermnestra agina, Corbet, 1943. *Proc. Roy. Ent. Soc. Lond.* (B) 12: 117–119.

ssp. sumbana Fruhstorfer, 1902

Elymnias nigrescens sumbana Fruhstorfer, 1902. **TL:** Sumba (Indonesia: East Nusa Tenggara, Sumba). **TS:** NHM. *Dt. ent. Z. Iris* 14 (2): 273.

ssp. decolorata Fruhstorfer, 190725

Elymnias nigrescens beatrice forma decolorata Fruhstorfer, 1907. unavailable name. **TL:** Sumatra (Indonesia: Sumatra). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 189.

Elymnias hypermnestra decolorata, Aoki, Yamaguchi & Uéuma, 1982. *Butterflies of the Southeast Asian Islands* 3: 175–176.

ssp. sumbawana Fruhstorfer, 1907

Elymnias nigrescens sumbawana Fruhstorfer, 1907. **TL:** Tambora, Sumbawa (Indonesia: West Nusa Tenggara, Sumbawa, Mt. Tambora). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 197.

*trice and agina became available for representing the populations in Malay Peninsula and Singapore. Determination of their validity, therefore, depends on the priority. Considering the fact that Corbet’s (1943) use of agina is much later than Fruhstorfer’s (1902a) proposal of a nomen novum, we conclude that beatrice should be used to represent the populations in southern part of the Malay Peninsula, including Singapore. The syntype series of both names contain more than one subspecies, so designation of a lectotype for both names will be necessary to fix the concept and use the names. This work will be published elsewhere.*

25 de Nicéville and Martin (1895) stated that they had “great difficulty in identifying satisfactorily the common species of *Elymnias* of the *undularis* group occurring in Sumatra”. They decided to follow Distant’s (1882a) concept of “nigrescens” but still noticed that the Sumatran population of *Elymnias hypermnestra* (as nigrescens or protogenia) had smaller wings and duller coloration. Fruhstorfer (1907) noticed the opinion of de Nicéville & Martin, and decided to give the Sumatran population a status as a color form, and name it *decolorata*. However, since it was originally published as an infrasubspecific taxon, the name is not available under the Code unless another author uses the name to represent a valid taxon. In 1982, Aoki and colleagues enumerated the subspecies of *Elymnias hypermnestra* that occur throughout its range. They became the first authors to use *decolorata* to represent the Sumatran population. According to the Code (Article 45.5.1), the authorship of *decolorata* should be attributed to Aoki et al. (1982) because they made it available for use for the first time.
ssp. *timorensis* Fruhstorfer, 1907
*Elymnias nigrescens timorensis* Fruhstorfer, 1907. **TL:** Timor. **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 198.

ssp. *alorensis* Talbot, 1932
*Elymnias nigrescens alorensis* Talbot, 1932. **TL:** Alor (Indonesia: East Nusa Tenggara, Alor). **TS:** NHM. *Bull. Hill Mus. Witley* 4: 167.

ssp. *nimota* Corbet, 1937
*Elymnias hypermnestra nimota* Corbet, 1937. **TL:** Tioman (Peninsular Malaysia: Pahang, Rompin, Tioman Island). **TS:** NHM. *Proc. R. ent. Soc. Lond.* 6 (5): 97.

ssp. *kangeana* Aoki & Uémura, 1982
*Elymnias hypermnestra kangeana* Aoki & Uémura, 1982. **TL:** Kangean (Indonesia: East Java, Sumenap Regency, Kangean). **TS:** TPC. *Mem. Tsukada Coll.* 4: 2.

ssp. *robinsona* Monastyrskii & Devyatkin, 2003
*Elymnias hypermnestra robinsona* Monastyrskii & Devyatkin, 2003. **TL:** Con Dao, Con Son Island (Vietnam: Ba Ria–Vung Tau Province, Con Dao Archipelago, Con Son Island). **TS:** NHM. *Atalanta* 34 (1/2): 81, pl. 5, figs 5, 7–8.

ssp. *jennifferae* Suzuki, 2006. comb. n.
*Elymnias cottonis jennifferae* Suzuki, 2006. **TL:** Little Andaman (India: Andaman Islands, Little Andaman Island). **TS:** KMSPC. *Futao* (52): 13.

ssp. *uemurai* Lamas, 2010 (replaced *Elymnias nigrescens meliophila* Fruhstorfer, 1896a). **SHILAP** 38 (150): 198.

*Elymnias nigrescens meliophila* Fruhstorfer, 1896a. **TL:** Lombok (Indonesia: West Nusa Tenggara, Lombok). **TS:** NHM. *Soc. Ent.* 11 (18): 147. (preoccupied by *Elymnias hewitsoni meliophila* Fruhstorfer 1896b).

**caudata** Butler, 1871
Specimens: Fig. 8J–K; Male Genitalia: Fig. 23L; Distribution: Fig. 41

*Elymnias caudata* Butler, 1871. **TL:** Canara (India: Karnataka, Kanara). **TS:** NHM. *Proc. Zool. Soc. Lond.* 1871: 520, pl. 42, fig. 4.

**merula** Swinhoe, 1915. incertae sedis
Specimen: Fig. 8K; Distribution: Fig. 42

*Elymnias merula* Swinhoe, 1915. **TL:** Kandy, Ceylon (Sri Lanka: Central Province, Kandy). **TS:** NHM. *Ann. Mag. nat. Hist.* 16 (93): 171.

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26 Although *caudata* was originally proposed as a species of its own, some authors (Gupta 2007; Wynter-Blyth 1957) treated it as a subspecies of *hypermnestra* (or *undularis*) due to the similarity in the *Danaus*-mimicking females. Our morphological and molecular studies demonstrate that *caudata* is a distinct, monophyletic taxon that is sister to *hypermnestra*.

27 Swinhoe’s *merula* is based on a single male type collected from Sri Lanka. Having examined the type deposited in the Natural History Museum, London, we are convinced that *merula* should be a synonym of *hypermnestra*. Lamas (pers. comm.) suggests synonymizing *merula* with the Sri Lankan *fraterna*; however, the male of Sri Lankan *fraterna* is quite different from *merula* and we cannot at present conclude that synonymizing it with this subspecies is warranted. We presume that the single specimen of *merula* was accidentally introduced with imported palms or is an aberration; we treat this name as *incertae sedis*. 
**leucocyma Godart, 1819. incertae sedis**

**Distribution:** Fig. 43

*Biblis leucocyma* Godart, 1819. **TL:** Java (**Indonesia:** Java). **TS:** unknown. *Encyc. Méth.* 9: 326.

**nepheronides-group**

**nepheronides Fruhstorfer, 1907**

**Specimens:** Fig. 8L–N; **Male Genitalia:** Fig. 23M; **Distribution:** Fig. 44

**ssp. nepheronides Fruhstorfer, 1907**

*Elymnias nepheronides* Fruhstorfer, 1907. **TL:** Flores Island (**Indonesia:** East Nusa Tenggara, Flores). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 228.

*Elymnias detanii* Aoki & Uémura, 1982. **TL:** Flores (**Indonesia:** East Nusa Tenggara, Flores). **TS:** NODAI. *Butterflies of the Southeast Asian Islands* 3: 208.

**ssp. tamborana Okubo, 2010**

*Elymnias tamborana* Okubo, 2010. **TL:** Mt. Ngegep, Sumbawa (**Indonesia:** West Nusa Tenggara, Sumbawa, Mt. Sengenges). **TS:** OPC. *Trans. Lep. Soc. Jpn.* 60 (4): 255–257.

**harterti-group**

**harterti Honrath, 1889**

**Specimens:** Fig. 9A–F; **Distribution:** Fig. 45

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28 The true identity of Godart’s *leucocyma* has been problematic since its description in 1819. Godart specified “Java” as the source of the specimen but gave a vague description without any figure. Doubleday (1844) suggested that northern India (near the border with Myanmar) might be the source of the specimen. Moore (1878a) mentioned the name *leucocyma* in his checklist without providing any further information. In 1882, Marshall & de Nicéville recognized the validity of *leucocyma* and synonymized *malelas* with it. However, Moore (1894) considered *leucocyma* to be the name that should be validated rather *malelas*. Fruhstorfer (1907), based on Godart’s simple description, doubted that the origin of specimen was Java or northern India, and suggested placing *leucocyma* closer to *hypermnestra*. There are more than 2 species with color patterns similar to *leucocyma* (viz. forewing with metallic blue sheen and hindwing with undulate margin) in Java and northern India, so we cannot specify the use of this name until more evidence becomes available. Moreover, Hewitson’s figure (1861: pl. 9, fig. 34) of *leucocyma* was a misidentification of *bewitsoni* and has no relevance to this problem.

29 Our molecular phylogenetic analysis confirms that *detanii* and *nepheronides* represent opposite sexes of the same species as Araya (2016) demonstrated using morphology. We also accept Araya’s (2016) decision to include *tamborana* as a subspecies of *nepheronides* on morphological grounds; we currently have no genetic data from *tamborana*.

30 Having examined specimens deposited in the NHM, we are confident that *harterti* and *brookei* should be regarded as different subspecies of the same species. Moulton’s *smithi* is identical to Shelford’s *brookei* so they are synonymized in the present study.
ssp. *harterti* Honrath, 1889
*Elymnias harterti* Honrath, 1889. **TL**: Perak (Peninsular MALAYSIA: Perak). **TS**: NHM. *Berl. ent. Z.* 33 (1): 165.

ssp. *brookei* Shelford, 1904
*Elymnias brookei* Shelford, 1904. **TL**: Sarawak (East MALAYSIA: Sarawak). **TS**: NHM. *J. Straits Asiat. Soc.* (41): 102.

*Elymnias smithi* Moulton, 1915. **syn. n. TL**: Mt. Molu (East MALAYSIA: Sarawak, Mt. Molu). **TS**: NHM. *Entomologist* 48: 98.

ssp. *lautensis* Medicielo & Hanafusa, 1994
*Elymnias harterti lautensis* Medicielo & Hanafusa, 1994. **TL**: Laut Island (Indonesia: South Kalimantan, Kota Baru Regency, Laut Island). **TS**: HPC. *Futao* (15): 17, pl. 4, figs 17–18.

ssp. *arbaimuni* Hanfusa, 2005
*Elymnias harterti* [sic] *arbaimuni* Hanfusa, 2005. **TL**: INDONESIA: Jambi Province, Kuala Tungkal, Suban. **TS**: HPC. *Futao* (49): 11, pl. 1, figs 11–12.

**parce** Staudinger, 1889
Specimens: Fig. 9G–J; Male Genitalia: Fig. 23N; Distribution: Fig. 46

ssp. *parce* Staudinger, 1889
*Elymnias panthera parce* Saudinger, 1889. **TL**: Palawan (PHILIPPINES: Palawan). **TS**: ZMHB. *Dt. ent. Z. Iris* 2 (1): 39.

ssp. *justini* Schröder & Treadaway, 2003
*Elymnias parce justini* Schröder & Treadaway, 2003. **TL**: PHILIPPINES: Palawan, Busuanga Island. **TS**: SMFD. *Nachr. ent. Ver. Apollo* 23 (4): 194, pl. 1, fig. 21.

**panthera**-group

**panthera** (Fabricius, 1787)
Specimens: Figs 9K, 10A–P; Male Genitalia: Figs 23O, 24A; Distribution: Fig. 47

ssp. *panthera* (Fabricius, 1787)
*Papilio panthera* Fabricius, 1787. **TL**: Tranquebariae (INDIA: Tamil Nadu, Tharangambadi). **TS**: ZMUC. *Mantissa Ins.* 2: 39.

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31 Staudinger (1889) placed *parce* as a subspecies of *panthera*, but morphological and molecular evidence suggest that *parce* does not belong to the *panthera*-group; it is more closely allied to *harterti*.

32 Fabricius stated that the type locality of the nominotypical *panthera* is Tranquebar (Tharangambadi, Tamil Nadu) in southern India, but the current distribution of this species in India seems to be restricted to the north. It is necessary to confirm the actual distribution of the species in India to verify whether the type locality falls in the actual distribution range or is simply a port from which the specimen was exported during the colonial period.
ssp. *dusara* (Horsfield, [1829])\(^{33}\)

*Melanitis dusara* Horsfield, [1829]. **TL**: West Java (Indonesia: West Java). **TS**: NHM. *Descr. Cat. lep. Ins. Mus. East India Coy.* 2: pl. 5, f. 7.

**ssp. minus** Wood-Mason & de Nicéville, 1881

*Elymnias minus* Wood-Mason & de Nicéville, 1881. **TL**: Nicobar Islands (India: Nicobar Islands). **TS**: unknown. *J. Asiat. Soc. Bengal* 50: 230.

**ssp. dolorosa** Butler, 1883.

*Elymnias dolorosa* Butler, 1883. **TL**: Nias Island (Indonesia: North Sumatra, Indonesia, Nias). **TS**: NHM. *Ent. mon. Mag.* 20: 53.

**ssp. lutescens** Butler, 1867. **comb. n., stat. n.**\(^{34}\)

*Elymnias lutescens* Butler, 1867. **TL**: Malacca, Singapore and Penang (Singapore & Peninsular Malaysia: Penang and Malacca). **TS**: NHM. *Ann. Mag. nat. Hist.* 20 (120): 404, pl. 9, f. 10.

*Elymnias panthera* var. *labuana* Staudinger, 1889. **syn. n.** **TL**: Labuan Island (East Malaysia: Labuan). **TS**: ZMHB. *Dt. ent. Z. Iris* 2 (1): 39.

*Elymnias panthera* *lacrima* Fruhstorfer, 1904. **syn. n.** **TL**: [North Borneo], [Ban-ka] (Indonesia: Banka-Belitung Province, Banka Island). **TS**: NHM. *Berl. ent. Z.* 49: 188.

*Elymnias defasciata* Fruhstorfer, 1911, **syn. n.** **TL**: Borneo. **TS**: NHM. *Gross-Schmett. Erde* 9: 372.

*Elymnias panthera* *alfredi* Fruhstorfer, 1907. **syn. n.** **TL**: Southeast Borneo. **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 220.

*Elymnias panthera* *alfredi* f. *pantherina* Fruhstorfer, 1907. **unavailable name.** **TL**: Southeast Borneo. **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 220.

*Elymnias panthera* *alfredi* f. *alfredi* Fruhstorfer, 1907. **unavailable name.** **TL**: Southeast Borneo. **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 220.

**ssp. enganica** Doherty, 1891

*Elymnias enganica* Doherty, 1891. **TL**: Engano (Indonesia: Bengkulu, Enggano Island). **TS**: NHM. *J. Asiat. Soc. Bengal. Part 2*, 60 (1): 24.

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33 The subspecies *dusara* and *dulcibella* were both described from Java, suggesting the names might be synonymous. However, many lepidopteran species have distinctive populations western and eastern parts of the island (Aoki et al. 1982; Tsukada and Nishiyama 1982; Yata and Morishita 1985), and we therefore retain these two subspecies as valid.

34 Butler’s *lutescens* was proposed as a full species based on specimens from Borneo (collected by Lowe), Malacca, Singapore, and Penang (from Roberts’ collection), and according to Butler (1867: 404), *lutescens* was similar to *dusara*. This taxon, however, has been synonymized with the Indian nominotypical subspecies for long with no clear reason. In the present study, we revalidate the name and use it to represent the population in Borneo, as Borneo is the first locality mentioned in Butler’s original description. The other conspecific taxa described from Borneo, such as *labuana, lacrima, defasciata, alfredi*, and *pantherina* are therefore newly synonymized with *lutescens* in the present study. It is not clear whether *panthera* from peninsular Malaysia is genetically distinct from Bornean populations, so we do not further revise the plethora of subspecific names associated with *panthera*. 
ssp. *lacrimosa* Fruhstorfer, 1898
*Elymnias panthera lacrimosa* Fruhstorfer, 1898. **TL:** Bawean Island (INDONESIA: East Java, Gresik Regency, Bawean). **TS:** NHM. *Berl. ent. Zs.* 43: 196.

ssp. *suluana* Fruhstorfer, 1899
*Elymnias panthera suluana* Fruhstorfer, 1899. **TL:** Sulu Island (PHILIPPINES: Sulu Province, Sulu Island). **TS:** NHM. *Berl. ent. Zs.* 44: 57.

ssp. *bangueyana* Fruhstorfer, 1899
*Elymnias panthera bangueyana* Fruhstorfer, 1899. **TL:** Banguey Island (MALAYSIA: Sabah, Banggi Island). **TS:** NHM. *Berl. ent. Zs.* 44: 58.

ssp. *dulcibella* Fruhstorfer, 1907
*Elymnias panthera* f. *dulcibella* Fruhstorfer, 1907. **TL:** East Java (INDONESIA: East Java). **TS:** NHM *Dt. ent. Z. Iris* 20 (3): 223.31

ssp. *tautra* Fruhstorfer, 1907
*Elymnias panthera tautra* Fruhstorfer, 1907. **TL:** Northeast Sumatra (INDONESIA: North Sumatra). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 218 (repl. *E. lutescens* Martin & de Nicéville, 1896)

ssp. *arikata* Fruhstorfer, 1907
*Elymnias panthera arikata* Fruhstorfer, 1907. **TL:** Natuna Island (INDONESIA: Riau Province, Natuna Island). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 219.

ssp. *balina* Martin, 1909
*Elymnias panthera balina* Martin, 1909. **TL:** Bali Island (INDONESIA: Bali). **TS:** NHMT. *Dt. ent. Z. Iris* 22 (1): 58.

ssp. *exsulata* van Eecke, 1918
*Elymnias panthera exsulata* van Eecke, 1918. **TL:** Pulu [sic] Lasia (INDONESIA: North Sumatra, Lasia Island). **TS:** NBC. *Zoologische Mededeelingen* 4 (2): 82.

ssp. *winkleri* Kalis, 1933
*Elymnias panthera winkleri* Kalis, 1933. **TL:** Sabang, Weh Island (INDONESIA: Aceh, Sabang, Weh Island). **TS:** MEPR. *Tijdschrift voor Entomologie* 76 (1–2): 80.

ssp. *mira* Corbet, 1942
*Elymnias panthera mira* Corbet, 1942. **TL:** Sipora Island (INDONESIA: West Sumatra, Mentawai Regency, Sipora). **TS:** NHM. *Ann. Mag. nat. Hist.* (11) 9 (56): 612.

ssp. *tiomanica* Eliot, 1978
*Elymnias panthera tiomanica* Eliot, 1978. **TL:** Tioman (Peninsular MALAYSIA: Pahang, Rompin, Tioman Island). **TS:** NHM. *Butterflies of the Malay Peninsula*, 3rd ed: 413.

ssp. *belitungensis* Okano, 1986
*Elymnias panthera belitungensis* Okano, 1986. **TL:** Belitung Island (INDONESIA: Bangka-Belitung Province, Belitung). **TS:** OMPC. *Tokurana* 11 (1): 1, figs 1–6.

ssp. *ruricolaris* Hanafusa, 1989
*Elymnias panthera ruricolaris* Hanafusa, 1989. **TL:** Karimata Island (INDONESIA: West Kalimatan Province, Karimata Island). **TS:** HPC. *Futao* (3): 10, pl. 3, figs 1–4.
ssp. banyakensis Hanafusa, 1993
_Elymnias panthera banyakensis_ Hanafusa, 1993. **TL:** Kepulauan Banyak (Indonesia: Aceh, Banyak Islands). **TS:** HPC. _Futao_ (13): 8.

ssp. attenuata Hanafusa, 1994
_Elymnias panthera attenuata_ Hanafusa, 1994. **TL:** Tanahmasa Island (Indonesia: North Sumatra Province, Tanahmasa Island). **TS:** HPC. _Futao_ (4): 13.

ssp. redangensis Hanafusa, 2001
_Elymnias panthera redangensis_ Hanafusa, 2001. **TL:** Redang Island (Peninsular Malaysia: Terengganu, Redang Island). **TS:** HPC. _Futao_ (37): 14, pl.1, figs 5–8.

ssp. zeta Abang, Treadaway & Schröder, 2004
_Elymnias panthera zeta_ Abang, Treadaway & Schröder, 2004. **TL:** Balambangan Island (East Malaysia: Sabah, Balambangan Island). **TS:** MUS. _Futao_ (47): 10, pl. 3, figs 33–36.

obnubila Marshall & de Nicéville, 1883
Specimens: Fig. 11A–B; Male Genitalia: Fig. 24B; Distribution: Fig. 48
_Elymnias obnubila_ Marshall & de Nicéville, 1883. **TL:** Mergui (Myanmar: Thanintharyi, Mergui Archipelago). **TS:** IM. _Butts India Burmah Ceylon_ 1 (2): 272.

congruens Semper, 1887
Specimens: Fig. 11C–G; Male Genitalia: Fig. 24C; Distribution: Fig. 49

ssp. congruens Semper, 1887
_Elymnias congruens_ Semper, 1887. **TL:** N. Mindanao (Philippines: northern Mindanao). **TS:** SMFD. _Reisen. Philipp._ 2: 61, pl. 11, fig. 8–10.
_Elymnias congruens photinus_ Fruhstorfer, 1907. **syn. n.** **TL:** N. Mindanao (Philippines: northern Mindanao). **TS:** NHM. _Dt. ent. Z. Iris_ 20 (3): 199.
_Elymnias congruens phaios_ Fruhstorfer, 1907. **syn. n.** **TL:** S. Mindanao (Philippines: southern Mindanao). **TS:** NHM. _Dt. ent. Z. Iris_ 20 (3): 200.
_Elymnias congruens rafaela_ Fruhstorfer, 1907. **syn. n.** **TL:** Bazilan (Philippines: Sulu Archipelago, Basilan). **TS:** NHM. _Dt. ent. Z. Iris_ 20 (3): 200.

ssp. subcongruens Semper, 1892
_Elymnias subcongruens_ Semper, 1892. **TL:** Mindoro (Philippines: Mindoro). **TS:** SMFD. _Reisen. Philipp._ 7: 329.

ssp. endida Fruhstorfer, 1911
_Elymnias congruens endida_ Fruhstorfer, 1911. **TL:** Bohol (Philippines: Bohol). **TS:** NHM. _Gross-Schmett. Erde_ 9: 379.

Having examined the type material described by Fruhstorfer and Semper, we are convinced that only one subspecies of _congruens_ is distributed on the island Mindanao, and therefore synonymize _photinus, phaios, and rafaela_ with the nominotypical _congruens._
**ssp. salipi** Schroeder & Treadaway, 1989
*Elymnias salipi* Schroeder & Treadaway, 1989. **TL:** Philippines: Tawi-Tawi Archipelago, Sanga Sanga Island, Boloboc. **TS:** SMFD. *Ent. Z.* 99 (22): 327, fig. 6.

**ssp. jekei** Schroeder & Treadaway, 1989
*Elymnias jekei* Schroeder & Treadaway, 1989. **TL:** Philippines: Luzon, Nueva Ecija, near Carranglan. **TS:** SMFD. *Ent. Z.* 99 (22): 328, fig. 6.

**ssp. neergaardorum** Schroeder & Treadaway, 2003
*Elymnias neergaardorum* Schroeder & Treadaway, 2003. **TL:** Philippines: Masbate. **TS:** SMFD. *Nachr. ent. Ver. Apollo* 23 (4): 194, pl. 1, figs 14–15.

**miyagawai** Saito & Kishi, 2012
Specimens: Fig. 11H–I; Distribution: Fig. 50
*Elymnias miyagawai* Saito & Kishi, 2012. **TL:** Vietnam: Lam Dong. **TS:** SPC. *Butterflies* (62): 4, figs 1–2, 10.

**nesaea-group**

**nesaea** (Linnaeus, 1764)
Specimens: Fig. 12A–O; Male Genitalia: Fig. 24D–G; Distribution: Fig. 51

**ssp. nesaea** (Linnaeus, 1764)36
*Papilio (Nymphalis) nesaea* Linnaeus, 1764. **TL:** [Java] (Indonesia: Java). **TS:** LSL. *Mus. Lud. Ulr. Reg.*: 302.

*Papilio lais* Cramer, 1777. **TL:** Java (Indonesia: Java). **TS:** unknown. *Uitl. Kapellen* 2 (10): 21, pl. 110, f. A–B.

*Elymnias nesaea hermia* Fruhstorfer, 1907. **syn. n. TL:** near Lawang, (Indonesia: East Java, Lawang). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 206.34

**ssp. timandra** Wallace, 186937
*Elymnias timandra* Wallace, 1869. **TL:** Sylhet (Bangladesh: Sylhet Division), Moulmein (Myanmar: Mon State, Mawlamyine). **TS:** NHM. *Trans. ent. Soc. Lond.* 1869 (4): 326.

*Elymnias nesaea cortona* Fruhstorfer, 1911. **syn. n. TL:** Burma (Myanmar). **TS:** NHM. *Gross-Schmett. Erde* 9: 379.

**ssp. laisidis** de Nicéville, 1896
*Elymnias (Melynias) laisidis* de Nicéville, 1896. **TL:** Sumatra (Indonesia: Sumatra). **TS:** IM. *J. Asiat. Soc. Bengal, Part 2*, 64 (3): 390.

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36 Linnaeus did not indicate from which part of Java his specimen of *nesaea* was collected, and we found no consistent differences among Javan *nesaea* populations based on examination of specimens at several different museums, so we combine Fruhstorfer’s *hermia* with the nominotypical *nesaea*.

37 Wallace’s *timandra* from Sylhet, Bangladesh, is not different from Fruhstorfer’s *cortona* from Myanmar, so we synonymize them.
An illustrated checklist of the genus Elymnias Hübner, 1818 (Nymphalidae, Satyrinae)

ssp. baweana Hagen, 1896
_Elymnias baweana_ Hagen, 1896. **TL:** Bawean Island (Indonesia: East Java, Gresik, Bawean). **TS:** NHMT. _Jahrb. Nass. Nat._ 49: 184, pl. 4, fig. 6.

ssp. neolais de Nicéville, 1898
_Elymnias (Melynias) neolais_ de Nicéville, 1898. **TL:** Nias Island (Indonesia: North Sumatra, Nias). **TS:** IM. _J. Bomb. nat. Hist. Soc._ 12 (1): 136, pl. X, fig. 6.

ssp. apelles Fruhstorfer, 1902
_Elymnias lais apelles_ Fruhstorfer, 1902. **TL:** Bangkok (Thailand: Bangkok). **TS:** NHM. _Soc. Ent._ 16 (22): 169

ssp. vordemani Snellen van Vollenhoven, 1902
_Elymnias vordemani_ Snellen van Vollenhoven, 1902. **TL:** Kangean Island (Indonesia: East Java, Sumenap, Kangean). **TS:** NBC. _Tijdschr. Ent._ 45: 77, pl. 8, fig. 1.

ssp. hypereides Fruhstorfer, 1903 36
_Elymnias lais hypereides_ Fruhstorfer, 1903. **TL:** North Borneo. **TS:** NHM. _Dt. ent. Z._ Iris 15 (2): 315
_Elymnias nesaea coelifrons_ Fruhstorfer, 1907. **syn. n. TL:** Southeast Borneo (Indonesia: South or East Kalimantan). **TS:** NHM. _Dt. ent. Z._ Iris 20 (3): 205. 38

ssp. kamarina Fruhstorfer, 1906
_Elymnias lais kamarina_ Fruhstorfer, 1906. **TL:** Batu Island (Indonesia: North Sumatra, South Nias Regency, Batu Islands). **TS:** NHM. _Ent Zs._ 20 (15): 98.

ssp. lioneli Fruhstorfer, 1907
_Elymnias nesaea lioneli_ Fruhstorfer, 1907. **TL:** Malaysia. **TS:** NHM. _Dt. ent. Z._ Iris 20 (3): 203.

ssp. tawicola Schröder & Treadaway, 1989
_Elymnias nesaea tawicola_ Schröder & Treadaway, 1989. **TL:** Philippines: Tawi-Tawi Archipelago, Sibutu Island, Cavan Cavan. **TS:** SMFD. _Ent. Z._ 99 (22): 326, fig. 4.

casiphone Geyer, [1827]
_Specimens:_ Fig. 12A–M; _Male Genitalia:_ Fig. 24H–L; _Distribution:_ Fig. 52

ssp. casiphone Geyer, [1827]
_Elymnias casiphone_ Geyer, [1827]. **TL:** not indicated. **TS:** unknown. _Samml. exot. Schmett._ 3: pl. [9], f. 1–2. 39, 40

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38 We examined many _nesaea_ from different regions of Borneo and found no consistent difference among them. Frustorfer’s _coelifrons_ is therefore treated as a junior synonym of _hypereides_. The relationship between the Malayan _lioneli_ with _hypereides_ can be addressed in future phylogenetic studies.

39 Lamas (pers. comm.) regards _casiphone_ and _kamara_ as different species, so _erinyes_, _exclusa_, and _lombokiana_ are therefore regarded as subspecies of _kamara_. Our phylogenetic study based on morphology and DNA sequence data, however, show that _kamara_ is conspecific with _casiphone_; _kamara_ seems to represent a sexually dimorphic, mimetic form in which both males and females differ from the sexually dimorphic mimetic forms of _casiphone_. We therefore associate all subspecies previously included under _kamara_ with _casiphone_.

40 Geyer, when describing _casiphone_, did not specify the geographical provenance of his specimen. Westwood (1851) and Fruhstorfer (1907) suspected that Java was possibly the origin of Geyer’s _casiphone_.

**Elymnias kamara** Moore, [1858]. *syn. n. TL*: Java (Indonesia: Java). *TS*: NHM. *Cat. lep. Ins. Mus. East India Coy* 1: 239.

**Elymnias kamara pareuploea** Fruhstorfer, 1911. *TL*: [Java] (Indonesia: Java). *TS*: NHM. *Gross-Schmett. Erde* 9: 382, pl. 87e.

**Elymnias kamara pseudalumna** Fruhstorfer, 1911. *TL*: Java (Indonesia: Java). *TS*: NHM. *Gross-Schmett. Erde* 9: 382.

ssp. *erinyes* de Nicéville, 1895. *comb. rev.*

**Elymnias (Melynias) erinyes** de Nicéville, 1895. *TL*: Battak Mountains (Indonesia: North Sumatra). *TS*: IM. *J. Bomb. nat. Hist. Soc.* 10 (1): 19, pl. R, figs 9–10.

**Elymnias kamara pseudalumna** Fruhstorfer, 1911. *TL*: Java (Indonesia: Java). *TS*: NHM. *Gross-Schmett. Erde* 9: 382.

**Elymnias kamara pareuploea** Fruhstorfer, 1911. *TL*: [Java] (Indonesia: Java). *TS*: NHM. *Gross-Schmett. Erde* 9: 382.

**Elymnias kamara lombokiana** Fruhstorfer, 1911. *syn. n.* *TL*: Lombok Island (Indonesia: West Nusa Tenggara, Lombok). *TS*: NHM. *Gross-Schmett. Erde* 9: 383.

ssp. *exclusa* de Nicéville, 1898. *comb. n.*

**Elymnias (Melynias) exclusa** de Nicéville, 1898. *TL*: Bali (Indonesia: Bali). *TS*: IM. *J. Asiat. Soc. Bengal, Part II* 66 (4): 681.

**Elymnias casiphone djilantik** Martin, 1909, *syn. n.* *TL*: Bali (Indonesia: Bali). *TS*: NHMT. *Dt. ent. Z. Iris* 22 (1): 49.

**Elymnias casiphone djilantik** Martin, 1909, *syn. n.* *TL*: Bali (Indonesia: Bali). *TS*: NHMT. *Dt. ent. Z. Iris* 22 (1): 49.

**Elymnias casiphone alumna** Fruhstorfer, 1907. *TL*: East Java (Indonesia: East Java). *TS*: NHM. *Dt. ent. Z. Iris* 20 (3): 209.

**malelas** (Hewitson, 1863) *44*

Specimens: Fig. 14A–D; Male Genitalia: Fig. 24M; Distribution: Fig. 53

ssp. *malelas* (Hewitson, 1863)

**Melanitis malelas** Hewitson, 1863. *TL*: East India. *TS*: NHM. *Ill. exot. Butts.* 4: [70], pl. [36], f. 6–7.

**Elymnias malelas malelas** ab. *subdecorata* Fruhstorfer, 1911. *unavailable name.*

**TL**: Assam (India: Meghalaya). *TS*: NHM. *Gross-Schmett. Erde* 9: 381.

**Elymnias malelas ivena** Fruhstorfer, 1911. *syn. n.* *TL*: Thailand, N. Vietnam. *TS*: NHM. *Gross-Schmett. Erde* 9: 381.

Having compared the original drawing of *casiphone* and the specimens from Java, Sumatra, Bali and Lombok, we conclude that the color pattern of the Javanese population matches well with Geyer’s figure.

**de Nicéville’s erinyes** was originally described as a full species, and then downgraded to be a subspecies of *casiphone* by Fruhstorfer (1907) or *kamara* (Corbet et al. 1992). Since we now consider this subspecies should be associated with *casiphone*, Fruhstorfer’s combination should be revived.

Since we regard *kamara* as a junior synonym of *casiphone*, the name *lombokiana*, originally described as a subspecies of *kamara*, is treated as a new junior synonym of *praetextata* in the present study.

Martin’s *djilantik* and de Nicéville’s *exclusa* were previously placed under *casiphone* and *kamara*, respectively. We regard them as different color forms.

We examined many specimens from northeast India to Vietnam and found no consistent morphological differences to support the current subspecies classification. We therefore synonymize *ivena* and *nilamba* with *malelas.*
**Elymnias malelas nilamba** Fruhstorfer, 1911. **syn. n.** **TL:** India. **TS:** NHM. *Gross-Schmett. Erde* 9: 381.

*saueri* Distant, 1882\(^{45}\)
Specimens: Fig. 14E–F; Distribution: Fig. 54

ssp. *saueri* Distant, 1882
*Elymnias saueri* Distant, 1882. **TL:** Malaysia, Province Wellesley (Peninsular Malaysia: Penang, Seberang Perai). **TS:** NHM. *Rhopalocera Malayana* p. 65, pl. 9, fig. 3.

*kochi* Semper, 1887\(^{46}\)
Specimens: Fig. 14G–H; Male Genitalia: Fig. 24N; Distribution: Fig. 55

ssp. *kochi* Semper, 1887
*Elymnias kochi* Semper, 1887. **TL:** Philippines: Central Luzon. **TS:** SMFD. *Reisen Philipp.* (2) 55: 63, pl. 12, fig. 4.

*casiphonides* Semper, 1892\(^{47}\)
Specimens: Fig. 14I–J; Male Genitalia: Fig. 24O; Distribution: Fig. 56

ssp. *casiphonides* Semper, 1892
*Elymnias casiphonides* Semper, 1892. **TL:** Philippines: Mindanao. **TS:** SMFD. *Reisen Philipp.* (7): 330.

ssp. *sanrafaela* Schröder & Treadaway, 1980
*Elymnias casiphonides sanrafaela* Schröder & Treadaway, 1980. **TL:** Philippines: Samar, San Rafael **TS:** SMFD. *Ent. Z.* 90 (21): 238, fig. 3.

*nelsoni* Corbet, 1942
Specimens: Fig. 14K–L; Male Genitalia: Fig. 25A; Distribution: Fig. 57

ssp. *nelsoni* Corbet, 1942
*Elymnias nelsoni* Corbet, 1942. **TL:** Mentawei Islands (Indonesia: West Sumatra, Mentawai Islands). **TS:** NHM. *Ann. Mag. nat. Hist.* (11) 9 (56): 612, fig. 5.

*amoena* Tsukada & Nishiyama, 1979
Specimens: Fig. 14M; Distribution: Fig. 58

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\(^{45}\) Distant’s *saueri* was originally described as a full species and then placed under *casiphone* as a subspecies by Fruhstorfer (1907) due to the similarity in wing pattern. Recently, Araya and Saito (2014) separated them into two morphologically defined species. Our phylogenetic analysis reveals that these taxa are not even sister to each other. The sister species of *saueri* is *saola*, and we therefore affirm the species status of *saueri*.

\(^{46}\) Semper (1887) described *kochi* as a full species, while Fruhstorfer downgraded it to be a subspecies of *beza* due to the similarity of their wing patterns. Treadaway and Schroeder (2012) considered *kochi* a full species, and our phylogenetic study places *kochi* as the sister group of *kanekoi* from Negros, so its status as a full species is upheld.

\(^{47}\) The physiognomy of *casiphonides* is remarkably similar to female *casiphone* and female *malelas*, however, our molecular phylogenetic study places it as the sister group of *nesaea*. The similarity is almost certainly the result of these different lineages mimicking the same widespread model: female *Euploea mulciber*. 
ssp. amoena Tsukada & Nishiyama, 1979
_Elymniass amoena_ Tsukada & Nishiyama, 1979. **TL:** Sumba (Indonesia: East Nusa Tenggara, Sumba). **TS:** TPC. Mem. Tsukada Coll. 1: 15, figs 19–20.

_kanekoi_ Tsukada & Nishiyama, 1980
Specimens: Fig. 14N–O; Male Genitalia: Fig. 25B; Distribution: Fig. 59
ssp. _kanekoi_ Tsukada & Nishiyama, 1980
_Elymniass kanekoi_ Tsukada & Nishiyama, 1980. **TL:** north Negros (Philippines: Negros Occidental). **TS:** TPC. Mem. Tsukada Coll. 2: 14, f. 8–9, 14

_saola_ Monastyrskii, 2004
Specimens: Fig. 14P; Distribution: Fig. 60
ssp. _saola_ Monastyrskii, 2004
_Elymniass saola_ Monastyrskii, 2004. **TL:** Vietnam: Nghe An Province, Pu Mat Nature Reserve. **TS:** NHM. _Atalanta_ 35 (1/2): 45, pl. 2a, figs 1–2; fig. 1A, 3

_melias_-group

_melias_ (C. & R. Felder, 1863)
Specimens: Fig. 15A–D; Male Genitalia: Fig. 25C; Distribution: Fig. 61
ssp. _melias_ (C. & R. Felder, 1863)
_Melanitiss melias_ C. & R. Felder, 1863. **TL:** Lugban (Philippines: Luzon, Quezon, Lucban) and Burias Island (Philippines: Masbate, Burias Island). **TS:** NHMW. Wien. ent. Monats. 7 (4): 120.
ssp. _malis_ Semper, 1887
_Elymniass melias malis_ Semper, 1887. **TL:** Casiguran (Philippines: Central Luzon, Aurora, Casiguran). **TS:** SMFD. _Reisen Philipp._ (2): 62, pl. 12, figs 2–3.
_Elymniass palmifolia_ Schultze, 1908. **TL:** Cagayang (Philippines: Northern Luzon, Cagayan). **TS:** ECMP. _Philipp. J. Sci_ 3 (1): 27, pl. 1, fig. 1.

_bezav_ (Hewitson, 1877)
Specimens: Fig. 15E–F; Male Genitalia: Fig. 25D; Distribution: Fig. 62.
ssp. _beza_ (Hewitson, 1877)
_Melanitiss beza_ Hewitson, 1877. **TL:** Philippines: Mindanao. **TS:** NHM. _Ent. Mon. Mag._ 13: 179.

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48 According to the current taxonomy, two subspecies of _melias_ are recognized and distributed in Luzon, and it seems unusual for a single island to harbor more than one subspecies. The biotic regions of Luzon, however, are complex. The northern Sierra Madre mountains may serve as a geographical barrier within the island as suggested by Vallejo (2014).
Elymnias kochi plateni Fruhstorfer, 1907. syn. n. TL: Philippines: Mindanao. TS: NHM. Dr. ent. Z. Iris 20 (3): 228.49

ssp. samarana Schröder & Treadaway, 1980
Elymnias beza samarana Schröder & Treadaway, 1980. TL: Philippines: Samar, San Rafael. TS: SMFD. Ent. Z. 90 (21): 236, fig. 2.

sansoni Jumalon, 1975
Specimens: Fig. 15G–J; Male Genitalia: Fig. 25E; Distribution: Fig. 63

ssp. sansoni Jumalon, 1975
Elymnias sansoni Jumalon, 1975. TL: Philippines: Negros. TS: JPC. Trans. Lep. Soc. Jpn. 26 (2): 47.

ssp. aklanensis Uémura & Kitamura, 2001
Elymnias sansoni aklanensis Uémura & Kitamura, 2001. TL: Philippines: Panay, Aklan Province, Makato, Castillo. TS: TME. Butterflies 29: 5.

luteofasciata Okubo, 1980
Specimens: Fig. 15K–L; Distribution: Fig. 64
Elymnias luteofasciata Okubo, 1980. TL: Philippines: Mindanao, Davao, Penangudloton, Upian River, Calinan. TS: OPC. Tyô to Ga 31 (1,2): 60.

vitellia-group

vitellia (Stoll, [1781])
Specimens: Fig. 15M–P; Male Genitalia: Fig. 25F–G; Distribution: Fig. 65

ssp. vitellia (Stoll, [1781])
Papilio vitellia Stoll, [1781]. TL: Ambon (Indonesia: Maluku, Ambon). TS: unknown. Uitl. Kapellen. 4 (30): 116, pl. 349, fig. E–F.
Melanitis stellaris Snellen van Vollenhoven, 1861. TL: [New Guinea]. TS: NBC. Tijdschr. Ent. 4 (5/6): 159, pl. 8, fig. 3.
Elymnias vitellia f. basium Fruhstorfer, 1907. unavailable name. TL: Saparua (Indonesia: Maluku, Saparau). TS: NHM. Dr. ent. Z. Iris 20 (3): 230.
Elymnias vitellia ceramensis Martin, 1909. TL: Ceram (Indonesia: Maluku, Seram). TS: NHMT. Dt. ent. Z. Iris 22 (1): 65.

ssp. viminalis Wallace, 1869
Elymnias viminalis Wallace, 1869. TL: Buru Island (Indonesia: Maluku, Buru). TS: NHM. Trans. ent. Soc. Lond. 1869 (4): 328.

49 Fruhstorfer (1907) placed plateni as a subspecies of kochi, but our molecular phylogenetic analysis reveals that kochi is the sister species of kanekoi. Therefore, plateni should be synonymized with the nominotypical beza, which is a member of the melias group.
agondas (Boisduval, 1832)\(^5\)
Specimens: Figs 16A–H, 17A–I, 18A–M, 19A–M; Male Genitalia: Fig. 25H–N; Distribution: Fig. 66

ssp. agondas (Boisduval, 1832)\(^5\)
_Dyctis agondas_ Boisduval, 1832. **TL:** Vanikoro (Solomon Islands: Temotu Province, Vanikoro). **TS:** unknown. Voy. Astrolabe. 1: 138.
_Dyctis bioculatus_ Westwood, 1851. **syn. n. TL:** Arfak Mountains (Indonesia: West Papua). **TS:** NHM. Gen. diurn. Lep. 2: 354, pl. 54, fig. 4.
_Elymnias agondas muscosa_ Fruhstorfer, 1907. **TL:** Kapaur (Indonesia: West Papua, Fakfak). **TS:** NHM. Dt. ent. Z. Iris 20 (3): 243.
_Elymnias agondas tampyra_ Fruhstorfer, 1907. **TL:** Kumusi River (Papua New Guinea: Northern Province, Kumusi River). **TS:** NHM. Ent. Rundschau 31 (5): 25.
_Elymnias agondas hagias_ Fruhstorfer, 1914. **TL:** Eilandenfluß (Indonesia: Papua, Pulau River). **TS:** NHM. Ent. Rundschau 31 (5): 25

ssp. melane (Hewitson, 1858)
_Melanitis melane_ Hewitson, 1858. **TL:** [Key Island] (Indonesia: Maluku, Kei Island). **TS:** NHM. Proc. zool. Soc. Lond. 1858: 465, pl. 55, figs 2, 4.
_Elymnias (Dyctis) mela_ de Nicéville, 1902. **TL:** Key Island (Indonesia: Maluku, Kei Island). **TS:** IM. J. Bomb. nat. Hist. Soc. 14 (2): 238, pl. FF, figs 4–5.
_Elymnias (Dyctis) meletus_ de Nicéville, 1902. **TL:** Key Island (Indonesia: Maluku, Kei Island). **TS:** IM. J. Bomb. nat. Hist. Soc. 14 (2): 241.
_Elymnias (Dyctis) melitia_ de Nicéville, 1902. **TL:** Key Island (Indonesia: Maluku, Kei Island). **TS:** IM. J. Bomb. nat. Hist. Soc. 14 (2): 242.

ssp. melantho Wallace, 1869
_Elymnias melancho_ Wallace, 1869. **TL:** Gagie Island (Indonesia: West Papua, Raja Ampat Regency, Gag Island). **TS:** NHM. Trans. ent. Soc. Lond. 1869 (4): 330.

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\(^5\) The species _agondas_ has long been considered a highly variable species, the females of which mimic various _Taenaris_ spp. throughout its range in New Guinea and the surrounding islands. Our phylogenetic analysis, however, reveals that _thryallis_, which was currently placed as a subspecies of _cybele_, is nested within _agondas_, and the branch support for this relationship is strong. We therefore conclude that both _agondas_ and _cybele_ are not monophyletic species as currently circumscribed. We sink _thryallis_ into _agondas_, thus forming a monophyletic species, but further clarification of the subspecific nomenclature is difficult because of the myriad described taxa, vague descriptions of many type localities (frequently “New Guinea”), and our lack of access to material of several rare “subspecies” of _agondas_, _cybele_, and other members of the species group.

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\(^5\) The true identity of _agondas_ is mysterious. Boisduval stated that the source of the type specimen was the Solomon Islands (Boisduval 1832: 138, pl. 3, fig. 5). However, no _Elymnias_ are known from the Solomon Islands at present (Tennent 2002), and the easternmost point in the range of this species is Woodlark Island in Milne Bay Province, Papua New Guinea—approximately 350 km from the Solomon Islands across the Solomon Sea. Although the circumscription of “Solomon Islands” has changed throughout history, an area with that name has never included Woodlark Island. Bougainville Island can be included in the Solomon Islands, but _Elymnias agondas_ has never been found there. The original drawing of _agondas_ is a male, and since the highly variable wing pattern of male _agondas_ is not a reliable diagnostic character, we tentatively retain the nominotypical _agondas_ as a taxon with questionable geographical provenance, but the nominal subspecies should not be applied to any population until the true collection locality of the type can be discerned.
Elymnias agondas moranda Fruhstorfer, 1904. TL: Waigeu (Indonesia: West Papua, Raja Ampat Regency, Waigeo). TS: NHM. Dt. ent. Z. Iris 16 (2): 322.

ssp. glaucopis Staudinger, 1894
Elymnias glaucopis Staudinger, 1894. TL: Sattelberg (Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg). TS: ZMHB. Dt. ent. Z. Iris 7 (1): 116.

Elymnias agondas glaucopis Fruhstorfer, 1907. TL: New Guinea. TS: NHM. Dt. ent. Z. Iris 20 (3): 243.

ssp. melanippe Grose-Smith, 1894
Elymnias melanippe Grose-Smith, 1894. TL: Sattelberg (Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg). TS: NHM. Novit. Zool. 1 (3): 587.

Elymnias vertenteni Hulstaert, 1925. TL: Irian Jaya (Indonesia: Papua or West Papua). TS: NBC. Ann. Mag. nat. Hist. (9) 15 (88): 447.

ssp. melanthes Grose-Smith & Kirby, 1897
Elymnias melanthes Grose-Smith & Kirby, 1897. TL: Woodlark Island (Papua New Guinea: Milne Bay, Woodlark Island). TS: NHM. Ann. Mag. nat. Hist. (6) 19: 178.

Elymnias agondas melanthes f. infernalis (♀) Fruhstorfer, 1914. TL: Not indicated. TS: NHM. Ent. Rundschau 31 (5): 26.

Elymnias agondas melanthes f. virginalis (♀) Fruhstorfer, 1914. TL: Not indicated. TS: NHM. Ent. Rundschau 31 (5): 26.

ssp. melagondas Fruhstorfer, 1900
Elymnias melagondas Fruhstorfer, 1900. TL: New Guinea. TS: NHM. Stett. ent. Ztg. 60 (10-12): 339.

Elymnias agondas melagondas f. taenarides (♀) Fruhstorfer, 1914. TL: Milnebai (Papua New Guinea: Milne Bay). TS: NHM. Ent. Rundschau. 31 (5): 26.

ssp. australiana Fruhstorfer, 1900
Elymnias australiana Fruhstorfer, 1900. TL: Cape York (Australia: Queensland, Cape York). TS: NHM. Stett. ent. Ztg. 60 (10-12): 339.

ssp. aruana Fruhstorfer, 1900
Elymnias aruana Fruhstorfer, 1900. TL: Aru (Indonesia: Maluku, Indonesia). TS: NHM. Stett. ent. Ztg. 60 (10-12): 341.

ssp. goramensis Fruhstorfer, 1900
Elymnias goramensis Fruhstorfer, 1900. TL: Goram Island (Indonesia: Maluku, East Seram Regency, Gorong Island). TS: NHM. Stett. ent. Ztg. 60 (10-12): 341.

ssp. agondina Fruhstorfer, 1904
Elymnias agondina Fruhstorfer, 1904. TL: Salewatti (Indonesia: West Papua, Raja Ampat Islands, Salawati). TS: NHM. Dt. ent. Z. Iris 16 (2): 322.

ssp. dampierensis Rothschild, 1915
Elymnias dampierensis Rothschild, 1915. TL: Dampier (Papua New Guinea: Madang, Karkar Island). TS: NHMT. Novit. Zool. 22 (2): 201.

ssp. multocellata van Eecke, 1915
Elymnias multocellata van Eecke, 1915. TL: Kloofbivak (Indonesia: Papua). TS: NBC. Nova Guinea 13 (1): 66, pl. 3, f. 6.
Elymnias thryallis Kirsch, 1876. **comb. n.**
*Elymnias thryallis* Kirsch, 1876. **TL**: Mysore, Kordo (Indonesia: Papua, Biak). **TS**: SMTD. *Mitt. zool. Mus. Dresden* 1: 119, pl. 6, fig. 4.

*Elymnias glauconia* Staudinger, 1894. **TL**: Kubary (Papua New Guinea: Jiwaka, Mt. Kubari). **TS**: ZMHB. *Dt. ent. Z. Iris* 6 (2): 362, pl. 6, fig. 2.

*Elymnias glauconia* var. *chloera* Staudinger, 1894. **TL**: New Guinea. **TS**: ZMHB. *Dt. ent. Z. Iris* 6 (2): 363.

*Elymnias thryallis* f. *brunnescens* Fruhstorfer, 1911. **TL**: New Guinea. **TS**: NHM. *Gross-Schmett. Erde* 9: 389.

*Elymnias thryallis* f. *psuedosalpinx* Fruhstorfer, 1911. **TL**: New Guinea. **TS**: NHM. *Gross-Schmett. Erde* 9: 389.

*Elymnias thryallis* f. *terentilina* Fruhstorfer, 1911. **TL**: New Guinea. **TS**: NHM. *Gross-Schmett. Erde* 9: 389.

*Elymnias thryallis* f. *violacea* Fruhstorfer, 1911. **TL**: Waigiu Island (Indonesia: West Papua, Raja Ampat Regency, Waigeo). **TS**: NHM. *Gross-Schmett. Erde* 9: 389.

**cybele** (C. & R. Felder, 1860)

**Specimens**: Fig. 20A–F; Male Genitalia: Figs 25O, 26A; Distribution: Fig. 67

**ssp. cybele** (C. & R. Felder, 1860)**52**

*Melanitis cybele* C. & R. Felder, 1860. **TL**: Batschian Island (Indonesia: North Maluku, Bacan). **TS**: NHMW. *Wien. ent. Monats.* 4 (8): 248.

*Dyctis astrifera* Butler, 1874. **TL**: Batchian (Indonesia: North Maluku, Bacan). **TS**: NHM. *Trans. ent. Soc. Lond.* 1874 (4): 425.

*Elymnias cybele opaca* Fruhstorfer, 1907. **syn. n.** **TL**: Halmahera (Indonesia: North Maluku, Halmahera). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 229.

*Elymnias cybele ternatana* **syn. n.** Fruhstorfer, 1907. **TL**: Ternate (Indonesia: North Maluku, Ternate). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 229.

**ssp. obiana** Fruhstorfer, 1904

*Elymnias obiana* Fruhstorfer, 1904. **TL**: Obi Island (Indonesia: North Maluku, Obi). **TS**: NHM. *Dt. ent. Z. Iris* 16 (2): 321.

**ssp. adumbrata** Fruhstorfer, 1907. **subsp. rev.**53

*Elymnias cybele adumbrata* Fruhstorfer, 1907. **TL**: Buru (Indonesia: Maluku, Buru). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 228.

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52 Our phylogenetic analysis shows that *cybele cybele* from Bacan is nested within *cybele opaca* from Halmahera. Morphological examination failed to distinguish these two subspecies; we therefore synonymize them.

53 The subspecies *adumbrata* was described from Buru, but it was synonymized with the nominotypical *cybele* by previous authors. Since the wing pattern of *adumbrata* is different from that of *cybele*, and Buru island is presently ~280 km from Halmahera, we revive this subspecies from synonymy with *cybele cybele*. 
An illustrated checklist of the genus Elymnias Hübner, 1818 (Nymphalidae, Satyrinae)

**cumaea** (C. & R. Felder, [1867])

Specimens: Fig. 20G–H; Male Genitalia: Fig. 26B; Distribution: Fig. 68

**ssp. cumaea** (C. & R. Felder, [1867])

*Melanitis cumaea* C. & R. Felder, [1867]. **TL**: Halmahera (Indonesia: North Maluku Halmahera). **TS**: NHMW. *Reise. Fregatte. Novara*. 2 (3): 452, pl. 452., pl. 61, f. 9–10.

**ssp. thyone** Fruhstorfer, 1904. **comb. n., stat. n.**

*Elymnias thyone* Fruhstorfer, 1904. **TL**: [North Celebes] (Indonesia: North Sulawesi, Indonesia). **TS**: NHM. *Soc. Ent.* 19: 53.

**ssp. toliana** Fruhstorfer, 1899

*Elymnias cumaea toliana* Fruhstorfer, 1899. **TL**: Toli Toli (Indonesia: Central Sulawesi, Tolitoli). **TS**: NHM. *Berl. Ent. Zs.* 44 (1/2): 53.

**ssp. hewitsoni** Wallace, 1869

*Elymnias hewitsoni* Wallace, 1869. **TL**: Macassar (Indonesia: South Sulawesi, Makassar). **TS**: NHM. *Trans. ent. Soc. Lond.* 1869 (4): 327.

**ssp. meliophila** Fruhstorfer, 1896

*Elymnias meliophila* Fruhstorfer, 1896. **TL**: Saleyer (Indonesia: South Sulawesi, Selayar Islands, Selayar). **TS**: NHM. *Soc. Ent.* 11 (4): 25.

**ssp. atys** Fruhstorfer, 1904

*Elymnias hewitsoni atys* Fruhstorfer, 1904. **TL**: Bouthain, south Celebes (Indonesia: South Sulawesi, Moncong Lompobatang). **TS**: NHM. *Soc. Ent.* 19 (8): 60.

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54 According to our phylogenetic analysis, *cumaea* is not a monophyletic group and is part of a radiation on Sulawesi that includes *hicetas* and *hewitsoni*. The subspecies *phrikonis* is not allied with other *cumaea* subspecies, but comprises the sister group to a clade including *cybele*, *vitellia*, *holofernes* and *agondas*. We therefore elevate *phrikonis* to the species level. Fruhstorfer (1907) described *relicina* from Sanana (Sula Besi), and we consider this name should be synonymized with *phrikonis* as they are not different from each other morphologically.

55 Nomino-typical *cumaea* is only reported from Halmahera. We have not been able to obtain specimens for inclusion in the molecular phylogeny so we have no indication of how many subspecies previously associated with *cumaea* should be retained.

56 Having examined specimens of *thyone*, we conclude that this taxon should not be regarded as a junior synonym of *cumaea cumaea*, but we tentatively place *thyone* as a subspecies of *cumaea* pending molecular data for inclusion in a phylogenetic study.

57 In our phylogenetic study, a specimen from North Sulawesi identified as *toliana* is sister to *hicetas*, and this pair is sister to *bornemanni*, which we regard as a full species. Since we have no genetic data from nominotypical *cumaea*, we are unsure were to place this taxon and tentatively retain *toliana* as a subspecies of *cumaea*, even though this arrangement makes *cumaea* polyphyletic.
**mimalon** (Hewitson, 1861)
Specimens: Fig. 20K–N; Male Genitalia: Fig. 26D; Distribution: Fig. 70

**ssp. mimalon** (Hewitson, 1861)
*Melanitis mimalon* (Hewitson, 1861). **TL**: Toli-Toli (Indonesia: Central Sulawesi, Tolitoli). **TS**: NHM. Proc. zool. Soc. Lond. 1861: 52, pl. 9, figs 1–2.
*Elymnias mimalon mimalon* f. leucostigmata Fruhstorfer, 1907. **TL**: Toli-Toli (Indonesia: Central Sulawesi, Tolitoli). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 239.

**ssp. ino** Fruhstorfer, 1904
*Elymnias mimalon ino* Fruhstorfer, 1904. **TL**: Tawaya, Celebes (Indonesia: Central Sulawesi, Towaya). **TS**: NHM. Soc. Ent. 19 (7): 53.

**ssp. nysa** Fruhstorfer, 1907
*Elymnias mimalon nysa* Fruhstorfer, 1907. **TL**: South Celebes (Indonesia: South-east Sulawesi). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 239, pl. 7, fig. 5.

**bicetas** Wallace, 1869
Specimens: Fig. 20O–P; Male Genitalia: Figs 26E–F; Distribution: Fig. 71

**ssp. bicetas** Wallace, 1869
*Elymnias bicetas* Wallace, 1869. **TL**: Macassar, south Celebes (Indonesia: South Sulawesi, Makassar). **TS**: NHM. Trans. ent. Soc. Lond. 1869 (4): 327.
*Elymnias bicetas bonthainensis* Fruhstorfer, 1899. **syn. n. TL**: Bua Kraeng (Indonesia: South Sulawesi, Mt. Bawakaraeng). **TS**: NHM. Berl. ent. Zs. 44 (1/2): 55. 58

**ssp. bicetina** Fruhstorfer, 1904
*Elymnias bicetas bicetina* Fruhstorfer, 1904. **TL**: Tombugu (Indonesia: Central Sulawesi, Tombuko). **TS**: NHM. Soc. Ent. 19 (7): 53.

**ssp. butona** Fruhstorfer, 1904
*Elymnias bicetas butona* Fruhstorfer, 1904. **TL**: North Buton (Indonesia: South-east Sulawesi, Buton). **TS**: NHM. Soc. Ent. 19 (7): 53.

**ssp. rarior** Martin, 1929
*Elymnias bicetas rarior* Martin, 1929. **TL**: Celebes (Indonesia: Sulawesi). **TS**: NHMT. Mitt. münchn. ent. Ges. 19: 160.

**holofernes** (Butler, 1882)
Specimens: Fig. 21A–B; Male Genitalia: Fig. 26G; Distribution: Fig. 72
*Dyctis holofernes* Butler, 1882. **TL**: Duke-of-York Island (Papua New Guinea: East New Britain, Duke of York Island). **TS**: NHM. Ann. Mag. nat. Hist. 10 (55): 42.

58 Having examined the type specimens of *bonthainensis* and *bicetas*, we failed to find any distinguishing morphological characters. These two names are therefore synonymized.

59 Martin described *rarior* as a subspecies of *bicetas* without a clear indication of its type locality in Sulawesi. In our phylogenetic study, two specimens identified as *rarior* are paraphyletic with regard to *bicetas* and *butona*. Since the type locality of *rarior* is unclear, we retain *rarior* as a subspecies of *bicetas*. 
**bornemanni Ribbe, 1889.** stat. n.\(^6^0\)
Specimens: Fig. 21C–D; Male Genitalia: Fig. 26H; Distribution: Fig. 73
_Elymnias bornemanni_ Ribbe, 1889. **TL:** Bangkai (**Indonesia:** Central Sulawesi, Banggai). **TS:** SMTD (?). *Dt. ent. Z. Iris* 2 (1): 183, pl. 3, f. 1–2.

**phrikonis Fruhstorfer, 1899.** stat. n.\(^6^1\)
Specimens: Fig. 21E–F; Male Genitalia: Fig. 26I; Distribution: Fig. 74
_Elymnias cumaea phrikonis_ Fruhstorfer, 1899. **TL:** Sula Besi and Sula-Mangoli (**Indonesia:** North Maluku, Sula Islands, Sanana and Mangole). **TS:** NHM. *Berl. ent. Zs.* 44 (1/2): 53.
_Elymnias cumaea relicina_ Fruhstorfer, 1907. **syn. n.** **TL:** Sula Besi (**Indonesia:** North Maluku, Sula Islands, Sanana). **TS:** NHM. *Dt. ent. Z. Iris* 20 (3): 234.

**sangira Fruhstorfer, 1899**
Specimens: Fig. 21G–H; Male Genitalia: Fig. 26J; Distribution: Fig. 75
_Elymnias cumaea sangira_ Fruhstorfer, 1899. **TL:** Sangir, Sulawesi (**Indonesia:** North Sulawesi, Sangihe Islands, Sangir Besar). **TS:** NHM. *Berl. ent. Zs.* 44 (1/2): 54.

**umbratilis Joicey & Noakes, 1915.** stat. n.\(^6^2\)
Specimens: Fig. 21I–J; Male Genitalia: Fig. 26K; Distribution: Fig. 76
_Elymnias cybele umbratilis_ Joicey & Noakes, 1915. **TL:** Biak (**Indonesia:** Papua, Biak). **TS:** NHM. *Trans. ent. Soc. Lond.* 1915 (2): 195.

**resplendens Martin, 1929.** stat. n.\(^6^3\)
Specimens: Fig. 21K–L; Male Genitalia: Fig. 26L; Distribution: Fig. 77
_Elymnias cumaea resplendens_ Martin, 1929. **TL:** Celebes (**Indonesia:** Sulawesi). **TS:** NHMT. *Mitt. münchn. ent. Ges.* 19: 162.

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\(^6^0\) The situation of _bornemanni_ is similar to that of _phrikonis_. It is not closely related to other _cumaea_ subspecies, so we treat it as a full species.

\(^6^1\) _phrikonis_ has been regarded as a subspecies of _cumaea_. Our phylogenetic analysis, however, places it as the sister to a clade consisting of _cybele, holofernes, umbratilis, vitellia_, and _agondas_. We therefore elevate _phrikonis_ to full species status. Since _relicina_ was described from the same locality as _phrikonis_ we synonymize these two names in the present study.

\(^6^2\) _Elymnias cybele umbratilis_ was originally described based on five syntypes from Biak and synonymized with _thryallis_ by subsequent authors. Our phylogenetic analysis, however, reveals that _umbratilis_ is a distinct taxon, not closely related to any subspecies of _cybele_, and sister to _holofernes_. We therefore revive this taxon and give it full species status.

\(^6^3\) Martin (1929) placed _resplendens_ with _cumaea_, but our analysis suggests that _resplendens_ is closely related to _bewitsoni_ and deserves full species status.
Species not placed in any group

**singhala** Moore, [1875]

Specimens: Fig. 21M–N; Male Genitalia: Fig. 26M; Distribution: Fig. 78

*Elymnias singhala* Moore, [1875]. **TL:** Colombo, Ceylon (Sri Lanka: Western Province, Colombo). **TS:** NHM. *Proc. zool. Soc. Lond.* 1874 (4): 568.

**Discussion**

Wing patterns of *Elymnias* butterflies appear to be highly evolvable, which facilitates Batesian mimetic resemblance to a variety of phenotypically dissimilar model species. Many *Elymnias* are found on islands in the Indo-Australian Archipelago, and the isolation provided by islands seems to provide the opportunity for divergence and local adaptation, facilitating resemblance to different model species in different locales. The remarkable capacity for phenotypic evolution of wing patterns has resulted in sexually dimorphic mimicry, convergence of distantly related taxa on similar wing patterns, and marked phenotypic divergence among conspecific populations. These phenomena have previously confounded attempts to produce an accurate taxonomic framework because few if any morphological characters are taxonomically or phylogenetically informative. Wing veination, male genitalia, and female genitalia are remarkably uniform among species of *Elymnias*; only slight variation in male genitalia might be useful for discriminating some species. Species delimitation and diagnosis in *Elymnias* has therefore traditionally relied almost entirely on wing patterns. Our molecular phylogeny, which uses genetic markers presumed to be unrelated to wing phenotypes, has detected multiple instances of similar wing patterns in non-sister *Elymnias* lineages that mimic the same, widespread model species. This similarity seems to be the result of convergent evolution, and we have therefore split these taxa into two or more monophyletic lineages (*e.g.*, *E. cumaea* and *E. cybele* have each been split into four and three different species, respectively). On the other hand, some *Elymnias* species—like other mimetic butterfly taxa (Kunte et al. 2014; Merrill et al. 2015; Thompson and Timmermans 2014)—are polymorphic, with single species expressing different mimetic phenotypes in allopatric populations where they mimic different models. We have identified several instances of one nominal species nested within another, and synonymize these taxa under a single species name (*e.g.*, *E. cottonis* into *E. hypermnestra* and *E. cybele thryallis* into *E. agondas*).

Strong dimorphism caused many early workers to describe males and females as separate species, most of which have been synonymized. In this paper we confirmed

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64 We have been unable to obtain DNA sequence data from our tissue samples of *singhala* from old museum specimens. This species is probably not closely related to either the *hypermnestra* or *harterti* species group, but its true species group affinity cannot be deduced at this time.
Araya’s (2016) conclusion of synonymizing E. detanii, known only from males, into E. nepheronides, known only from females; this rare species is known only from the Indonesian islands of Flores and Sumbawa. Similarly, E. vasudeva oberthurii has been sunk into E. esaca andersonii, as these apparently represent different sexes of the same species.

Females of several Elymnias species, including E. agondas, E. hypermnestra, and E. esaca, are morphologically variable across their range. Rather than recognize every wing pattern variant as a different subspecies, we have synonymized many subspecies into geographically cohesive taxa, for example, within the islands of Borneo or New Guinea.

Much of the mismatch between Elymnias’ previous taxonomic framework and its evolutionary history is due to rapid evolutionary change. This resulted in morphologically-delimited nominal species that were polyphyletic. In these cases, our molecular phylogenetic results make delimiting species relatively straightforward. However, there are several cases that are not as clear-cut. For example, we elected to retain E. esaca and E. vasudeva as distinct species despite their paraphyletic relationship because of marked, species-specific morphological differences in these two parapatrically distributed taxa. Population genetic theory predicts incomplete lineage sorting of genetic loci to persist for some time after speciation, resulting in paraphyletic species; the probability of reciprocal monophyly increases with time since divergence (Avise and Ball 1990). Thus, requiring all species to be monophyletic would underestimate true species diversity (Hickerson et al. 2006), particularly in recently diverged species (Knowles and Carstens 2007) such as esaca and vasudeva. However, we decided to sink E. kamara into E. casiphone despite their morphological differences because both taxa are wholly sympatric and because morphologically intermediate specimens are known. We included four specimens of E. c. casiphone and four of E. “kamara” from Java, Bali, and Lombok in our molecular phylogeny, and the topology of all genetic loci individually and together clearly indicated these taxa were conspecific. We suspect that a genetic switch is responsible for the distinct pair of E. casiphone casiphone male and female phenotypes (which mimic Euploea mulciber males and females) and the different, sexually dimorphic forms of E. casiphone kamara, which mimic other Euploea species.

Our molecular phylogeny identifies several examples of allopatrically or parapatrically distributed populations that form distinct, monophyletic sister groups: E. sansoni sansoni on Negros and E. sansoni aklanensis on Panay; E. patna from India and E. patna from peninsular Malaysia; E. vitellia vitellia from Seram and E. vitellia viminalis from Buru; and E. hypermnestra from Java and the Lesser Sundas and E. hypermnestra from everywhere else. These monophyletic sister lineages would likely be considered different species under a strict phylogenetic species concept, and, in most cases, preliminary Bayesian species delimitation analyses with the program Bayesian Phylogenetics and Phylogeography (BPP; Yang and Rannala 2010) suggest the sister lineages are different species. However, we refrain from splitting these species because we regard the geographic sampling of our phylogenetic work as too sparse, consider the degree of phylogenetic distance between the lineages to be too small, or otherwise fail to find convincing evidence that
reciprocal monophyly is the result of anything more than geographical isolation. In addition, a recent simulation study suggests that programs such as BPP delimit population structure, not species (Sukumaran and Knowles 2017). Further work may find convincing evidence to split one or more of these pairs into two species.

Although there is one African and several mainland Asian species, most of Elymnias’ diversity is found on the islands of the Indo-Australian Archipelago. Islands are considered laboratories for the study of evolution because they promote isolation and divergence while simplifying the task of delimiting populations and other taxa. Evolutionary study of this taxon provides an excellent opportunity to study the role of archipelagoes in diversification, and the evolutionary genetics of evolutionary novelty and speciation.

**List of taxonomic changes**

**New synonyms**

*Elymnias papua bivittata* van Eecke, 1915, of *Elymnias papua papua* Wallace, 1869
*Elymnias* (Mimadelias) *esaca taeniola* Fruhstorfer, 1907, of *Elymnias esaca borneensis*, Wallace, 1869
*Elymnias* (Mimadelias) *oberthuri* Fruhstorfer, 1902, of *Elymnias esaca andersonii* (Moore, 1885)
*Elymnias thycana* Wallace, 1869, of *Elymnias vasudeva vasudeva* Moore, 1857
*Mimadelias deva* Moore, 1894, of *Elymnias vasudeva vasudeva* Moore, 1857
*Mimadelias burmensis* Moore, 1893, of *Elymnias vasudeva vasudeva* Moore, 1857
*Elymnias vacuera [sic] sinensis* Chou, Zhang & Xie, 2000, of *Elymnias vasudeva vasudeva* Moore, 1857
*Melanyias patnoides* Moore, 1893, of *Elymnias patna patna* (Westwood, 1851)
*Elymnias patna stictica* Fruhstorfer, 1902, of *Elymnias patna patna* (Westwood, 1851)
*Elymnias kuenstleri mariae* Toxopeus, 1936, of *Elymnias kuenstleri* Honrath, [1885]
*Elymnias nigrescens tonkiniana* Fruhstorfer, 1902, of *Elymnias hypermnestra hainana* Moore, 1878
*Elymnias hypermnestra nigrescens* f. *depicta* Fruhstorfer, 1907, of *Elymnias hypermnestra hainana* Moore, 1878
*Elymnias hypermnestra septentrionalis* Chou & Huang, 1994, of *Elymnias hypermnestra hainana* Moore, 1878
*Elymnias smithi* Moulton, 1915, of *Elymnias harterti brookei* Shelford, 1904
*Elymnias panthera* var. *labuana* Staudinger, 1889, of *Elymnias panthera lutescens* Butler, 1867
*Elymnias panthera lacrima* Fruhstorfer, 1904, of *Elymnias panthera lutescens* Butler, 1867
*Elymnias defasciata* Fruhstorfer, 1911, of *Elymnias panthera lutescens* Butler, 1867
*Elymnias panthera alfredi* Fruhstorfer, 1907, of *Elymnias panthera lutescens* Butler, 1867
*Elymnias congruens photinus* Fruhstorfer, 1907, of *Elymnias congruens congruens* Semper, 1887
Elymnias congruens phaios Fruhstorfer, 1907, of Elymnias congruens congruens Semper, 1887
Elymnias congruens rafaela Fruhstorfer, 1907, of Elymnias congruens congruens Semper, 1887
Elymnias nesaea hermia Fruhstorfer, 1907, of Elymnias nesaea nesaea (Linnaeus, 1764)
Elymnias nesaea cortona Fruhstorfer, 1911, of Elymnias nesaea timandra Wallace, 1869
Elymnias nesaea coelifrons Fruhstorfer, 1907, of Elymnias nesaea hypereides Fruhstorfer, 1903
Elymnias kamara Moore, [1858], of Elymnias casiphone casiphone Geyer, [1827]
Elymnias kamara lombokiana Fruhstorfer, 1911, of Elymnias casiphone praetextata Fruhstorfer, 1896
Elymnias casiphone djilantik Martin, 1909, of Elymnias casiphone exclusa de Nicéville, 1898
Elymnias malelas ivena Fruhstorfer, 1911, of Elymnias malelas malelas (Hewitson, 1863)
Elymnias malelas nilamba Fruhstorfer, 1911, of Elymnias malelas malelas (Hewitson, 1863)
Elymnias kochi plateni Fruhstorfer, 1907, of Elymnias beza beza (Hewitson, 1877)
Dyctis bioculatus Westwood, 1850, of Elymnias agondas agondas (Boisduval, 1832)
Elymnias cybele opaca Fruhstorfer, 1907, of Elymnias cybele cybele (C. & R. Felder, 1860)
Elymnias cybele ternata Fruhstorfer, 1907, of Elymnias cybele cybele (C. & R. Felder, 1860)
Elymnias hicetas bonthainensis Fruhstorfer, 1899, of Elymnias hicetas hicetas Wallace, 1869
Elymnias cumaea relicina Fruhstorfer, 1907, of Elymnias phrikonis Fruhstorfer, 1899

New combinations
Elymnias hypermnestra cottonis (Hewitson, 1874) (Melanitis cottonis)
Elymnias hypermnestra beatrice Fruhstorfer, 1902 (Elymnias nigrescens beatrice)
Elymnias hypermnestra jennifferae Suzuki, 2006 (Elymnias cottonis jennifferae)
Elymnias panthera lutescens Butler, 1867 (Elymnias lutescens)
Elymnias casiphone exclusa de Nicéville, 1898 (Elymnias (Melynias) exclusa)
Elymnias agondas thryallis Kirsch, 1876 (Elymnias thryallis)
Elymnias cumaea thyone Fruhstorfer, 1904 (Elymnias thyone)

Resurrected combination
Elymnias casiphone erinyes de Nicéville, 1895

Resurrected subspecies
Elymnias cybele adumbrata Fruhstorfer, 1907

Status changes
Elymnias ceryxoides de Nicéville, 1895 stat. rev.
Elymnias panthera lutescens Butler, 1867 stat. n.
Elymnias cumaea thyone Fruhstorfer, 1904 stat. n.
*Elymnias bornemanni* Ribbe, 1889 stat. n.
*Elymnias phrikonis* Fruhstorfer, 1899 stat. n.
*Elymnias umbratilis* Joicey & Noakes, 1915 stat. n.
*Elymnias resplendens* Martin, 1929 stat. n.

**Incertae sedis**
*Elymnias merula* Swinhoe, 1915
*Elymnias leucocyna* Godart, 1819

**Species not placed in any group**
*Elymnias singhala* Moore, [1875]

**Plates**

**Format of each legend for specimen figures (1–22):**
valid species or subspecies name_♂♀_dorsal/ventral_specimen repository_current name of collection locality (COUNTRY: State/Province, Locality). D = dorsal; V = Ventral; ♂ = male ♀ = female.

**Format of each legend for male genitalia figures (22–26):**
valid species or subspecies_specimen repository_current locality name.

See pages 4–5 for abbreviations of specimen repositories.

Each distribution map (Figs 27–78) indicates the subspecies distributions for a single species. The species name is indicated in the lower left corner, and subspecies distributions are indicated with different colors. Red dots indicate the species type locality and black dots indicate subspecies type localities. If the type locality is vague, then the dot is positioned in the center of the area specified. Type localities are not indicated on small islands, where a dot would obscure the landmass on the map.
Figure 1. A bammakoo bammakoo ♂ D NHM central Africa B bammakoo bammakoo ♀ D NHM collection locality unknown C bammakoo bammakoo ♂ D NMNH Central African Republic: Bangui D bammakoo rattrayi ♂ D NMNH Uganda: Bwamba E paradoxa ♂ D NHM Indonesia: Papua, Weyland Mountains F paradoxa ♀ D NHM Indonesia: Papua, Weyland Mountains G papua papua ♂ D NHM Indonesia: Papua, Yog Sudarso Bay; Syntype of Elymnias papua viridescens H papua papua ♀ D NHM Indonesia: Papua, Yog Sudarso Bay; Syntype of Elymnias papua viridescens I papua papua ♂ D NHM Papua New Guinea J papua papua ♀ D NHM Papua New Guinea K papua cinereomargo ♂ D NHM Indonesia: Papua, Biak L papua cinereomargo ♀ D NHM Indonesia: Papua, Biak M papua lactentia ♂ D NHM Indonesia: West Papua, Raja Ampat Regency, Waigeo N esaca andersonii ♂ D KUTH Thailand: Yala, Than To O esaca maheswara ♂ D NHM Indonesia: Java P esaca maheswara ♀ D NHM Indonesia: Java.
Figure 2. A eoteca leontina ♂ D+V NHM Indonesia: North Sumatra, Nias B eoteca leontina ♀ D+V NHM Indonesia: North Sumatra, Nias C eoteca eoteca ♂ D KUTH Thailand: Yala, Than To D vasudeva ♂ D KUTH Thailand: Kanchanburi, Sri Sawat E vasudeva ♀ D KUTH Thailand: Chaiyaphum, Phu Khieo F vasudeva ♂ D+V NHM India: Assam G vasudeva ♀ D+V NHM India: Assam H vasudeva ♂ D NHM India: Meghalaya, Khasi Hills I vasudeva ♀ D NHM India: Meghalaya, Khasi Hills J vasudeva ♂ D DNPFIC Thailand: Kanchanaburi K vasudeva ♀ D NHM India: Assam.
Figure 3. A dara bengena ♂ D NHM Indonesia: West Java B dara bengena ♀ D NHM Indonesia: West Java C dara daedalion ♂ D NHM Myanmar D dara daedalion ♀ D NHM Myanmar E patna patna ♂ D NHM India: Sikkim F patna patna ♀ D NHM India: West Bengal, Darjeeling, Pedong G patna “inayoshii” (nomen nudum) ♂ D KUTH Thailand: Ranong; Holotype H patna “inayoshii” (nomen nudum) ♀ D KUTH Thailand: Trang, Khao Chong; Paratype I patna hanitschi ♂ D NHM Peninsular Malaysia J peali ♂ D NHM India: Assam, Sivasagar K peali ♀ D NHM India: Assam; Holotype L ceryx ♂ D NHM Indonesia: West Java, Mt. Gede M ceryx ♀ D NHM Indonesia: West Java, Mt. Gede N ceryxoides ♂ D MCZ Indonesia: North Sumatra, Mt. Sinabung O ceryxoides ♀ D UPC Indonesia: West Sumatra.
Figure 4. A kuenstleri kuenstleri ♂ D+V NHM Specimen locality unknown B kuenstleri kuenstleri ♀ D+V NHM Peninsular Malaysia: Selangor, Bukit Kuta C kuenstleri rileyi ♂ D NHM Borneo D pellucida ♂ D NHM Malaysia: Sabah, Mt. Kinabalu E pellucida ♀ D NHM Malaysia: Sabah, Mt. Kinabalu F penanga penanga ♀ D NHM Malaysia G penanga penanga ♀ D NHM Singapore; Allotype of Elymnias abrisa H penanga penanga ♀ D NHM Peninsular Malaysia: Penang; Holotype of Elymnias penanga penanga i. johnsoni I penanga sumatrana ♀ D NHM Indonesia: Sumatra; Holotype J penanga konga ♂ D NHM North Borneo K penanga konga ♀ D NHM North Borneo L penanga chelenis ♂ D NHM Thailand: Ranong.
Figure 5. A hypermnestra hypermnestra ♂ D+V NHM INDONESIA: Java, Bogor B hypermnestra hypermnestra ♀ D+V NHM INDONESIA: Java, Bogor C hypermnestra undularis ♂ D NHM INDIA: Assam D hypermnestra undularis ♀ D NHM INDIA: Sikkim E hypermnestra fraterna ♂ D NHM SRI LANKA F hypermnestra fraterna ♀ D NHM SRI LANKA G hypermnestra cottonis ♂ D NHM INDIA: Andaman Islands H hypermnestra cottonis ♀ D NHM INDIA: Andaman Islands I hypermnestra nigrescens ♂ D NHM BRUNEI: Tutong J hypermnestra nigrescens ♂ D NHM EAST MALAYSIA: Sarawak, Mt. Marapok K hypermnestra nigrescens ♂ D NHM EAST MALAYSIA: Labuan; Holotype of Elymnias hecate L hypermnestra nigrescens ♀ D NHM EAST MALAYSIA: Sarawak, Mt. Mulu M hypermnestra nigrescens "f. pseudagina" ♀ D NHM EAST MALAYSIA: Sarawak N hypermnestra nigrescens ♀ D NHM INDONESIA: Riau Islands.
Figure 6. A *Hypermnestra tinctoria* ♂ D NHM Myanmar: Bago B *Hypermnestra tinctoria* ♀ D NHM Myanmar: Ayeyarwady, Pathein C *Hypermnestra tinctoria* ♂ D NHM Thailand: Bangkok D *Hypermnestra tinctoria* ♀ D NHM Thailand: Bangkok E *Hypermnestra tinctoria* ♀ D NHM Myanmar: Tanintharyi; Syntype of *Elymnias hypermnestra tinctoria* f. *paraleuca* F *Hypermnestra tinctoria* ♀ D NHM Peninsular Malaysia: Kedah, Langkawi Island G *Hypermnestra discrepens* ♂ D NSYSU Peninsular Malaysia: Penang H *Hypermnestra discrepens* ♀ D NHM Peninsular Malaysia: Penang; Allotype I *Hypermnestra hainana* ♂ D NSYSU Taiwan: Kaohsiung J *Hypermnestra hainana* ♀ D NSYSU Taiwan: Kaohsiung K *Hypermnestra hainana* ♂ D NHM Vietnam L *Hypermnestra hainana* ♀ D NHM Vietnam M *Hypermnestra hainana* (f. *depicta*) ♀ D NHM Vietnam: Haiphong N *Hypermnestra hainana* (f. *depicta*) ♂ D NHM Vietnam: Haiphong O *Hypermnestra orientalis* ♂ D NHM Indonesia: East Nusa Tenggara, Flores, Ende Island; Holotype of *Elymnias nigrescens dohertyi* P *Hypermnestra orientalis* ♀ D NHM Indonesia: East Nusa Tenggara, Flores.
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Figure 7. A hypermnestra baliensis ♂ D NHM Indonesia: Bali B hypermnestra baliensis ♀ D NHM Indonesia: Bali; Holotype of Elymnias nigrescens bulelenga D hypermnestra tinctoria ♂ D KUTH Thailand: Chiang Mai E hypermnestra tinctoria ♀ D KUTH Thailand: Chanthaburi F hypermnestra violetta ♀ D NHM Thailand: Sri Racha; Holotype of Elymnias hypermnestra violetta f. obfuscata G hypermnestra meridonalis ♀ D NHM southern Vietnam; Holotype of Elymnias meridonalis f. orphnia H hypermnestra beatrice ♂ D NHM Peninsular Malaysia: Perak, Taiping I hypermnestra beatrice ♂ D NHM Peninsular Malaysia: Pahang, Gunung Tahan J hypermnestra beatrice ♂ D MCZ Peninsular Malaysia: Perak K hypermnestra beatrice ♀ D MCZ Singapore L hypermnestra sambana ♂ D NHM Indonesia: East Nusa Tenggara, Sumba M hypermnestra sambana ♀ D NHM Indonesia: East Nusa Tenggara, Sumba N hypermnestra decolorata ♂ D NHM Indonesia: Sumatra O hypermnestra decolorata ♀ D NHM Indonesia: Sumatra.
Figure 8. A *hypermnestra sumbawana* ♂ D NHM Indonesia: West Nusa Tenggara, Sumbawa B *hypermnestra sumbawana* ♀ D NHM Indonesia: West Nusa Tenggara, Sumbawa C *hypermnestra timorensis* ♂ D NHM East Timor: Dili D *hypermnestra timorensis* ♀ D NHM East Timor: Dili E *hypermnestra alorensis* ♂ D NHM Indonesia: East Nusa Tenggara, Adonara F *hypermnestra alorensis* ♀ D NHM Indonesia: East Nusa Tenggara, Adonara G *hypermnestra uemurai* ♂ D NHM Indonesia: West Nusa Tenggara, Lombok H *hypermnestra uemurai* ♀ D NHM Indonesia: West Nusa Tenggara, Lombok I *caudata* ♂ D NHM Myanmar (specimen is likely mislabeled) J *caudata* ♀ D NHM India: Kerala, Malabar K *merula* ♂ D NHM Sri Lanka: Central Province, Kandy; Holotype L *nepheronides nepheronides* ♂ D HSPC Indonesia: East Nusa Tenggara, Flores M *nepheronides nepheronides* ♀ D NHM Indonesia: East Nusa Tenggara, Flores N *nepheronides tamborana* ♂ D OPC Indonesia: Sumbawa, Mt. Sengenges; Holotype.
Figure 9. A *harterti harterti* ♂ D+V OPC MALAYSIA: Perak, Batang Padang, Tapah B *harterti harterti* ♀ D+V OPC MALAYSIA: Perak, Batang Padang, Tapah C *harterti brookei* ♂ D NHM collection locality unknown D *harterti lautensis* ♂ D OPC INDONESIA: South Kalimantan, Laut Island; Holotype E *harterti arbaimuni* ♂ D OPC INDONESIA: central Sumatra, Jambi; Holotype F *harterti arbaimuni* ♀ D OPC INDONESIA: central Sumatra, Jambi G *parce justini* ♂ D+V SMFD PHILIPPINES: Palawan Province, Calamian Islands, Busuanga Island, Coron; Holotype H *parce justini* ♀ D+V SMFD PHILIPPINES: Palawan Province, Calamian Islands, Busuanga Island, Coron; Paratype I *parce parce* ♂ D NHM PHILIPPINES: Palawan J *parce parce* ♀ D NHM PHILIPPINES: Palawan K *panthera enganica* ♀ D NHM INDONESIA: Bengkulu, Enggano Island.
Figure 10. A panthera panthera ♂ D NHM Peninsular Malaysia B panthera panthera ♀ D NHM Peninsular Malaysia C panthera dusara ♂ D NHM Indonesia: Java D panthera dusara ♀ D NHM Indonesia: Java E panthera mimus ♂ D NHM India: Nicobar Islands F panthera mimus ♀ D NHM India: Nicobar Islands G panthera dolorosa ♂ D NHM Indonesia: North Sumatra, Nias H panthera dolorosa ♀ D NHM Indonesia: North Sumatra, Nias I panthera lutescens ♂ D NHM North Borneo J panthera lutescens ♀ D NHM East Malaysia: Sarawak K panthera suluana ♂ D SMFD collection locality unknown L panthera suluana ♀ D SMFD Philippines: Tawi-tawi, Mapun Island M panthera tautra ♂ D NHM Indonesia: Sumatra, Bengkalis, Senggoro N panthera tautra ♀ D NHM Indonesia: Sumatra, Bengkalis, Senggoro O panthera arikata ♂ D NHM Indonesia: Riau Islands, Natuna P panthera arikata ♀ D NHM Indonesia: Riau Islands, Natuna.
Figure 11. A obnubila ♂ D+V NHM MALAYSIA: Perak B obnubila ♀ D+V NHM THAILAND: Ranong C congruens congruens ♂ D NHM PHILIPPINES: Cebu, Camotes Island D congruens subcongruens ♀ D NHM PHILIPPINES: Mindoro E congruens endida ♂ D SMFD PHILIPPINES: Bohol F congruens endida ♀ D SMFD PHILIPPINES: Bohol G congruens congruens ♀ D NMNH PHILIPPINES: Mindanao, Davao H miyagawai ♂ D SPC VIETNAM: Lam Dong, Loc Bao; Holotype I miyagawai ♀ D SPC VIETNAM: Lam Dong, Loc Bao; Paratype.
Figure 12. A *nesaea nesaea* ♂ D NHM Indonesia: Java B *nesaea nesaea* ♀ D NHM Indonesia: Java C *nesaea timandra* ♂ D NHM India: Meghalaya, Khasi Hills D *nesaea timandra* ♀ D NHM India: Meghalaya, Khasi Hills E *nesaea laisidis* ♂ D MCZ Indonesia: Sumatra F *nesaea laisidis* ♀ D MCZ Indonesia: West Sumatra, Padang G *nesaea baewana* ♂ D NHM Indonesia: East Java, Gresik Regency, Bawean H *nesaea baewana* ♀ D NHM Indonesia: East Java, Gresik Regency, Bawean I *nesaea neolais* ♂ D MCZ Indonesia: North Sumatra, Nias, Dymna J *nesaea neolais* ♀ D MCZ Indonesia: North Sumatra, Nias K *nesaea hypereides* ♂ D MCZ East Malaysia: Sabah, Sandakan L *nesaea hypereides* ♀ D MCZ East Malaysia: Sabah, Sandakan M *nesaea apelles* ♂ D KUTH Thailand: Samut Sakhon N *nesaea apelles* ♀ D KUTH Thailand: Bangkok, Bang Khen O *nesaea lioneli* ♀ D KUTH Thailand: Satun, Thale Ban.
Figure 13. A casiphone casiphone ♂ D+V NHM Indonesia: Java B casiphone casiphone ♀ D+V NHM Indonesia: Java C casiphone kamara ♂ D NHM Indonesia: Java D casiphone kamara ♀ D NHM Indonesia: Java E casiphone praetextata ♂ D NHM Indonesia: West Nusa Tenggara, Lombok F casiphone praetextata ♀ D NHM Indonesia: West Nusa Tenggara, Lombok G casiphone praetextata (= kamara lombokiana) ♂ D NHM Indonesia: West Nusa Tenggara, Lombok H casiphone praetextata (= kamara lombokiana) ♀ D NHM Indonesia: West Nusa Tenggara, Lombok I casiphone praetextata (= kamara lombokiana) ♂ D NHM Indonesia: West Nusa Tenggara, Lombok; Syntype of Elymnias kamara lombokiana J casiphone alumna ♂ D NHM Indonesia: East Java, Blitar K casiphone exclusa ♂ D NHM Indonesia: Bali L casiphone erinyes ♂ D NHM Indonesia: Sumatra M casiphone erinyes ♀ D NHM Indonesia: Sumatra.
Figure 14. A malelas ♂ D NHM India: Sikkim B malelas ♀ D NHM India: Sikkim C malelas ♂ D MCZ Vietnam D malelas ♀ D KUTH Thailand: Chiang Mai E saueri ♂ D IPC Thailand: Phetchabun F saueri ♀ D NMNH Malaysia: Johor, Mersing to Kluang G kochi ♂ D SMFD Philippines: Luzon, Sierre Madre Mountain Range H kochi ♀ D PNM Philippines: Luzon, Sierre Madre Mountain Range I casiphonides casiphonides ♂ D NHM Philippines: Mindanao J casiphonides casiphonides ♀ D NHM Philippines: Mindanao K nelsoni ♂ D UPC Indonesia: West Sumatra, Mentawai Regency, Sipora L nelsoni ♀ D UPC Indonesia: West Sumatra, Mentawai Regency, Sipora M amoena ♂ D MCZ Indonesia: Sumba, Kombapari Forest N kanekoi ♂ D NHM Philippines: Negros O kanekoi ♀ D SMFD Philippines: Negros P saola ♂ D NHM Vietnam; Holotype.
Figure 15. A mélia mélia ♂ D NMNH PHILIPPINES: Luzon, Cavite, Puerto Azul B mélia mélia ♀ D SMFD PHILIPPINES: Luzon, Sierr Madre Mountains C mélia malis ♂ D NHM PHILIPPINES: Quezon, Polillo Island D mélia malis ♀ D NHM PHILIPPINES: Luzon, Los Baños E beza beza ♂ D NHM PHILIPPINES: Mindanao F beza beza ♀ D NHM PHILIPPINES: Mindanao G sansoni sansoni ♂ D SMFD PHILIPPINES: Negros H sansoni sansoni ♀ D SMFD PHILIPPINES: Negros I sansoni aklanensis ♂ D UPC PHILIPPINES: Panay, Aklan; Paratype J sansoni aklanensis ♀ D UPC PHILIPPINES: Panay, Aklan; Paratype K luteofasciata ♂ D OPC PHILIPPINES: Mindanao, Penangulutan, Upian River, City of Davao; Holotype L luteofasciata ♀ D SMFD PHILIPPINES: Mindanao, South Cotabato, Mt. Matutum M vitellia vitellia ♂ D NHM INDONESIA: Maluku, Ambon N vitellia vitellia ♀ D NHM INDONESIA: Maluku, Ambon O vitellia viminalis ♂ D NHM INDONESIA: Maluku, Buru P vitellia viminalis ♀ D NHM INDONESIA: Maluku, Buru.
Figure 16. A *agondas agondas* ♂ D+V NHM Indonesia: West Papua B *agondas agondas* ♀ D+V NHM Indonesia: West Papua C *agondas melane* ♂ D+V NHM Indonesia: Maluku, Kei Island D *agondas melane* ♀ D+V NHM Indonesia: Maluku, Kei Island E *agondas glaucopis* ♂ D+V NHM Papua New Guinea: Oro Province, Kumusi River F *agondas glaucopis* ♀ D+V NHM Papua New Guinea: Oro Province, Kumusi River G *agondas melanippe* ♂ D+V NHM Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg H *agondas melanippe* ♀ D+V NHM Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg.
Figure 17. A. *agondas melanthes* ♂ D+V NHM Papua New Guinea: Milne Bay, Woodlark Island B. *agondas melanthes* ♀ D+V NHM Papua New Guinea: Milne Bay, Woodlark Island C. *agondas melanthes* ♀ D NHM Papua New Guinea: Milne Bay, Woodlark Island D. *agondas melanthes* ♀ D NHM Papua New Guinea: Milne Bay, Woodlark Island E. *agondas aruana* ♂ D+V NHM Indonesia: Maluku, Aru F. *agondas aruana* ♀ D+V NHM Indonesia: Maluku, Aru G. *agondas aruana* ♀ D+V NHM Indonesia: Maluku, Aru H. *agondas ssp.* ♂ D+V NHM Indonesia: Maluku, Tanimbar I. *agondas ssp.* ♀ D+V NHM Indonesia: Maluku, Tanimbar.
Figure 18. A agondas melagondas ♂ D+V NHM New Guinea B agondas melagondas ♀ D NHM New Guinea C agondas melagondas ♀ D NHM New Guinea D agondas melagondas ♀ D NHM New Guinea E agondas melagondas ♀ D NHM New Guinea F agondas melagondas ♀ D NHM New Guinea G agondas melagondas ♀ D NHM New Guinea H agondas melagondas ♀ D NHM New Guinea I agondas melagondas ♀ D NHM New Guinea J agondas melagondas ♀ D NHM New Guinea K agondas melagondas ♀ D NHM New Guinea L agondas melagondas ♀ D NHM New Guinea M agondas goramensis ♂ D+V NHM Indonesia: Maluku, East Seram Regency, Gorong Island.
Figure 19. A agondas dampierensis ♂ D NHM Papua New Guinea: Madang, Karkar Island; Syntype B agondas dampierensis ♂ D NHM Papua New Guinea: Madang, Karkar Island C agondas thryallis ♂ D NHM Papua New Guinea D agondas thryallis ♂ D NHM Papua New Guinea E agondas thryallis ♂ D+V NMNH Papua New Guinea: East Sepik, Maprik F agondas thryallis ♂ D+V NMNH Papua New Guinea: Regia, Mapuk G agondas thryallis ♂ D NHM Indonesia: Papua, Yos Sudarso Bay H agondas thryallis ♂ D NHM Indonesia: Papua, Yos Sudarso Bay I agondas thryallis ♂ D NHM Indonesia: Papua, Yos Sudarso Bay J agondas australiana ♂ D MCZ Australia: Queensland, Claudie River K agondas australiana ♂ D NHM Australia: Queensland, West Claudie River.
Figure 20. A cybele cybele ♂ D NHM Indonesia: North Maluku, Halmahera B cybele cybele ♀ D NHM Indonesia: North Maluku, Halmahera C cybele cybele ♂ D NHM Indonesia: North Maluku, Bacan D cybele cybele ♀ D NHM Indonesia: North Maluku, Bacan E cybele obiana ♂ D NHM Indonesia: North Maluku, Obi F cybele obiana ♀ D NHM Indonesia: North Maluku, Obi G cumaea cumaea ♂ D NHM Indonesia: North Sulawesi, Menado H cumaea cumaea ♀ D NHM Indonesia: North Sulawesi, Minahasa I hewitsoni hewitsoni ♂ D NHM Indonesia: South Sulawesi J hewitsoni hewitsoni ♀ D NHM Indonesia: South Sulawesi K mimalon mimalon ♂ D NHM Indonesia: Sulawesi L mimalon mimalon ♀ D NHM Indonesia: South Sulawesi, Menado M mimalon nysa ♂ D NHM Indonesia: South Sulawesi N mimalon ino ♂ D NHM Indonesia: Central Sulawesi; Holotype O hicetas hicetas ♂ D NHM Indonesia: South Sulawesi; P hicetas hicetas ♀ D NHM Indonesia: South Sulawesi.
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Figure 21. A holofernes ♂ D NHM Papua New Guinea: New Britain B holofernes ♀ D NHM Papua New Guinea: New Britain C bornemanni ♂ D NHM Indonesia: Central Sulawesi, Banggai D bornemanni ♀ D NHM Indonesia: Central Sulawesi, Banggai E phrikonis ♂ D NHM Indonesia: Sula Archipelago F phrikonis ♀ D NHM Indonesia: Sula Archipelago G sangira ♂ D NHM Indonesia: North Sulawesi, Talaud H sangira ♀ D NHM Indonesia: North Sulawesi, Talaud I umbratilis ♂ D NHM Indonesia: Papua, Biak; Holotype J umbratilis ♀ D OPC Indonesia: Papua, Biak K resplendens ♂ MCZ Indonesia: Central Sulawesi, Palu L resplendens ♀ MCZ Indonesia: Central Sulawesi, Palu M singhala ♂ D NHM Sri Lanka N singhala ♀ D NHM Sri Lanka.
Figure 22. A bammakoo bammakoo NHM Central Africa B paradoxa NHM Indonesia: Papua, Weyland Mountains C papua cinereomargo NHM Indonesia: Papua, Biak D esaca mabeswara NHM Indonesia: Java E esaca leontina NHM Indonesia: North Sumatra, Nias F vasudeva NHM India: Meghalaya, Khasi Hills G dara albofasciata MCZ Philippines: Palawan H dara bengena NHM Indonesia: Java I dara darina MCZ Peninsular Malaysia: Pahang, Cameron Highlands J patna patna NHM India: Sikkim K peali NHM India: Assam L cerix NHM Indonesia: Java M kuenstleri NHM collection locality unknown N pellucida NHM East Malaysia: Sabah, Mt. Kinabalu O penanga chelensis NHM Thailand: Ranong.
Figure 23. A *hypermnestra hypermnestra* NHM Indonesia: West Java, Bogor B *hypermnestra hypermnestra* MCZ Indonesia: Maluku, Seram C *hypermnestra fraterna* MCZ Sri Lanka: Western Province D *hypermnestra cottonis* NHM India: Andaman Islands E *hypermnestra tinctoria* NSYSU Thailand: Trang, Khao Chong F *hypermnestra hainana* NSYSU Taiwan: Kaohsiung G *hypermnestra discrepans* NSYSU Peninsular Malaysia: Penang H *hypermnestra orientalis* MCZ Indonesia: East Nusa Tenggara, Flores I *hypermnestra baliensis* NSYSU Indonesia: Bali J *hypermnestra sumbana* MCZ Indonesia: East Nusa Tenggara, Sumba K *hypermnestra timorensis* MCZ Indonesia: East Nusa Tenggara, Timor L *caudata* NHM Myanmar (specimen is likely mislabeled) M *nepheronides nepheronides* MCZ Indonesia: East Nusa Tenggara, Flores N *parce* MCZ Philippines: Palawan O *panthera tautra* NHM Indonesia: Sumatra, Bengkalis, Senggoro.
Figure 24. A *panthera balina* MCZ Indonesia: Bali B *obnubila* NHM Peninsular Malaysia: Perak C *congruens congruens* NHM Philippines: Cebu, Camotes Island D *nesaeae nesaeae* NHM Indonesia: Java E *nesaeae nesaeae* NSYSU Indonesia: Bali F *nesaeae timandra* NHM India: Meghalaya, Khasi Hills G *nesaeae vordemani* NSYSU Indonesia: East Java, Kangean Islands H *casiphone casiphone* NHM Indonesia: Java I *casiphone casiphone* NHM Indonesia: Java J *casiphone praetextata* NHM Indonesia: East Nusa Tenggara, Lombok K *casiphone exclusa* NSYSU Indonesia: Bali L *casiphone alumna* NSYSU Indonesia: Java M *malelas* NSYSU Thailand: Chiang Mai N *kochi* MCZ Philippines: Luzon, Sierra Madre Range, Isabela O *casiphonides casiphonides* NHM Philippines: Mindanao
Figure 25. **A** nelsoni MCZ INDONESIA: West Sumatra, Pagai Island **B** kanekoi NHM PHILIPPINES: Negros **C** melias malis NHM PHILIPPINES: Quezon, Polillo Island **D** beza beza NHM PHILIPPINES: Mindanao **E** sansoni aklanensis MCZ PHILIPPINES: Panay, Aklan, Mt. Madiaas **F** vitellia vitellia NHM INDONESIA: Maluku, Ambon **G** vitellia viminalis MCZ INDONESIA: Maluku, Buru **H** agondas glaucopis NHM PAPUA NEW GUINEA: Oro Province, Kumusi River **I** agondas agondas (previously E. a. bioculatus) NSYSU INDONESIA: West Papua, Sorong **J** agondas melagondas MCZ INDONESIA: West Papua, Sorong **K** agondas melagondas MCZ INDONESIA: Papua, Asiki **L** agondas aruana MCZ INDONESIA: Papua, Aru **M** agondas thryallis NHM PAPUA NEW GUINEA: New Britain **N** agondas thryallis MCZ INDONESIA: West Papua, Yapen **O** cybele cybele NHM INDONESIA: North Maluku, Bacan.
Figure 26. A *cybele cybele* NHM Indonesia: North Maluku, Halmahera B *cumaea toliana* MCZ Indonesia: North Sulawesi C *hewitsoni meliophila* NHM Indonesia: Maluku, Kisar D *mimalon mimalon* NHM Indonesia: Sulawesi E *hicetas hicetas* NHM Indonesia: Sulawesi F *hicetas hicetina* NHM Indonesia: Sulawesi G *holofernes* NHM Papua New Guinea: New Britain H *hornemannii* NHM Indonesia: Central Sulawesi, Banggai I *phrikonis* MCZ Indonesia: North Maluku, Sula Regency, Sanana J *sangira* NMNH Indonesia: North Sulawesi, Sangir island K *umbratilis* MCZ Indonesia: Papua, Biak L *resplendens* MCZ Indonesia: Central Sulawesi, Palu M *singhala* NHM Sri Lanka
Figure 27. Distribution map of *Elymnias bammakoo*.

Figure 28. Distribution map of *Elymnias paradoxa*. 
Figure 29. Distribution map of *Elymnias papua*.

Figure 30. Distribution map of *Elymnias esaca*. 
An illustrated checklist of the genus Elymnias Hübner, 1818 (Nymphalidae, Satyrinae)

Figure 31. Distribution map of Elymnias vasudeva.

Figure 32. Distribution map of Elymnias dara.
Figure 33. Distribution map of *Elymnias patna*.

Figure 34. Distribution map of *Elymnias peali*. 
Figure 35. Distribution map of *Elymnias ceryx*.

Figure 36. Distribution map of *Elymnias kuenstleri*. 
**Figure 37.** Distribution map of *Elymnias ceryxoides*.

**Figure 38.** Distribution map of *Elymnias pellucida*.
An illustrated checklist of the genus *Elymnias* Hübner, 1818 (Nymphalidae, Satyrinae)

Figure 39. Distribution map of *Elymnias penanga*.

Figure 40. Distribution map of *Elymnias hypermnestra*. 
Figure 41. Distribution map of *Elymnias caudata*.

Figure 42. Distribution map of *Elymnias merula*.
An illustrated checklist of the genus Elymnias Hübner, 1818 (Nymphalidae, Satyrinae)

Figure 43. Distribution map of *Elymnias leucocyma*.

Figure 44. Distribution map of *Elymnias nepheronides*.
**Figure 45.** Distribution map of *Elymnias harterti*.

**Figure 46.** Distribution map of *Elymnias parce*. 
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Figure 47. Distribution map of Elymnias panthera.

Figure 48. Distribution map of Elymnias obnubila.
Figure 49. Distribution map of *Elymnias congruens*.

Figure 50. Distribution map of *Elymnias miyagawai*. 
An illustrated checklist of the genus Elymnias Hübner, 1818 (Nymphalidae, Satyrinae)

Figure 51. Distribution map of *Elymnias nesaea*.

Figure 52. Distribution map of *Elymnias casiphone*.
Figure 53. Distribution map of *Elymnias malelas*.

Figure 54. Distribution map of *Elymnias saueri*. 
Figure 55. Distribution map of *Elymnias kochi*.

Figure 56. Distribution map of *Elymnias casiphonides*. 
Figure 57. Distribution map of Elymnias nelsoni.

Figure 58. Distribution map of Elymnias amoena.
Figure 59. Distribution map of Elymnias kanekoi.

Figure 60. Distribution map of Elymnias saola.
Figure 61. Distribution map of *Elymnias melias*.

Figure 62. Distribution map of *Elymnias beza*.
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Figure 63. Distribution map of Elymnias sansoni.

Figure 64. Distribution map of Elymnias luteofasciata.
Figure 65. Distribution map of *Elymnias vitellia*.

Figure 66. Distribution map of *Elymnias agondas*.
**Figure 67.** Distribution map of *Elymnias cybele*.

**Figure 68.** Distribution map of *Elymnias cumaea*. 
**Figure 69.** Distribution map of *Elymnias hewitsoni*.

**Figure 70.** Distribution map of *Elymnias mimalon*.
An illustrated checklist of the genus Elymnias Hübner, 1818 (Nymphalidae, Satyrinae)

Figure 71. Distribution map of Elymnias hicetas.

Figure 72. Distribution map of Elymnias holofernes.
**Figure 73.** Distribution map of *Elymnias bornemanni*.

**Figure 74.** Distribution map of *Elymnias phrikonis*.
Figure 75. Distribution map of *Elymnias sangira*.

Figure 76. Distribution map of *Elymnias umbratilis*.
Figure 77. Distribution map of *Elymnias resplendens*.

Figure 78. Distribution map of *Elymnias singhala*.
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