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Search for mesophotic octocorals (Cnidaria, Anthozoa) and their phylogeny. II. A new zooxanthellate species from Eilat, northern Red Sea

Yehuda Benayahu[1], Catherine S. McFadden[2], Erez Shoham[1], Leen P. van Ofwegen[3]

1 *School of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv, 69978, Israel* **2** *Department of Biology, Harvey Mudd College, Claremont, CA 91711-5990, USA* **3** *Department of Marine Zoology, Naturalis Biodiversity Centre, P.O. Box 9517, 2300 RA Leiden, the Netherlands*

Corresponding author: *Yehuda Benayahu* (yehudab@tauex.tau.ac.il)

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Abstract

An octocoral survey conducted in the mesophotic coral ecosystem (MCE) of Eilat (Gulf of Aqaba, northern Red Sea) yielded a new species of the speciose reef-dwelling genus *Sinularia*. It features encrusting colony morphology with a thin, funnel-shaped polypary. *Sinularia mesophotica* **sp. n.** (family Alcyoniidae) is described and compared to the other congeners with similar morphology. Both the morphological and molecular examination justified the establishment of the new species, also assigning it to a new genetic clade within *Sinularia*. The results highlight its unique phylogenetic position within the genus, and this is the first described species of a mesophotic zooxanthellate octocoral.

Keywords

Octocorallia, taxonomy, new species, mesophotic coral ecosystem, Eilat, Red Sea

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Introduction

The taxonomy of the northern Red Sea octocorals has been quite extensively studied, albeit mostly confined to the reefs above 30 m (references in Shoham and Benayahu 2017). Studies have demonstrated a high octocoral richness in the Red Sea, revealing new taxa and new zoogeographical records (e.g., Verseveldt and Benayahu 1978, 1983; Haverkort-Yeh et al. 2013; Ofwegen et al. 2013, 2016). Octocorals of the mesophotic coral ecosystems (MCEs), in contrast, have remained little studied (Shoham and Benayahu 2017). To date, the only newly-described mesophotic Red Sea octocoral is the azooxanthellate *Scleronephthya lewinsohni* Verseveldt and Benayahu, 1978 of the family Nephtheidae, discovered at a depth of 55–82 m. Recently, Shoham and Benayahu (2017) recorded a higher species richness and higher number of species in Eilat's upper MCEs (30-45 m) compared to the shallower reefs there. The latter study also revealed an almost exclusive dominance of zooxanthellate octocorals in the upper MCE. Following an octocoral survey conducted in Eilat's MCEs, we describe here a new species of the genus *Sinularia*.

Materials and methods

Samples were collected by ROV (ECA H800) operated by the Sam Rothberg R/V of the Interuniversity Institute for Marine Sciences in Eilat. *In-situ* photography was carried out using a low light black and white camera VS300 (Eca Robotics) and 1CAM Alpha HD camera (SubCimaging). Samples were obtained using the ROV arm. Colony fragments were removed and preserved in 100% ethanol for molecular work. The original samples were placed in 70% ethanol for taxonomic identification, for which sclerites from different parts of the colonies (polyp, polypary surface and interior, base surface and interior) were obtained by dissolving the tissues in 10% sodium hypochlorite, followed by rinsing in fresh water. Sclerites were then prepared for scanning electron microscopy as follows: rinsed with double-distilled water; dried at room temperature, coated with gold-palladium; and examined with a SEM Jeol 6480LV electron microscope and at high vacuum under an environmental scanning electron microscope (ESEM, JSM-6700 Field Emission Scanning Electron Microscope, operated at 10 kV). Wet preparations of tissue smears were examined under a light microscope (X 200) in order to verify presence of symbiotic algae (zooxanthellae). Material studied is deposited at the Steinhardt Museum of Natural History, National Center for Biodiversity Studies, Tel Aviv University, Israel (ZMTAU) and Naturalis Biodiversity Center, formerly Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands (RMNH).

Molecular phylogenetic analyses

DNA was extracted from the EtOH-preserved samples, and two mitochondrial gene regions (*mtMutS*, *igr1* + *COI*) were sequenced using previously published primers and

protocols (McFadden et al. 2011). Sequences were aligned to a dataset that included published sequences from 143 specimens representing >85 nominal species of *Sinularia* (McFadden et al. 2009, 2014; Benayahu et al. 2013). Maximum likelihood analyses of each gene region separately as well as the concatenated sequence were conducted using PhyML (Guindon et al. 2003) with 100 bootstrap replicates. A GTR+I+G model of evolution was substituted for the best-fit TVM+I+G model selected using ModelTest 3.0 (Posada and Crandall 1998) but not available in PhyML. MEGA v. 5 (Tamura et al. 2011) was used to calculate pairwise genetic distance values (Kimura 2-parameter) between sequences. New sequences have been deposited in GenBank (KY971524–KY971525), and alignments and treefiles in TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S20934).

Results

Systematic description
Order Alcyonacea Lamouroux, 1912
Family Alcyoniidae Lamouroux, 1912
Genus *Sinularia* May, 1898

***Sinularia mesophotica* sp. n.**
http://zoobank.org/658B7592-DE2D-4929-AF61-C11FABCF2879
Figs 1–4

Type material examined. Holotype: ZMTAU Co 37425, Israel, northern Red Sea, Gulf of Aqaba, Eilat, Dekel Beach (29°32'2.49"N, 34°57'44.56"E), 62 m, 31 May 2016, coll. M. Weis; three paratypes: ZMTAU Co 37492 same collection details.

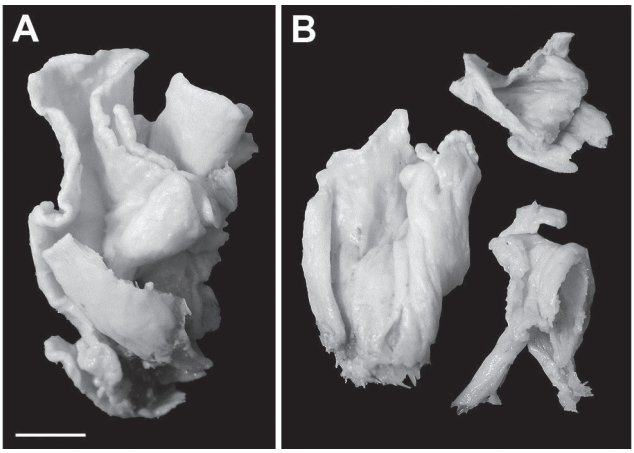

Figure 1. *Sinularia mesophotica* sp. n.; **A** Holotype ZMTAU Co 37425 **B** paratypes ZMTAU Co 37492. Scale bar: 1 cm (**A** also applies to **B**).

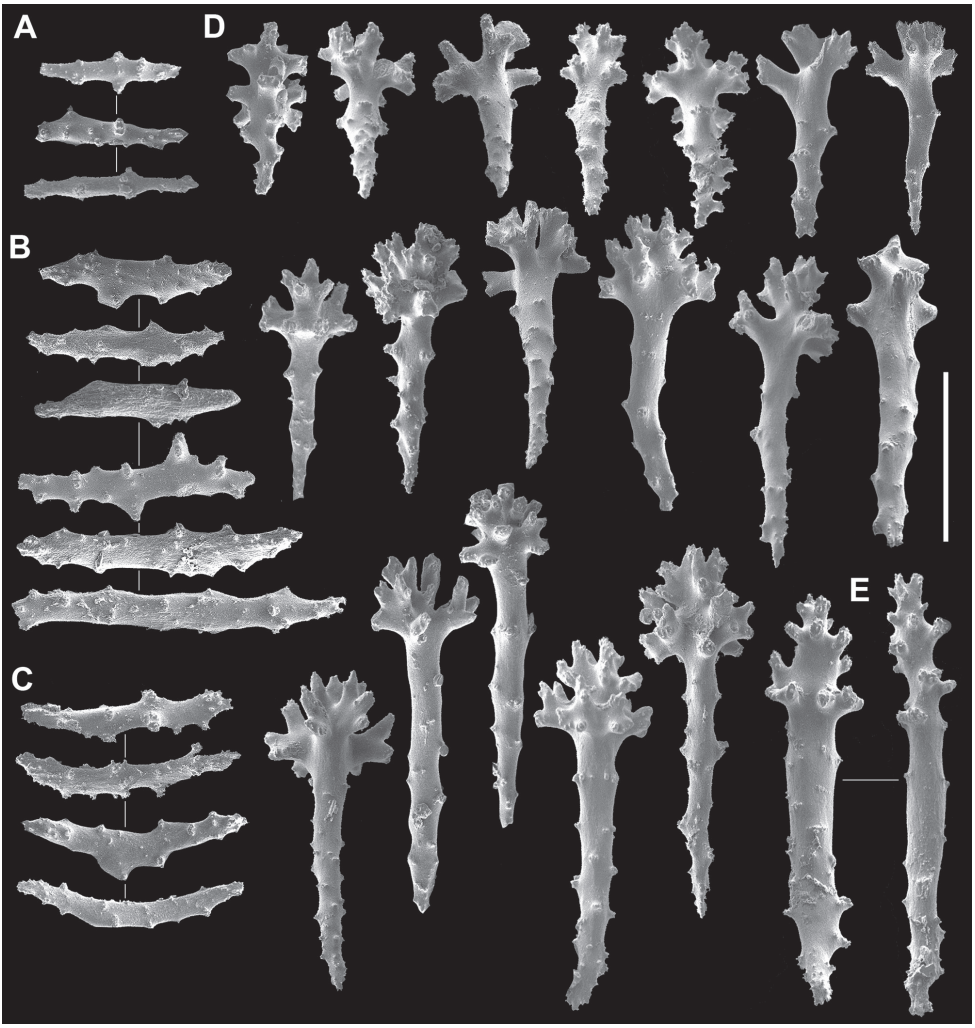

Figure 2. *Sinularia mesophotica* sp. n., holotype ZMTAU Co 37425. Sclerites from the polypary. **A** tentacle rods **B** straight collaret spindles **C** bent collaret spindles **D** clubs **E** larger clubs. Scale bar: 0.10 mm.

Diagnosis. The holotype is part of an encrusting colony with a thin, funnel-shaped polypary, also featuring a curly margin (Fig. 1A). In a side-view its maximum dimensions are 5 × 2.5 cm. Polyps with tentacle rods and collaret sclerites (Fig. 2A–C). Tentacle rods up to 0.10 mm long (Fig. 2A). Collaret consists of almost straight spindles, up to 0.20 mm long (Fig. 2B), and shorter bent ones, up to 0.14 mm long (Fig. 2C). Surface layer of the polypary with clubs (Fig. 2D), some featuring a central wart, while in others it is less discernible, or even absent. Clubs vary from 0.10 mm long to 0.25 mm long, and a few with poorly developed heads attain 0.27 mm (Fig. 2E). Surface layer of the colony base contains clubs up to 0.22 mm; some similar to those of polypary, and others have wide heads (Fig. 3A). Polypary

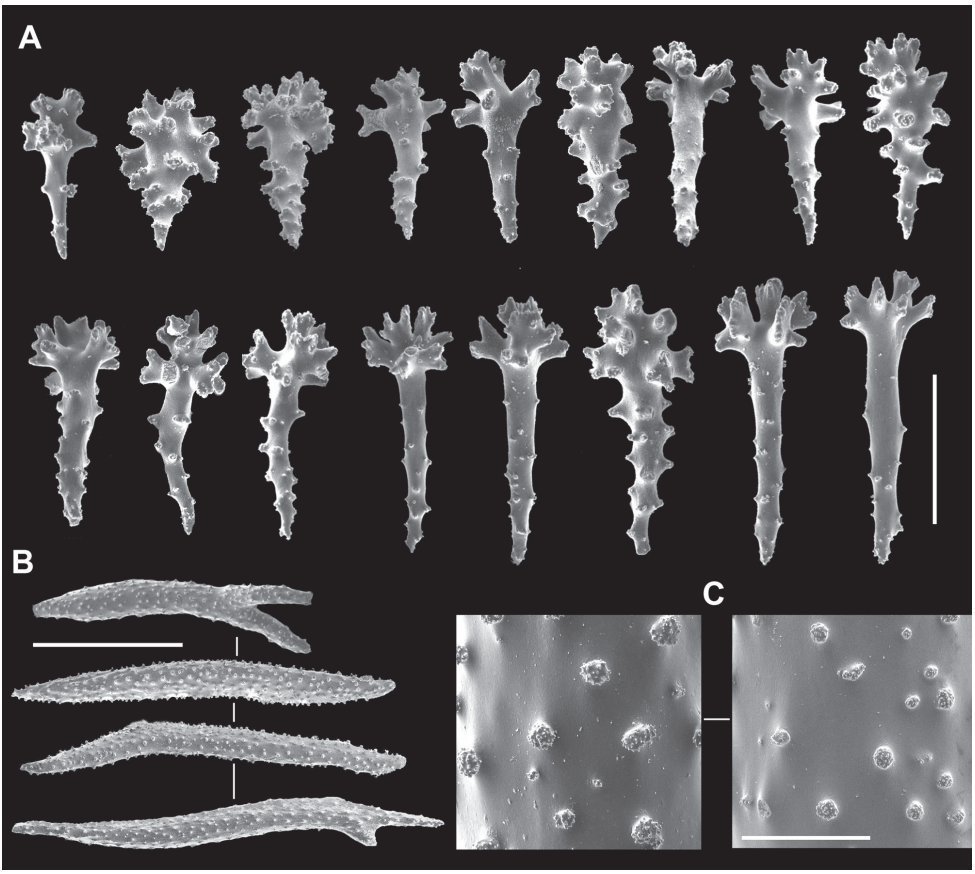

Figure 3. *Sinularia mesophotica* sp. n., holotype ZMTAU Co 37425. Sclerites of the base of colony. **A** clubs of the surface layer **B** spindles of interior **C** tuberculation of the spindles. Scale bars: 0.10 mm (**A, C)**, 1 mm (**B**).

and base interior bear spindles, some branched, up to 3.2 mm long (Fig. 3B), with well-spaced simple tubercles (Fig. 3C).

Color. The ethanol-preserved holotype is beige.

Etymology. The new species name reflects its mesophotic habitat.

Living features. Colonies grow as dense patches over reefal-calcareous substrate. Their polypary is flat and horizontally oriented (Fig. 4A) or funnel-shaped (Fig. 4B), with upper part dark-brown, due to dense zooxanthellae as verified by light microscopy, and lower part brighter, almost white. The flexibility and softness of the living colonies was recognized by their movement in the water currents generated by the ROV arm.

Variability. ZMTAU Co 37492 comprises three paratypes, each of them represented by fragments of colonies (Fig. 1B). Their general morphology and sclerites are identical to those of the holotype ZMTAU Co 37425.

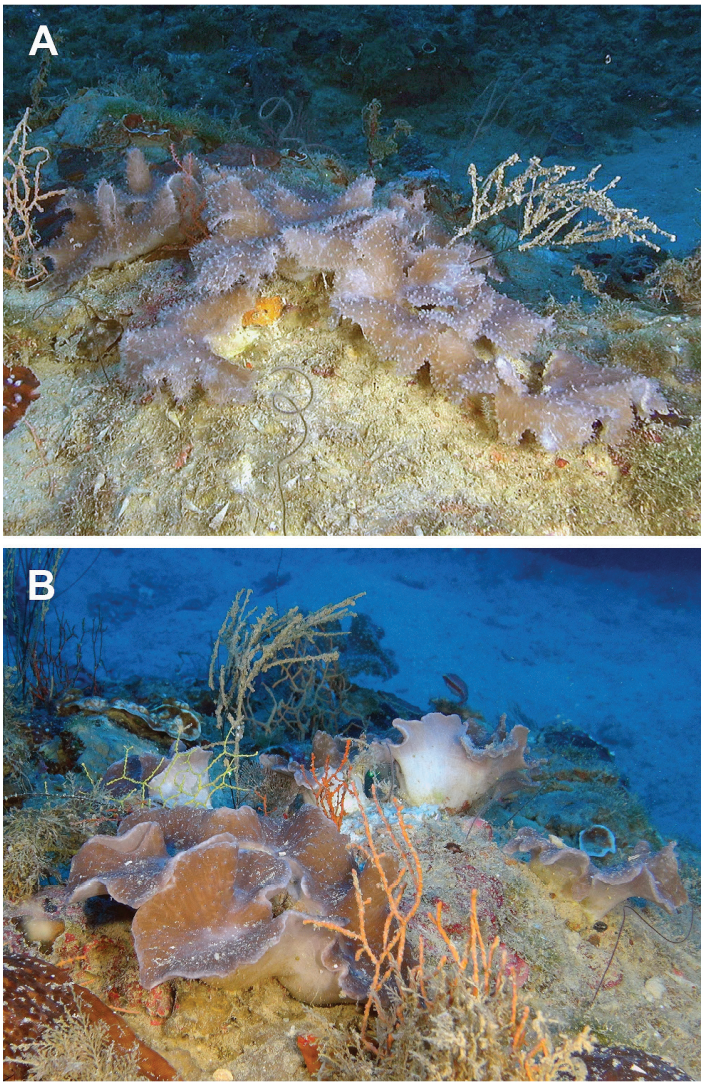

Figure 4. Underwater photographs of *Sinularia mesophotica* sp. n. **A** patch of colonies **B** funnel-shaped morphology of colonies.

Molecular phylogenetic analyses of *Sinularia mesophotica*

Phylogenetic analyses of *mtMutS*, *igr1* + *COI* (not shown) and the concatenated sequence (Fig. 5) all placed *Sinularia mesophotica* n. sp. in a unique position outside the five previously recognized clades of *Sinularia* (McFadden et al. 2009). The mean genetic distance (Kimura 2-parameter) between *S. mesophotica* n. sp. and all other species was 5.7% (s.d. ± 1.0%), comparable to the mean distances between different clades (2.8–7.2%), and much greater than what is typically observed between species within each clade (0.2–2.9%) (McFadden et al. 2009). The *mtMutS* tree (not shown)

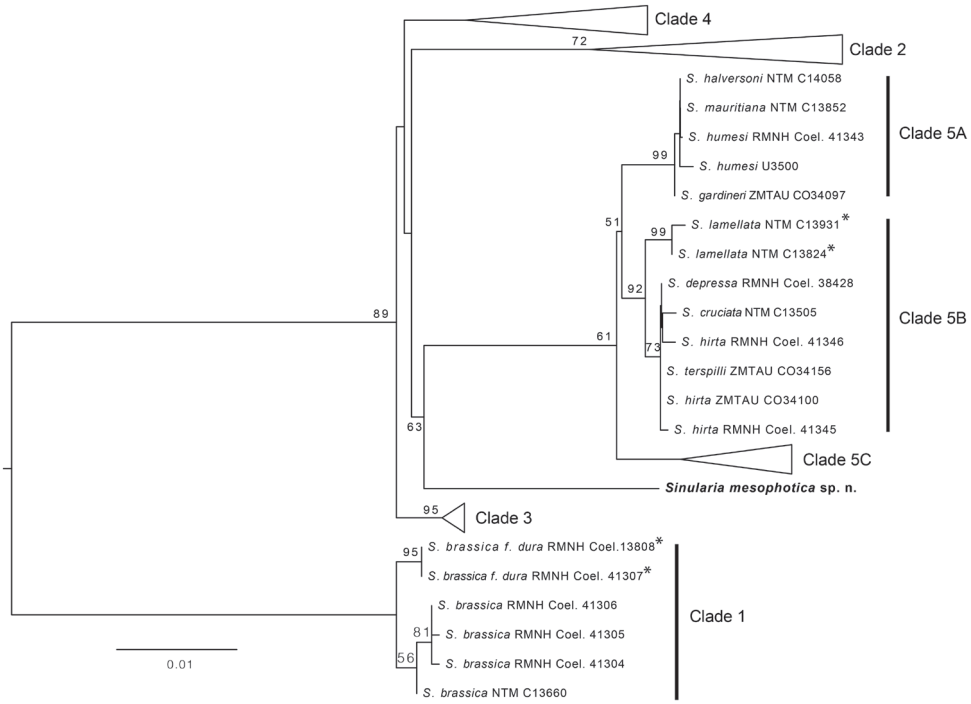

Figure 5. Maximum likelihood tree of concatenated *mtMutS* and *igr1+COI* mitochondrial gene sequences. Clade numbering system follows McFadden et al. (2009); some clades have been collapsed to facilitate readability. Asterisks indicate species with a funnel-shaped morphology similar to that of *Sinularia mesophotica* sp. n. Bootstrap values >50% are indicated adjacent to nodes.

suggested that *S. mesophotica* n. sp. is a sister taxon to clade 5 (bootstrap support = 78%), but neither *igr1+COI* (not shown) nor the concatenated gene tree resolved the basal relationships among *S. mesophotica* sp. n. and clades 2–5 (Fig. 5).

Discussion

Prior to the present study two *Sinularia* species have been described as possessing a distinct funnel-shaped polypary. Certain morphologies of *S. brassica* May, 1898, originally assigned to *S. dura* (Pratt 1903), share such morphology (see Benayahu et al. 1998: figs 6, 7, 9, 13, 25). Notably, *S. brassica* features club-sclerites with heads consisting of two or three diverging, wide-toothed prominences, markedly different from those of *S. mesophotica*.

The holotype of *Sinularia lamellata* Verseveldt and Tursch, 1979 features a "thin, plate-like funnel-wall" (see p. 143, plate 6), thus also resembling the colonies of *S. mesophotica* (this study: Figs 1, 4). For comparison, in the current study we re-examined the sclerites of the holotype of *S. lamellata* (RMNH Coel no. 12864), and

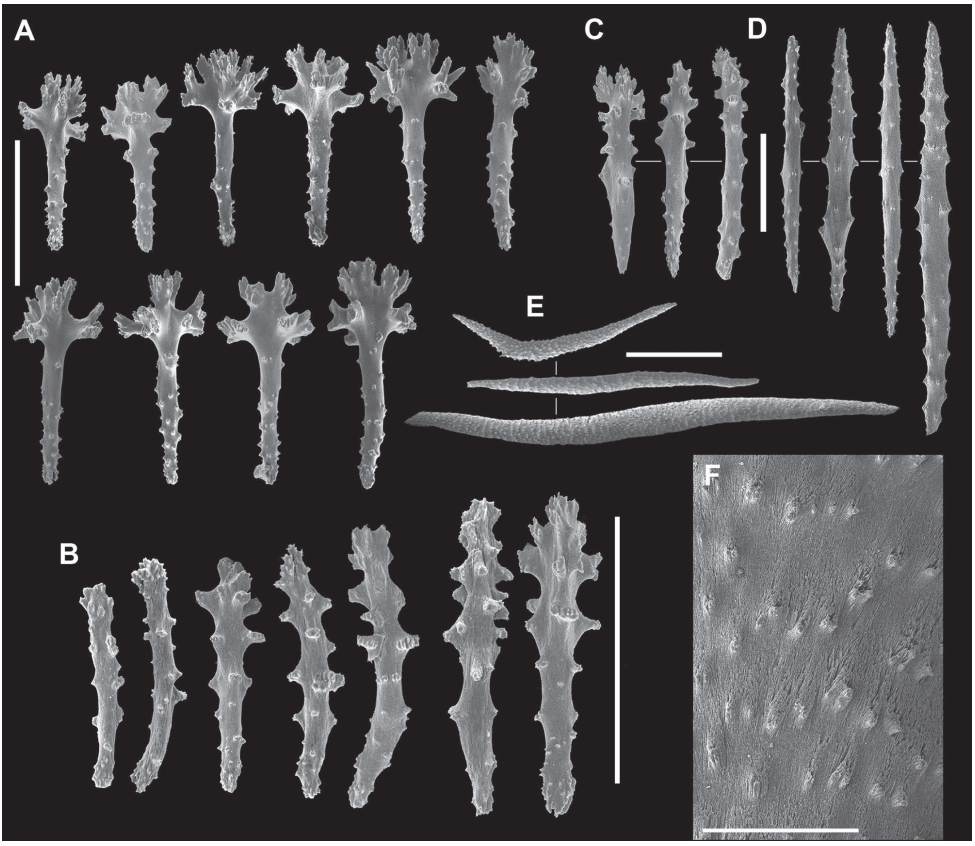

Figure 6. *Sinularia lamellata* RMNH Coel no. 12864. Sclerites of the polypary. **A** clubs of surface layer **B–C** point sclerites **D** spindles from surface **E** spindles from interior **F** tuberculation. Scale bars: 0.10 mm (**A–D, F**), 1 mm (**E**).

SEM images are provided (Figs 6, 7). The surface layer of the polypary contains clubs, up to 0.16 mm long, some featuring a central wart comprised of a markedly spiny head (Fig. 6A). The polyps have point sclerites with head either poorly developed or distinct, up to 0.12 mm long (Fig. 6B), along with longer ones, up to 0.23 mm (Fig. 6C). There are no collaret or tentacle sclerites. The lack of collaret and tentacle sclerites in this specimen was observed previously (McFadden et al. 2009), and is probably caused by storing the specimen in formalin as many sclerites showed damage. A specimen from Palau identified as *S. lamellata* was also examined by McFadden et al. (2009), and that specimen showed collaret, point and tentacle sclerites (in situ photograph of that specimen available in WoRMS). The surface of the polypary contains some pointed spindles, up to 0.40 mm long (Fig. 6D). The longer ones might be transitional forms to the internal spindles of the polypary (Fig. 6E). Neither the point sclerites nor the spindles of the polypary were mentioned in the original description (see Verseveldt and Tursch 1979). The surface of the colony base contains clubs

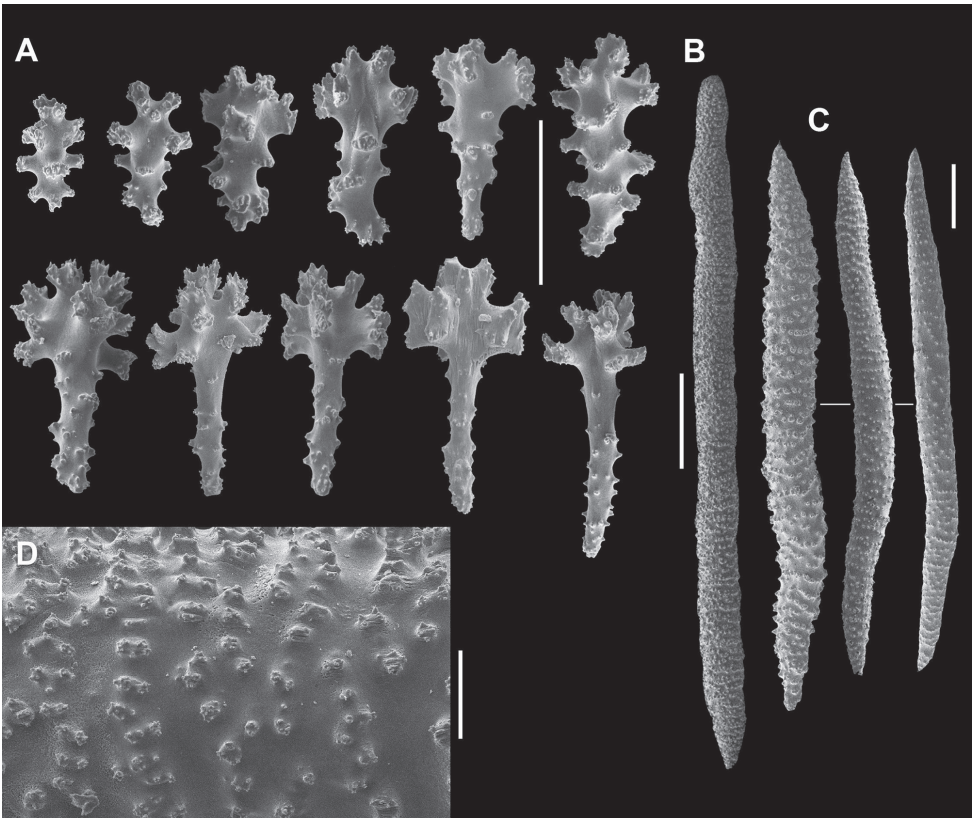

Figure 7. *Sinularia lamellata* RMNH Coel no. 12864. Sclerites of the colony base; **A** clubs of surface layer **B–C** spindles from interior base **D** tuberculation of spindles. Scale bars: 0.10 mm (**A, D**), 1 mm (**B, C**).

similar to those of the polypary, measuring up to 0.18 mm long, but some feature a wider head (Fig. 7A).

The interior of the polypary has almost straight spindles or slightly bent ones, up to 4.8 mm long (Fig. 6E), ornamented with simple low conical warts (Fig. 6F). The interior of the colony base has slightly bent or almost straight spindles, up to 6.3 mm long (Fig. 7B, C), with simple warts (Fig. 7D).

A comparison of *Sinularia lamellata* with *S. mesophotica* reveals that the club heads of the two species are quite different, as the former feature terminal prominences consisting of closely-packed, pointed, thin spikes (see also Verseveldt and Tursch 1979), while in the latter they are mostly truncate. Furthermore, *S. lamellata* possesses spindles on the surface of the polypary, where none exist in *S. mesophotica*. The polyp sclerites of both species markedly differ, with *S. mesophotica* having only collaret and tentacle sclerites while *S. lamellata* has points as well as collaret and tentacle sclerites. Similarly, the coenenchymal spindles of *S. lamellata* are longer and their ornamentation differs from that of *S. mesophotica*. It is thus evident that *S. mesophotica* differs

morphologically from both *S. brassica* and *S. lamellata*, the two previously described *Sinularia* species that possess a similar funnel-shaped polypary.

Sinularia frondosa Verseveldt, 1978 also has somewhat similar sclerites, but this species does not have the funnel-shaped polypary. Moreover, McFadden et al. (2009) re-examined the type of *S. frondosa* and found that it shares the morphological characters of clade 5B, like *S. lamellata*.

The phylogenetic analyses also support the genetic distinction of *Sinularia mesophotica* sp. n. from *S. brassica*, *S. lamellata*, and all other species of *Sinularia* for which molecular data are available (Fig. 5). *Sinularia brassica*, including the morphologically and genetically distinct *dura* form with a funnel shape, is phylogenetically distinct from all other *Sinularia* species, comprising the previously described clade 1 (McFadden et al. 2009), whereas reference specimens identified morphologically as *S. lamellata* belong to clade 5B. In contrast, *S. mesophotica* occupies a unique phylogenetic position outside of any of the five recognized clades to which all other known *Sinularia* species belong, and can be considered to represent a sixth, phylogenetically distinct clade (Fig. 5).

The five previously recognized clades of *Sinularia*, as well as distinct subclades within the two large clades 4 and 5, can be distinguished morphologically based on a suite of four primary morphological characters. These include the presence of sclerites in the (a) tentacles, (b) collaret, and (c) points regions of the polyp, as well as (d) the shape of the club sclerites in the colony surface tissues (McFadden et al. 2009). For example, clade 1 (*S. brassica*) has scales in the tentacles but lacks a collaret and points, and the surface club sclerites are characterized by very wide heads of unique form. In contrast, species belonging to clade 5B (which includes *S. lamellata*) have sclerites in the tentacles, a collaret and points, and surface clubs with a distinct central wart. Clade 6 (*S. mesophotica* sp. n.) can be distinguished from all other clades by the presence of rods in the tentacles, a collaret but no points, and surface clubs with a central wart that may be indistinct or absent. It is evident that *S. mesophotica* differs both morphologically and genetically from all other congeners, and is thus justified to be a new species.

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RESEARCH ARTICLE

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A new species of *Phyllocomus* Grube, 1878 from the Yellow Sea, China (Annelida, Ampharetidae)

Jixing Sui[1,2], Xinzheng Li[1,2,3]

1 *Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China* **2** *Laboratory for Marine Biology and Biotechnology, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266071, China* **3** *University of Chinese Academy of Sciences, Beijing 100049, China*

Corresponding author: *Xinzheng Li* (lixzh@qdio.ac.cn)

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Abstract

A new species of the ampharetid genus *Phyllocomus*, *P. chinensis* **sp. n.**, is described based on material from the Yellow Sea. The new species is distinguished from the known species of this genus by having two thoracic regions, with segments of the anterior region (up to thoracic chaetiger 10) approximately half as long as those of the posterior region, neuropodia of the anterior region are large while those of the posterior region become gradually smaller, thoracic neuropodia without dorsal cirrus, and abdominal neuropodia with a papillary dorsal cirrus. A key to all species of *Phyllocomus* is given.

Keywords

Polychaete, *Phyllocomus chinensis* sp. n., *Schistocomus*, taxonomy

Introduction

Ampharetids are small to medium-sized, tubiculous worms which have a worldwide marine distribution from the intertidal to 8292 m deep (Jirkov 2011; Jumars et al. 2015). Ampharetidae comprise approximately 230 species distributed among 62 genera, 34 of them monotypic (Read 2017). The genus *Phyllocomus* was erected in 1878 by Grube for the species *P. crocea* Grube, 1878. Holthe (2000) described the species *P. balinensis*

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Holthe, 2000 and characterized the genus *Phyllocomus* as having four pairs of branchiae, at least two of these foliate, twelve thoracic uncinigers and a long abdomen.

The genus *Schistocomus* Chamberlin, 1919 resembles *Phyllocomus* in having four pairs of branchiae, twelve thoracic uncinigers, and a long abdomen. It differs from the latter in having branchiae of two types, one pair smooth and awl-shaped, and the other three with one or two series of lamellar branches. However, in *Phyllocomus* the two known species also both have two types of branchiae, awl-shaped and foliate. So, we agree with Day (1964) that *Schistocomus* is a synonym of *Phyllocomus*. Although Reuscher et al. (2009) considered that *Schistocomus* was a valid genus, he now agrees with Day (1964) (pers. comm. Reuscher, 2016). Thus, five valid species have been described in the genus *Phyllocomus*: *P.crocea* Grube, 1878 from the Southern Ocean; *P. balinensis* Holthe, 2000 from the Bali Sea; *P. hiltoni* (Chamberlin, 1919) from Laguna Beach (USA); *P. fauveli* (Hartman, 1955) from India; and *P. sovjeticus* (Annenkova, 1937) from the Japanese Sea.

Recently, two *Phyllocomus* specimens were identified and separated during sorting of material of Ampharetidae deposited in the Marine Biological Museum of the Chinese Academy of Sciences (MBMCAS). These specimens represent an undescribed species. They are described herein and proposed as a new species to science.

Materials and methods

The two specimens were collected using a 1.5×0.5 m Agassiz trawl from the Yellow Sea by the team investigating a project entitled "The key processes, mechanism and ecological consequences of jellyfish blooms in China coastal waters" in June 2012 (Qiu, 2014). They were fixed in ethanol and preserved in 75% ethanol. The specimens are deposited in the Marine Biological Museum of the Chinese Academy of Sciences (**MBMCAS**). The specimens were photographed with a digital camera attached to a Nikon AZ100 microscope and drawn with camera lucida attached to a Nikon SMZ1500 microscope.

Systematics

Family Ampharetidae Malmgren, 1866
Genus *Phyllocomus* Grube, 1878

***Phyllocomus chinensis* sp. n.**
http://zoobank.org/ECA63BE1-2F58-4AB2-BA5F-A84D754E2F98
Figs 1–3

Type material. Holotype: complete. MBM285071. Yellow Sea, Station A3 (36°59'28"N, 123°58'17"E); depth 77 m; shell and sand; coll. Dong, D. and Sui J.; 28 June 2012.

Figure 1. *Phyllocomus chinensis* sp. n., tube of holotype. Scale bar 2 cm.

Paratype. complete. MBM285072, same locality.

Diagnosis. Prostomium with two rows of eyes, approximately ten in each row, appear to be crescent-shaped. Buccal tentacles smooth. Paleae and postbranchial hooks absent. Four pairs of branchiae. Twelve thoracic uncinigerous segments, 34 abdominal uncinigerous segments, without rudimentary notopodia. Pygidium with two pairs of long cirri.

Description. Holotype. Tube cylindrical, black, with broken shells and sand (Fig. 1). Length 36 mm, thorax width 5 mm without chaetae. Thorax and abdomen well defined; thorax approximately twice width of abdomen (Fig. 2A). Color in alcohol pale yellow; appear to be some pigmentation on prostomium.

Prostomium feebly developed on dorsum and forming lower triangular lobe ventrally with convex anterior margin. Two rows of eyes, approximately ten in each row, appear to be crescent-shaped. Buccal tentacles smooth (Fig. 2B). First segment achaetous. Paleae and postbranchial hooks absent. Four pairs branchiae. Innermost branchiae of anterior transverse row originating from segment II, outermost branchiae of anterior transverse row originating from segment III, outer pair awl-shaped, smooth (Fig. 3A), inner pair with single series of pectinate lamellae (Fig. 3B). Innermost branchiae of posterior transverse row originating from segment IV, outermost branchiae of posterior transverse row originating from segment V, two pairs of branchiae both with double rows of lamellae (Fig. 3C).

Notopodia begin on segment III, present in 15 segments. Notopodia well-developed, conical, bearing bundle of winged capillary chaetae. Notopodia and capillaries of third to fifth segments increasing gradually in size. Neuropodial uncini begin on fourth chaetiger (segment VI) and present in 12 thoracic segments. Thorax sharply subdivided into two regions. Segments of anterior region (up to thoracic chaetiger 10) approximately half as long as those of posterior region, neuropodia of anterior region large, and similar-sized, while those of posterior region become gradually smaller; the neuropodia of last thoracic unciniger is half size of first thoracic unciniger. Neuropodia of thoracic uncinigers are tori, without dorsal cirrus; neuropodia of abdominal uncinigerous are pinnules, with papillary dorsal cirrus (Fig. 2E). Continuous ventral shields present to approximately thoracic unciniger 7. Elevated or modified notopodia

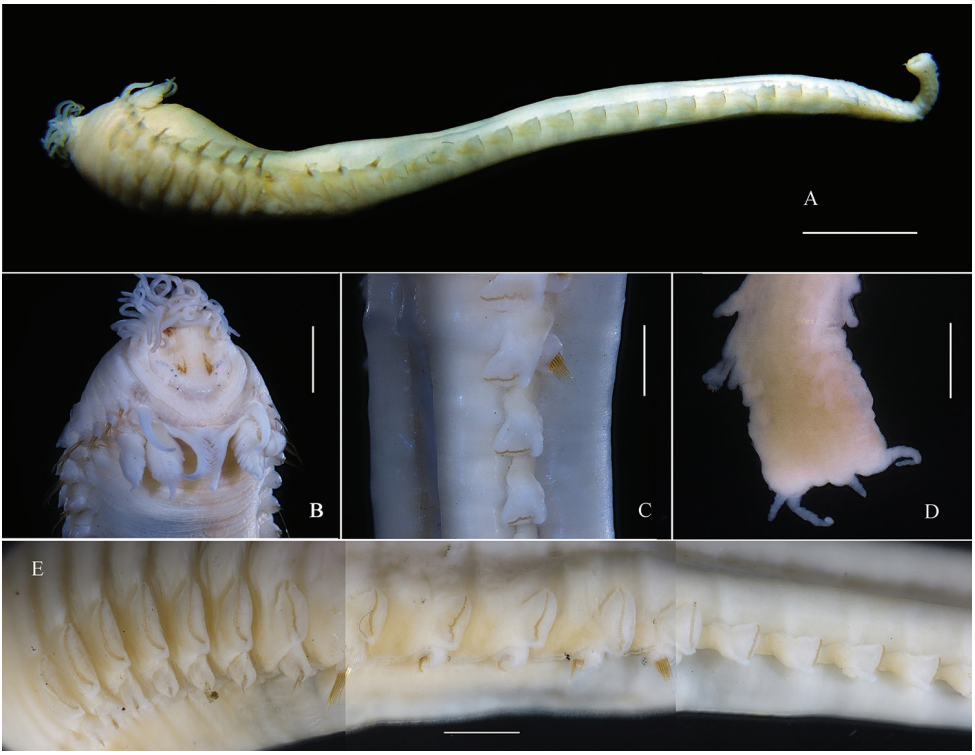

Figure 2. *Phyllocomus chinensis* sp. n. **A** whole specimen, lateral view **B** anterior end, dorsal view **C** last thoracic and first abdominal segments, lateral view **D** posterior region (with two pairs of long anal cirri) **E** consecutive variation of the neuropodia from segment 6 to segment 21. Scale bars **A**: 4 mm, **B, E**: 2mm, **C–D**: 1 mm.

absent. Thirty-four abdominal uncinigerous segments, without rudimentary notopodia (Fig. 2C). Thoracic torus 1 mm long, with approximately 68 uncini. Abdominal torus 0.5 mm long, with approximately 38 uncini. Uncini in abdominal segments are smaller than those of thorax. All uncini with single row of five teeth (Fig. 3D, E). Pygidium with two pairs of long cirri (Fig. 2D).

Variation. Paratype 25 mm long, 4 mm wide without chaetae, has 35 abdominal uncinigerous segments.

Etymology. The species is named after its type locality on the coast of China. The species name is an adjective in the nominative singular, derived from China, with the Latin suffix -ensis to indicate the Chinese seas.

Distribution. Yellow Sea at 77m depth. It is suspected that some species-list records of *P. hiltoni* and *P. sovjeticus* from China belong to *P. chinensis* sp. n. (Huang 1994; Liu 2008). Examination of more material from different localities will establish a more accurate distribution of the new species.

Remarks. Three species of *Phyllocomus*, *P. hiltoni* (Chamberlin, 1919), *P. fauveli* (Hartman, 1955) and *P. sovjeticus* (Annenkova, 1937), are similar to the new species. They

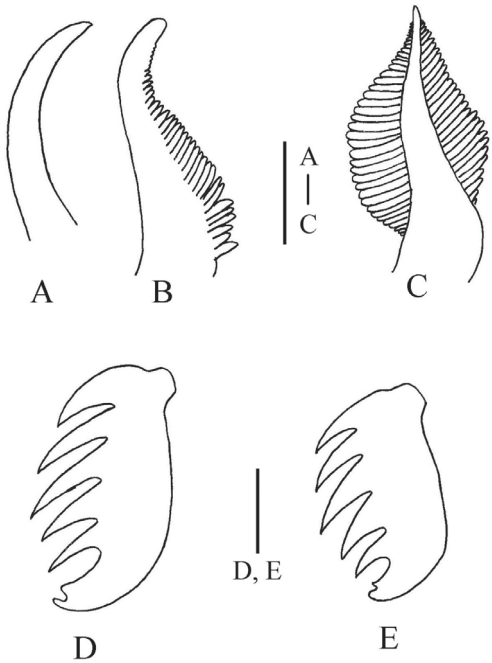

Figure 3. *Phyllocomus chinensis* sp. n. **A** awl-shaped branchiae from segment III **B** branchiae with one row of lamellae from segment II **C** branchiae with two rows of lamellae from segment 5 **D** thoracic uncinusfrom segment 7, lateral view; **E** abdominal uncinus from segment 20, lateral view. Scale bars **A–C**: 1 mm, **D–E**: 10 μm.

all have branchiae of the same type. *Phyllocomus hiltoni* and *P. fauveli* differ from the new species by having a long dorsal cirrus in the abdominal neuropodium, while the new species has a papillary dorsal cirrus. There are two major differences between the new species and *P. sovjeticus*: (1) the new species has thoracic neuropodia without dorsal cirri, while *P. sovjeticus* has large rounded, feebly-distinct papillary dorsal cirri (Annenkova 1937), (2) the new species has abdominal segments without rudimentary notopodia, while *P. sovjeticus* has a small and rounded rudimentary lobe (Annenkova 1937). Both are important characters to distinguish ampharetids species. Otherwise, the new species has two rows of eyes, approximately ten in each row, which appear to be crescent-shaped, 34–35 abdominal uncinigerous segments, and two pairs of long cirri in the pygidium, while the latter has no eyes, 44-54 abdominal uncinigerous segments, and a few rounded papillae on the pygidium (Okuda 1947). A key to all species of *Phyllocomus* is provided below.

Key to *Phyllocomus* species

1 At least two pairs foliate branchiae **2**
– Three of 4 pairs of lamellate branchiae **3**

2 Bases of last pair of branchiae as long as remaining branchial bases .... ***P. crocea*** **Grube, 1878**
– Bases of last pair of branchiae more than twice as long as remaining branchial bases ..... ***P. balinensis*** **Holthe, 2000**
3 Abdominal neuropodia with long dorsal cirri **4**
– Abdominal neuropodia with papillary dorsal cirri **5**
4 Awl-shaped and unipinnate pairs of branchiae in one transverse row .... ***P. fauveli*** **(Hartman, 1955)**
– Unipinnate pair of branchiae located in front of awl-shaped pair .... ***P. hiltoni*** **(Chamberlin, 1919)**
5 Thoracic neuropodia without dorsal cirri ..... ***P. chinensis*** **sp. n.**
– Thoracic neuropodia with large papillary dorsal cirri .... ***P. sovjeticus*** **(Annenkova, 1937)**

Acknowledgments

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RESEARCH ARTICLE

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Differentiation of three common deep-water hermit crabs (Crustacea, Decapoda, Anomura, Parapaguridae) from the South African demersal abundance surveys, including the description of a new species of *Paragiopagurus* Lemaitre, 1996

Jannes Landschoff[1], Rafael Lemaitre[2]

1 *Department of Biological Sciences and Marine Research Institute, University of Cape Town, Rondebosch 7701, South Africa* **2** *Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, 4210 Silver Hill Road, Suitland, MD 20746, U.S.A.*

Corresponding author: *Jannes Landschoff* (jannes@landschoff.net)

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Abstract

Deep-water hermit crabs of the family Parapaguridae can be abundant (up to 20 kg or 1000 hermit crab individuals per haul) in the trawl bycatch collected during South African demersal abundance research surveys. Until recently, only two parapagurid species had been recognized in the bycatch; *Parapagurus bouvieri* Stebbing, 1910, and *Sympagurus dimorphus* (Studer, 1883). Detailed examination of numerous samples of parapagurid specimens from research surveys revealed the existence of a third, undescribed species previously confounded with *S. dimorphus*, but in fact belonging to a different genus. This new species, *Paragiopagurus atkinsonae* **sp. n.** is the 25th in the genus *Paragiopagurus* Lemaitre, 1996, and has been found only in a small region on the West Coast shelf of South Africa, at depths of 199–277 m. The species is herein fully described and illustrated, including colour images, µCT scans of selected body parts, and CO1 barcode data. The new species is morphologically most similar to *P. ventilatus* Lemaitre, 2004, a species associated with hydrothermal vents, but differs in armature of the fourth antennal segment (armed with a spine on the dorsolateral distal angle vs. unarmed in *P. ventilatus*); setation of the antennal flagella (nearly naked vs. with dense setae in *P. ventilatus*); plumose setation on the third maxillipeds and basal segments of chelipeds (absent vs. present in *P. ventilatus*); number of rows of scales on the propodal rasp of

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pereopod 4 (two or three rows vs. one row in *P. ventilatus*); and degree of telson asymmetry (weakly asymmetrical vs. strongly asymmetrical in *P. ventilatus*). *Paragiopagurus atkinsonae* **sp. n.** is superficially similar to *S. dimorphus*, with males of the two species showing the same extreme degree of sexual dimorphism on the right cheliped, general light orange colouration, and frequent use of colonial zoanthid carcinoecia for pleonal protection. To aid in future identifications and to facilitate data gathering during surveys, a comparison of *P. atkinsonae* **sp. n.** with *S. dimorphus* is provided, along with descriptions of colouration and photographs of live specimens of all three parapagurid species. Information on taxonomy of the species is summarized, as well as knowledge of their distribution in the demersal research survey regions of South Africa.

Keywords

Crustacea, Parapaguridae, *Paragiopagurus*, new species, hake, *Merluccius* spp., South Africa

Introduction

The South African Department of Agriculture, Forestry and Fisheries (DAFF, formerly Department of Environmental Affairs and Tourism) has conducted biannual demersal fishery surveys since 1986. To assess the stock status of commercial fish species such as South African hake (*Merluccius* spp.), two 'demersal surveys' are usually conducted every austral summer (West Coast) or autumn (South Coast). In some years, the two surveys are repeated during the winter or spring. Each survey conducts between 100–120 trawls, the majority of these take place between the 100–500 m isobaths, but some trawls extend to depths >1000 m (Yemane et al. 2009). Among the invertebrate bycatch retained in research trawls, deep-water hermit crabs of the family Parapaguridae are particularly common and occasionally, remarkably abundant, although they have not always been adequately monitored. On the West Coast, a trawl can contain up to 20 kg (about 1000 individuals) of parapagurids per haul, and these can make up the vast majority of all invertebrates retained in the research trawls (Fig. 1; L. Atkinson, pers. comm.). Such parapagurid abundance is an indication of their ecological importance on the South African continental shelf. The exact role, however, that these anomuran crustaceans might play in the benthic community remains to be studied.

Since 2011, invertebrate bycatch, including parapagurids, have been monitored more consistently in research surveys, as part of DAFF's commitment to developing an ecosystem approach to management. Based on limited benthic taxonomic literature from the region, biologists identified only two abundant parapagurid species, *Sympagurus dimorphus* (Studer, 1883) and *Parapagurus bouvieri* Stebbing, 1910. However, during the January 2012 West Coast survey on the RS Africana, an unfamiliar male parapagurid specimen with "green eyes" was noticed and collected by Dr. Lara Atkinson, a researcher with the South African Environmental Observation Network (SAEON), leading the invertebrate monitoring component. The individual male specimen was sent for identification to the junior author who concluded that the specimen might represent an undescribed species of *Paragiopagurus* Lemaitre, 1996, but without additional specimens he was unable to make a final determination. Subsequently, during the 2015

and 2016 DAFF West Coast demersal surveys, numerous additional specimens were collected on request of the senior author, and proved to be conspecific with the first male specimen obtained by Dr. Atkinson. A detailed taxonomic study of all these specimens showed that indeed, they represent a new species of *Paragiopagurus* that co-occurs with the two common parapagurid species in the DAFF demersal research surveys, although in a comparatively confined area on the West Coast. Herein we fully describe and illustrate this new species, including colour photographs. Furthermore, to improve understanding of the parapagurid fauna occurring on the South African continental shelf, we compare this new species with the other two co-existing parapagurids, *S. dimorphus* and *P. bouvieri*. For the first time, live colour information is provided for the latter two hermit crab species. In combination, this diagnostic information on the three most common South African deep-water hermit crabs will facilitate improved accuracy in identification of the species, as well as future monitoring and ecological studies.

The systematics and taxonomy of deep-water hermit crabs of the family Parapaguridae has been revised in a number of broad studies over the last three decades. The family currently includes 91 species classified in 10 genera, of which five are monotypic (Lemaitre 1989; 1993; 1996; 1998; 1999; 2004a; 2004b; 2013; 2014; Osawa 1995; McLaughlin et al. 2010). The new species described herein within *Paragiopagurus* Lemaitre, 1996, is the 25th known for this genus. The other two genera represented in the bycatch of demersal research surveys, *Parapagurus* Smith, 1879, and *Sympagurus* Smith, 1883, each contain 17 species. Although many species of parapagurids are known to occur in the western Indian Ocean and vicinity of the east African coast, only eight species in four genera have previously been documented specifically from South Africa: *Oncopagurus africanus* (de Saint Laurent, 1972), *Parapagurus andreui* Macpherson, 1984, *P. bouvieri*, *P. richeri* Lemaitre, 1999, *P. stenorhinus* Lemaitre, 1999, *Strobopagurus sibogae* (de Saint Laurent, 1972), *Sympagurus dimorphus*, and *S. trispinosus* (Balss, 1911). In a recent catalogue of decapods, Emmerson (2016a, b) did list 13 species of parapagurids from the broad region that encompasses Namibia, South Africa and Mozambique, including two species of *Paragiopagurus*; however, the two latter species have only been reported from the Valdivia Bank, off Namibia. Thus, the new species of *Paragiopagurus* described herein represents the first report of a species of *Paragiopagurus* in waters of South Africa.

Several earlier reports of parapagurids from South Africa have been corrected in various taxonomic revisions of species in this family, as follows. Lemaitre (1989, 1999) concluded that reports by Kensley (1969, 1974, 1977) of *Parapagurus pilosimanus* Smith, 1879 actually represent *P. bouvieri*. The subspecies *Parapagurus pilosimanus bouvieri* proposed by de Saint Laurent (1972) in her division of the genus *Parapagurus*, and listed by Kensley (1981) in his zoogeographic study of Southern African decapods, was elevated to species status by Lemaitre (1989, 1999). *Parapagurus kilburni* Kensley, 1973, described from off Durban, South Africa, and subsequently listed by Kensley (1981), was determined by Lemaitre (2004a) to be conspecific, and thus a junior synonym, of *Strobopagurus sibogae*.

Materials and methods

Since 2011, targeted invertebrate specimens retained in the research trawl nets were collected during the DAFF demersal research abundance surveys, using a German otter trawl design with various configurations, and a 75 mm mesh cod-end fitted with a 35 mm mesh liner. Trawls were deployed for 30 minutes (bottom time) over all feasible habitats on the South African shelf (for detailed methods see Atkinson et al. 2011). During the 2015 research surveys, hermit crabs were pre-sorted on board by scientific staff, and all specimens of *S. dimorphus* and *P. bouvieri* were separated. Three male specimens with "green eyes" were obtained during the 2015 surveys. During the 2016 research surveys, a subsample of approximately 100 hermit crab specimens from each trawl were separated and frozen for further identification at the University of Cape Town (UCT). Three additional males and 23 females with "green eyes" were obtained from trawls at two West Coast stations during the 2016 surveys. All specimens with "green eyes" were found to be the new species of *Paragiopagurus* herein described. No specimens with "green eyes" were found in trawls from the South Coast. Live images of *S. dimorphus* and *P. bouvieri* were taken in the laboratory at the University of Cape Town, and in a photographic tank on board of the RS Africana during an additional South Coast spring survey in September/October of 2016.

The μCT scan of the holotype of the new species of *Paragiopagurus* was performed at the CT Scanner Facility at Stellenbosch University, South Africa, using a General Electric Phoenix V|Tome|X L240 with NF180 option (du Plessis et al. 2016). The specimen was defrosted and placed on top of a plastic rod with dense polystyrene foam as a platform, and consecutively scanned at an X-ray voltage of 100 kV and 100 μA, and a resolution of 35 μm. Images were recorded in 3200 steps in one full rotation of the sample averaging two image acquisitions at every step. Using a detector shift function between images reduced ring artifacts. The projection images were reconstructed using the system-supplied General Electric Datos reconstruction software, which were subsequently utilized for the visualization of the right cheliped using Volume Graphics VGStudioMax 3.1. (Heidelberg, Germany).

Illustrations were drawn using a Wild stereomicroscope equipped with a camera lucida, and digitally traced in Inkscape 0.91 (www.inkscape.com). Colour photographs were processed in Gimp 2.8 (www.gimp.com).

Specimens examined in this report are deposited in the Iziko South African Museum, Cape Town, South Africa (SAMC), the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), as well as in the Lee Kong Chian Natural History Museum, Singapore (ZRC). Morphological terminology for parapagurids is that used by Lemaitre (2013). Measurements of specimens, in millimeters (mm), listed in the material examined sections are for shield length (SL), taken from the tip of the rostrum to the midpoint of the posterior margin of the shield. Other abbreviations used are: ovig: ovigerous; SCDSA: South Coast Demersal Survey Autumn; SCDSS: South Coast Demersal Survey Spring; WCDSS: West Coast Demersal Survey Summer; sta: station; and in the material examined sections, months are abbreviated by the first three letters.

Muscular tissue, usually from the merus of the right cheliped, was extracted from freshly frozen specimens, placed in 96% ethanol, and sent to the South African Institute for Aquatic Biodiversity (SAIAB). At SAIAB, DNA extractions were carried out using a standard "salting out – ethanol precipitation" protocol (Sunnucks and Hales 1996), followed by the amplification of the 'barcoding' (Hebert et al. 2003) fragment of the cytochrome *c* oxidase subunit I (CO1) gene for each sample by Polymerase Chain Reaction (PCR), using the universal invertebrate primers (LCOI-1490 and HCOI-2198) of Folmer et al. (1994), or their degenerate variants (dgLCO1490 and dgHCO2198; Meyer 2003). PCR recipes and conditions followed Meyer (2003) and Gouws et al. (2015), with annealing performed at 48 °C for the latter. Successful amplification was determined by visualising products under UV light, following electrophoresis in 1% agarose gels, stained with ethidium bromide, in a TBE buffer. PCR products were purified with an Exonuclease I – Shrimp Alkaline Phosphate (Exo/SAP, ThermoFisher Scientific) protocol (Werle et al. 1994), sequenced in both the forward and reverse directions using BigDye v3.1 (Applied Biosystems, Austin, Texas) terminator chemistry and analyzed on an ABI-Hitachi 3500 Genetic Analyser (Applied Biosystems) at SAIAB. The resulting sequences were checked against their chromatograms for misreads and sequencing errors using ChromasLITE (Technylesium). Sequences were aligned, edited and the consensus DNA barcode compiled using Lasergene SeqMan Pro 9 (DNASTAR, Madison, Wisconsin). Barcodes were uploaded to the SeaKeys (SEAKY) project on BOLD (www.boldsystems.org; Ratnasingham and Hebert 2007) and were submitted to GenBank. For a number of specimens, tissues were submitted to the Canadian Centre for DNA Barcoding, Biodiversity Institute of Ontario, University of Guelph, for barcoding. These data were also uploaded to SEAKY on BOLD. For future reference and studies, the database gene codes are included under each species.

Results

Systematic account

Family Parapaguridae Smith, 1882
Genus *Paragiopagurus* Lemaitre, 1996

***Paragiopagurus atkinsonae* sp. n.**
http://zoobank.org/833540CC-B266-4010-A401-E7CA010CDE6A
Figs 2–6, 9

Type material. Holotype: male 7.0 mm, South Africa, West Coast, WCDSS2016, CCH008, sta D00723–3243, S31°52.81', E16°57.12', 265 m, 11 Mar 2016 (USNM 1292083).

Paratypes: *South Africa, West Coast*. WCDSS2012, AFR279: 1 male 7.6 mm [with zoanthid symbionts], sta A32208–3233, S31°39.79', E17°02.79', 259 m, 24 Jan

Figure 1. Abundance of deep-water hermit crabs in South African demersal research survey, Agulhas Bank, South Africa, Nan2007 401, sta 1294–008, S35°24.40', E19°10.70', 227 m, 12 Jan 2007: **A** contents of one trawl showing catch **B** close-up of parapagurid specimens and anthozoan symbionts (colonies of *Epizoanthus* sp.) in same. (Photographs by Kerry Sink).

2012, coll. L. Atkinson (USNM 1292086). WCDSS2015, AND004: 1 male 7.6 mm, sta C0416–3258, S32°08.05', E17°08.52', 230 m, 26 Feb 2015 (USNM 1292080); 1 male 7.0 mm (USNM 1292084), 1 male 6.2 mm (SAMC MB-A066814), sta C430–3237, S31°42.07', E16°58.53', 277 m, 1 Mar 2015. WCDSS2016, CCH008: 1 male 6.8 mm, sta D00724, S32°03.18', E17°03.11', 243 m, 11 Mar 2016 (SAMC MB-A066815); 1 male 7.8 mm (USNM 1292082), 3 females 6.4–7.0 mm (USNM 1292081), 4 females 5.9–7.1 (USNM 1292085), 1 ovig. female 6.8 mm (SAMC MB-A066809), 1 ovig. female 5.9 mm (SAMC MB-A066810), 1 ovig. female (SAMC MB-A066811), 3 ovig. females 6.6–7.2 mm, 7 females 7.2–8.0 mm (SAMC MB-A066812), 2 ovig. females 6.7–7.3 mm (SAMC MB-A066813), 1 ovig. female 6.4 mm (SAMC MB-A066816), sta D00726–2446, S32°22.98', E17°27.78', 199 m, 11 Mar 2016.

Description. Eleven pairs of biserial (Fig. 2A), or at most weakly divided quadriserial gills. Shield (Fig. 2B, 6C) about as broad as long; dorsal surface nearly naked or with scattered short setae, with weakly- to moderately-calcified median region extending from anterior margins of rostrum, anterior and lateral projections, to about proximal 0.2 length of shield; anterior, lateral and posterior margins with short setae. Rostrum broadly rounded, with short mid-dorsal ridge. Anterior margins weakly concave. Lateral projections subtriangular, armed with short terminal spine. Anterolateral margins sloping. Ventrolateral margin usually with small spine. Posterior margin broadly rounded. Anterodistal margin of branchiostegite rounded, unarmed, setose.

Ocular peduncles (Fig. 2B) about half, or slightly more than half, length of shield, each with longitudinal row of short setae on dorsal surface. Corneas weakly dilated. Ocular acicles subtriangular, about 0.3 as long as ocular peduncles, each terminating in strong, simple spine; separated basally by about 0.6 the width of 1 acicle.

Antennular peduncles exceeding distal margin of corneas by 0.8–0.9 length of ultimate segment; ventral flagellum with 5–7 articles. Ultimate segment twice, or more than twice, as long as penultimate, with scattered setae dorsally. Basal segment with strong ventromesial spine; lateral face with distal subrectangular lobe armed with 1 or 2 spines, and strong spine proximally.

Antennal peduncles (Fig. 2C) reaching to about distal margin of corneas. Fifth segment unarmed, with longitudinal row of setae on lateral and mesial margins. Fourth segment with strong spine on dorsolateral distal angle. Third segment with strong ventromesial distal spine. Second segment with dorsolateral distal angle produced, terminating in strong, simple spine extending to about half length of acicle and having 2 or 3 small spines dorsally; mesial margin with spine on dorsodistal angle. First segment with lateral surface armed with small spine; ventromesial angle not strongly produced, armed with 1–3 small, blunt spines. Antennal acicle slightly curved outward (dorsal view), overreaching proximal margin of cornea, but not exceeding distal margin of cornea, terminating in strong spine; mesial margin with row of about 10 strong spines of similar size and set at about 45^0 to longitudinal axis of acicle. Flagellum exceeding distal margin of extended right cheliped, nearly naked, or with scattered, short setae less than 1 flagellar article in length.

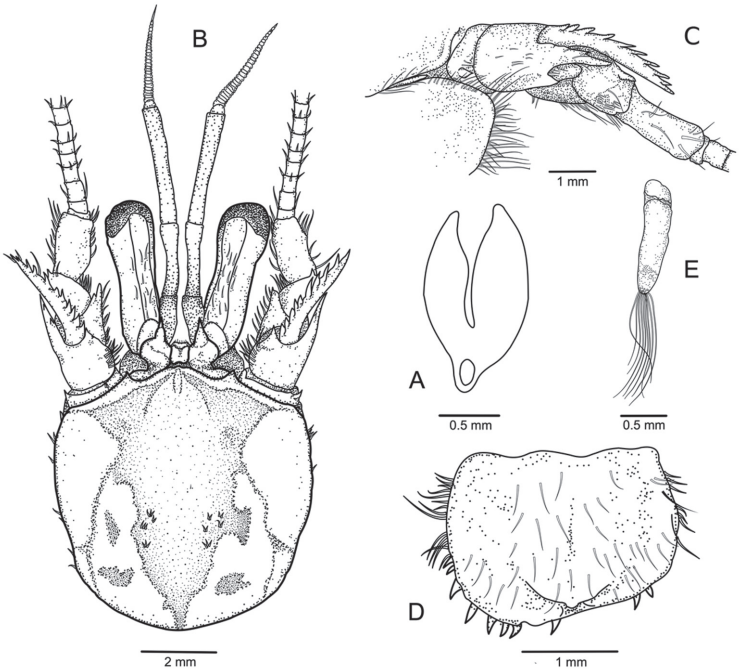

Figure 2. *Paragiopagurus atkinsonae* sp. n., South Africa, West Coast: **A** male paratype 7.0 mm, WCDSS2015 (USNM 1292084); **B–D** male holotype 7.0 mm, WCDSS2016 (USNM 1292083). **A** gill lamella of posterior-most arthrobranch **B** shield and cephalic appendages, dorsal view **C** right antennal peduncle and branchiostegite, lateral view **D** telson, dorsal view **E** left pleopod 2, lateral view.

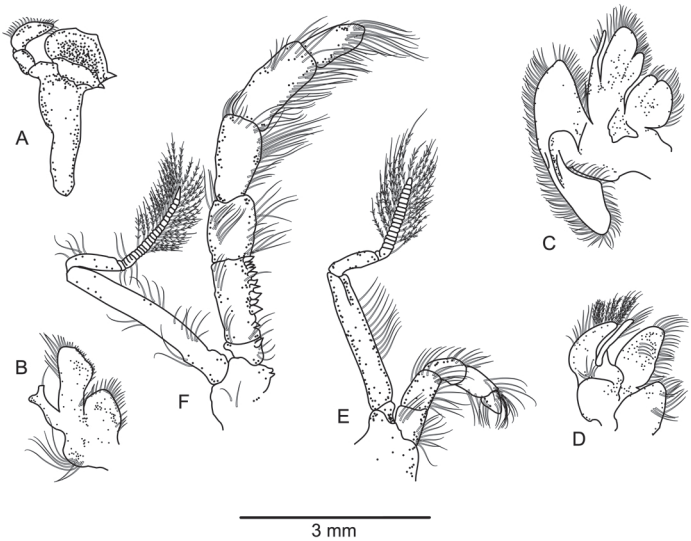

Figure 3. *Paragiopagurus atkinsonae* sp. n., South Africa, West Coast, male paratype 7.0 mm, WCDSS2015 (USNM 1292084). Left mouthparts, internal view. **A** mandible **B** maxillule **C** maxilla **D** first maxilliped **E** second maxilliped **F** third maxilliped.

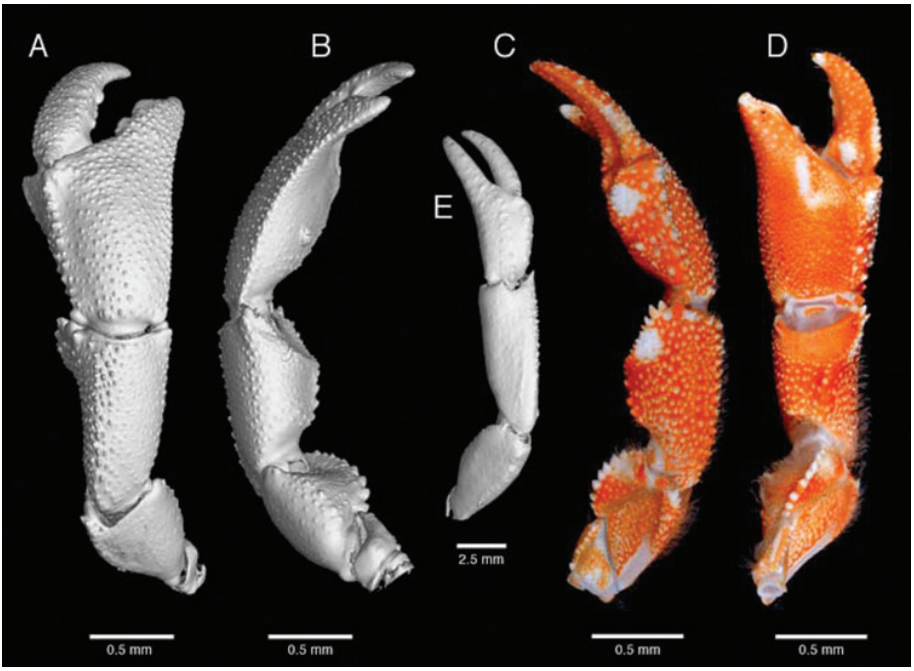

Figure 4. *Paragiopagurus atkinsonae* sp. n., South Africa, West Coast: **A, B, E** microCT scans, male holotype 7.0 mm, WCDSS2016 (USNM 1292083); **C, D** photographs, male paratype 6.8 mm, WCDSS2016 (SAMC MB-A066815). Right cheliped: **A** dorsal view **B** lateral view **C** mesial view **D** ventral view. Left cheliped: **E** dorsal view.

Mandible (Fig. 3A) with 3-segmented palp. Maxillule (Fig. 3B) with external lobe of endopod moderately-well developed, internal lobe with 1 long setae. Maxilla (Fig. 3C) with endopod well exceeding distal margin of scaphognathite. First maxilliped (Fig. 3D) with endopod exceeding distal margin of exopod. Second maxilliped (Fig. 3E) without distinguishing characters. Third maxilliped (Fig. 3F) with crista dentate with about 10 corneous teeth, decreasing in size distally; basis with 1 dorsomesial corneous tooth; coxa with 1 or 2 mesial teeth.

Chelipeds markedly dissimilar, proportions strongly affected by size and sexual dimorphism, males growing distinctly longer right chelipeds with narrower chela, than females. Right cheliped (Figs 4, 6A, B) massive; in males, about 1.5 times as long as left cheliped and 4.3 times as long as SL; in females, about 1.3 times as long as left cheliped and 3 times as SL; dorsal surfaces covered with sparse or inconspicuous short, simple or plumose setae. Chela operculate, somewhat dorsoventrally flattened, less so in males; males about twice as long as wide, or in females about 1.3 times as long as wide. Fingers moderately curving mesioventrally, each terminating in small corneous claw, dorsal surfaces covered with numerous small, blunt to sharp tubercles or spines, ventral surfaces covered with small tubercles; cutting edge of dactyl with 2 larger calcareous teeth and several small teeth in between, distal row of small fused corneous teeth; cutting edge of fixed finger with 2 large, rounded calcareous teeth and several small

calcareous teeth distally and proximally. Dactyl longer (female), or shorter (male), than mesial margin of palm, set at oblique angle to longitudinal axis of palm; mesial margin well defined by longitudinal row of spines or tubercles; proximal half of ventromesial face strongly concave. Fixed finger basally much broader in females than in males. Palm distinctly broader than long in females, or usually distinctly longer than broad in males; dorsal surface covered with numerous small tubercles or spines; lateral margin well defined by row of small tubercles or spines; dorsomesial margin with row of irregular spines (less strong in males); mesial face strongly sloping, slightly concave (less so in males), covered with small tubercles; ventromesial margin weakly delimited (less so in males) by row of low tubercles or spines; ventral surface nearly flat or weakly convex, with small tubercles or spines less numerous than on dorsal surface. Carpus similar to chela in general armature and setation, subtriangular in cross-section, longer in males than in females; dorsal surface covered with numerous small tubercles or spines, generally spines sharper in females than in males; dorsal margin with irregular row of spines, dorsodistal margin armed with strong (females) or weak (males) spines, increasing in size mesially; ventrolateral margin well defined (more so in females) by row of spines increasing in size distally; ventromesial distal margin somewhat expanded, wing-like, armed with row of strong spines. Merus subtriangular in cross-section, dorsal margin unarmed, or with low tubercles and row of short setae, and strong dorsodistal spine; lateral surface with minute tubercles; ventrolateral margin with row of blunt spines distally; mesial surface flat, unarmed, ventromesial margin with row of strong, mostly blunt spines; ventral surface smooth or with very low tubercles. Ischium with ventrolateral row of small spines, and moderately long setae mesioventrally. Coxa with row of small spines on ventrolateral distal margin and ventrodistal row of long setae.

Left cheliped (Figs 4E, 6A, B) generally well calcified, reaching to base of dactyl (females), or mid-length of palm (males), of right cheliped. Fingers weakly bent lateroventrally, gaping slightly when closed, each terminating in sharp corneous claw; dorsal and ventral surfaces unarmed, except for few tufts of short setae; cutting edges each with closely-set small, corneous teeth. Dactyl slightly longer than palm; proximal half of ventromesial face slightly concave. Palm longer than wide; dorsal surface with 2 median rows of small, low tubercles, and sparse tufts of short setae, somewhat depressed medially; dorsomesial margin with row of small tubercles or spines; dorsolateral margin rounded; ventral surface unarmed except for scattered setae. Carpus with moderately dense setation on dorsal, lateral and mesial surfaces; dorsal margin with irregular row of small tubercles or spines, and strong dorsodistal spine; lateral and mesial faces unarmed except for setae, and strong spine on lateroventral distal angle; ventral surface smooth, at most with tufts of sparse setae. Merus unarmed except for minute tubercles on lateral, mesial and ventral faces, and dense setation on dorsal ventromesial margins. Ischium unarmed and smooth except for dense setae on ventral surface. Coxa at most with minute spines on ventromesial distal margin and row of setae on ventrodistal margin.

Ambulatory legs or pereopods 2 and 3 (Figs 5A–D, 6A, B) similar from right to left, except for slightly longer meri on right; usually exceeding right cheliped by about

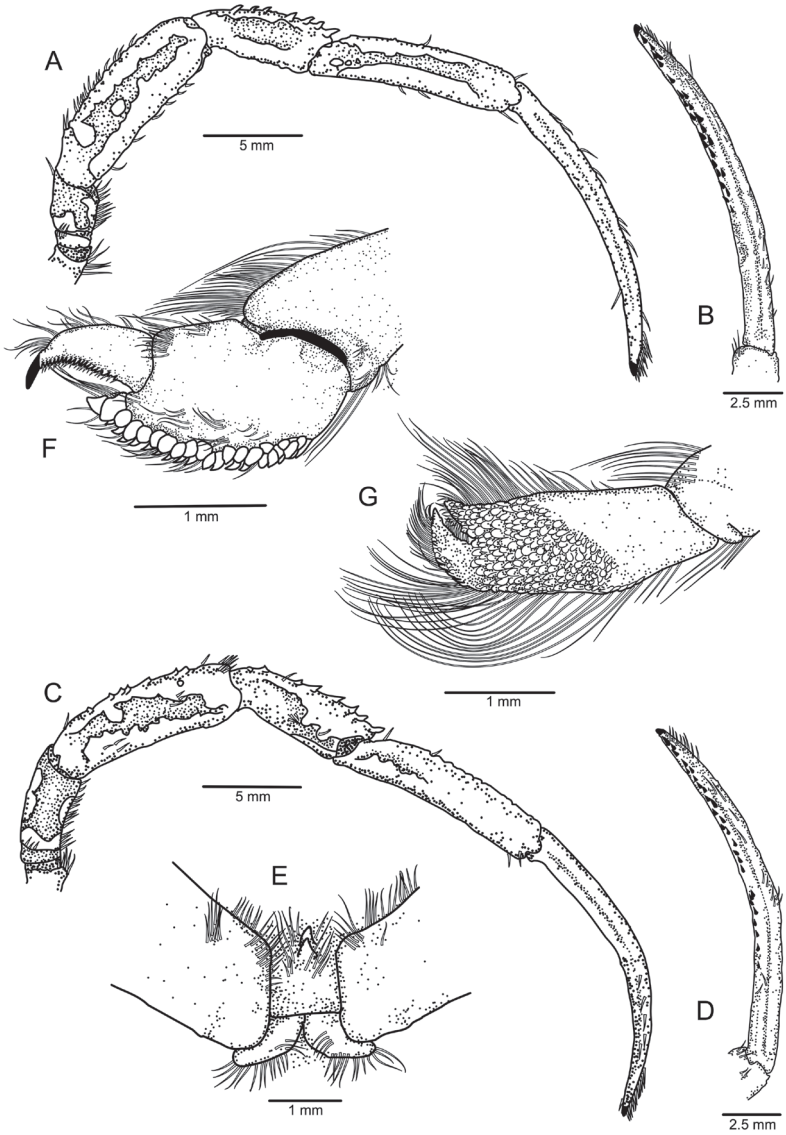

Figure 5. *Paragiopagurus atkinsonae* sp. n., South Africa, West Coast, male holotype 7.0 mm, WCDSS2016 (USNM 1292083). **A** pereopod 2, lateral view **B** dactyl of same, mesial view **C** pereopod 3, lateral view **D** dactyl of same mesial view **E** sternite XII and basal portion of coxae of pereopods 3, ventral view **F** propodus and dactyl of pereopod 4, lateral view **G** propodus and dactyl of pereopod 5, lateral view.

0.2 length of dactyl of legs when fully extended. Dactyl about 1.5–1.9 as long as propodus, broadly curved, terminating in sharp corneous claw; dorsal margin mostly with short setae, except for distal row of bristle-like setae; ventromesial margin (Fig. 5B, D) armed with 2 or 3 irregular rows of short, corneous spinules and usually terminat-

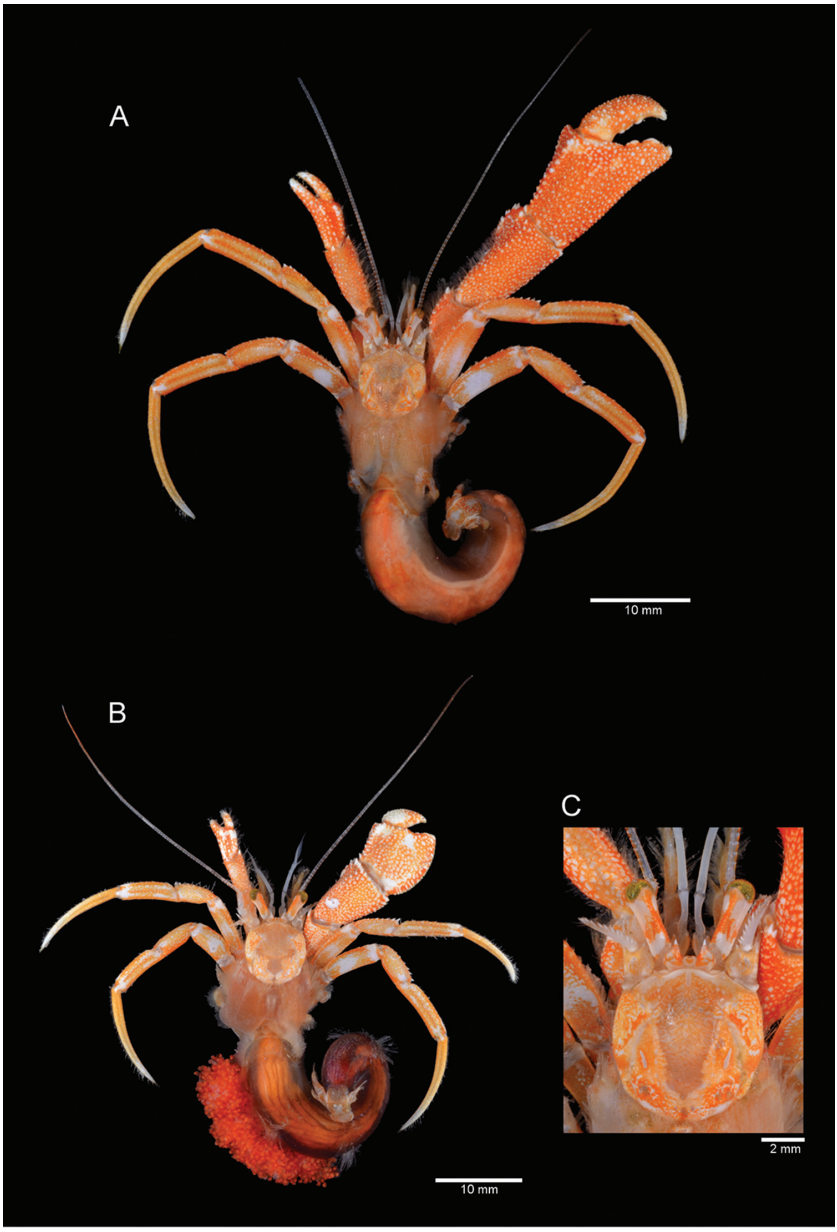

Figure 6. Colouration (in life or fresh). *Paragiopagurus atkinsonae* sp. n., South Africa, West Coast: **A** male holotype 7.0 mm, WCDSS2016 (USNM 1292083) **B** ovig. female 6.4 mm, WCDSS2016 (SAMC MB-A066816) **C** ovig. female 6.8 mm, WCDSS2016 (SAMC MB-A066809), shield and cephalic appendages, dorsal view.

ing as single row near claw; lateral and mesial face with shallow, longitudinal sulcus on proximal half, deeper on mesial face. Propodus nearly naked; dorsal margin with setae usually arising from low tubercles. Carpus nearly naked, or with sparse short

setae; dorsal margin armed with row of distinct, well-spaced small spines (stronger on pereopod 2) increasing slightly in size distally, and small dorsodistal spine. Merus unarmed except for scattered setae on dorsal margin. Ischium with dorsal and ventral row of setae. Coxa unarmed except for 1 or 2 minute spines on ventromesial proximal angle (pereopod 2 only) and ventromesial row of setae. Anterior lobe of sternite XII (of pereopods 3; Fig. 5E) subtriangular, setose, and terminating in simple or more frequently bifid spine.

Pereopod 4 (Fig. 5D) subchelate. Dactyl broadly curved, terminating in sharp, corneous claw, with ventrolateral row of small corneous teeth increasing in size distally. Propodus longer than wide; rasp consisting of 2 or 3 rows of rounded scales. Carpus with long setae on dorsal margin. Merus with rows of long setae on dorsal, ventromesial and ventrolateral margins.

Pereopod 5 (Fig. 5F) chelate. Propodal rasp extending slightly beyond mid-length of segment. Dactyl with row of minute, rounded scales on ventrolateral surface.

Uropods and telson asymmetrical. Telson (Fig. 2D) lacking transverse sutures separating anterior and posterior lobes; dorsal surface with scattered short setae; lateral margins with moderately long (left) and short (right) setae; posterior lobes separated by narrow, median cleft, terminal margins rounded, armed with row of 15–8 (left lobe) or 10–12 (right lobe) short corneous spines, some slightly curved.

Males lacking first gonopods; with unpaired left pleopods 2–5, of which pleopod 2 (Fig. 2E) is 2-segmented, uniramous, and other pleopods biramous. Females with unpaired pleopods 2–5, with well-developed rami on pleopods 2–4, and short endopod on pleopod 5.

Colour (in life; Figs 4C, D, 6A–C). Shield and cephalic appendages mottled orange and cream to white. Ocular peduncles white with basally and distally broadened dorsomedian orange stripe; orange pattern extending to ventromesial face just below midlength of ocular peduncle. Corneas usually green. Ocular acicles mottled orange with white spines. Chelipeds orange-red, with white tubercles and spines. Right chela often with dactyl and fixed finger each with cream patch proximally at about midline, fingertips white; propodus, merus and carpus with distinct cream to white spot on dorsomesial distal angle. Left chela with cream patches of different size, fingertips white. Ambulatory legs orange overall; dactyl light orange, distally cream; propodus with cream patch on distolateral and distomesial angles, lateral face with dark orange stripe; carpus orange overall, with lighter orange medially on lateral face. Merus with white band distally, large white patch on proximal half of lateral face, and darker orange on dorsodistal margin. Uropods and telson mottled orange and cream. Pleon orange, in some females dark red ventrally due to gonads with unspawned eggs. Eggs bright red.

Habitat. Occupying shells created by colonies of *Epizoanthus* sp. that incorporate sand grains in their tissue and form a carcinoecia that completely covers a minute gastropod shell. This *Epizoanthus* sp. appears the same to that frequently used by *Sympagurus dimorphus* in the South African region.

Distribution (Fig. 8). Known so far only from a small portion of the west coast of South Africa, between 31°42'S and 32°23'S, in a depth range of 199–277 m.

Etymology. This species is named after Dr. Lara Atkinson, a researcher from the South African Environmental Observation Network (SAEON), Egagasini Node for marine-offshore systems, who first noticed the presence of this new species and collected the first specimen. The name honours her research efforts to understand the benthic marine fauna of South Africa, and acknowledges the major role she played in organizing sampling of additional material of this new species.

Common name. "Green-eyed hermit crab".

Genetic data. Sta D00723-3243, S31°52.81', E16°57.12', 265 m, male 7.0 mm (holotype), BOLD: SEAKY1181-17 (USNM 1292083). Sta D00726–2446, S32°22.98', E17°27.78', 199 m, ovig. female 6.8 mm, BOLD: SEAKY1181-17 (MB-A066809); ovig. female 5.9 mm, BOLD: SEAKY1183-17 (MB-A066810); male 6.8 mm, BOLD: SEAKY1180-17 (MB-A066815).

Variations. In males with SL > 7.0 mm, the right cheliped (merus to dactyl) ranges from 3.6–4.8 times as long as the shield, and the chela varies from 1.7–2.4 as long as wide. In females with SL > 5.9 mm, the right cheliped (merus to dactyl) ranges from 2.6–3.2 times as long as the shield, and the chela varies from 1.3–1.6 as long as wide. The spination of both right and left chelae tends to be sharper, and stronger in females.

Remarks. Three characters present in *Paragiopagurus atkinsonae* sp. n. exemplify the morphological evolutionary tendencies that in general are observed (Lemaitre 2013) in species of *Paragiopagurus*. These three characters are: biserial gills that are, at most, weakly divided distally; the drastic sexual dimorphism exhibited on the right cheliped; and in males, the complete loss of paired first and second pleopods modified as gonopods. In sharing these three characters, this new species is most similar to *P. ventilatus* Lemaitre, 2004c, a northwestern Pacific species that is known to associate with hydrothermal vents in the northeastern coast of Taiwan and the Mariana Trough (Lemaitre 2004c; Komai et al. 2010). Additionally, both species share a rare armature condition in parapagurids for the ventromesial margin of the dactyls of the ambulatory legs, being armed in this new species with two or three irregular rows of numerous corneous spinules instead of a single regular row of relatively few spines, as in other species of this genus. In other respects, however, these two species are markedly different. In *P. atkinsonae* sp. n. the fourth antennal segment is armed with a spine on the dorsolateral distal angle, whereas in *P. ventilatus* the fourth segment is unarmed; the antennal flagella is nearly naked or with scattered short setae, whereas in *P. ventilatus* the flagella are densely covered with long setae; the third maxillipeds and basal segments of the chelipeds lack dense plumose setae, whereas in *P. ventilatus* these are present; the propodal rasp of pereopod 4 has two or three rows of ovate scales, whereas in *P. ventilatus* the rasp has only one row of ovate scales; the telson is weakly asymmetrical, whereas in *P. ventilatus* the telson is strongly asymmetrical. Furthermore, *P. atkinsonae* sp. n. is not associated with hydrothermal vent habitats, whereas *P. ventilatus* has been found exclusively in or close to vent habitats (Lemaitre 2004c; Komai et al. 2010).

In addition to *Paragiopagurus atkinsonae* sp. n., there are seven other species of *Paragiopagurus* in which the male lacks paired first and second gonopods: *P. trilineatus* Lemaitre, 2013, *P. bicarinatus* (de Saint Laurent, 1972), *P. hirsutus* (de Saint Laurent, 1972), *P. acutus* (de Saint Laurent, 1972), *P. ruticheles* (A. Milne-Edwards, 1891), *P.*

hobbiti (Macpherson, 1983), and *P. ventilatus*. The complete pleopod condition in the male for all these species is the same, i.e., presence of left unpaired pleopods 2–5. Pleopod 2 is uniramous, 2-segmented, with a short distal segment, and pleopods 3–5 are biramous. In both sexes of *P. atkinsonae* sp. n., the propodal rasp of pereopod 4 has two or three rows of ovate scales, a condition similar to that of three other congenerics: *P. trilineatus*, *P. pilimanus* (A. Milne-Edwards, 1880), and *P. tuberculosus* (de Saint Laurent, 1972). Other than the development of pleopods in the male, and the number of rows of scales on the propodal rasp of the pereopod 4, *P. atkinsonae* sp. n. differs significantly from all those species (see Lemaitre 2013).

When using Lemaitre's (2013) species identification key for specimens of *Paragiopagurus atkinsonae* sp. n., the user will reach couplet 19. To accommodate this new species to that key, couplet 19 can be replaced with the following two new couplets 19 and 20 (and changing the numbers of Lemaitre's couplets 20–23 by +1):

19 Ventromesial margins of ambulatory legs (pereopods 2, 3) armed with several irregular rows of numerous corneous spinules **20**

– Ventromesial margins of ambulatory legs (pereopods 2, 3) armed with single, regular row of corneous spinules **21**

20 Propodal rasp of pereopod 4 with 2 or 3 rows of ovate scales; antennal flagella naked or with scattered short simple setae; fourth antennal segment armed with spine on dorsolateral distal angle; telson weakly asymmetrical ..... ***Paragiopagurus atkinsonae* sp. n.**

– Propodal rasp of pereopod 4 with 1 row (at least distally) of ovate scales; antennal flagella densely covered with long mostly plumose setae; fourth antennal segment lacking spine on dorsolateral distal angle; telson strongly asymmetrical ..... ***P. ventilatus***

Genus *Sympagurus* Smith, 1883

Sympagurus dimorphus (Studer, 1883)

Fig. 7A, B, 8

Primary synonyms: *Eupagurus dimorphus* Studer, 1883: 24, figs 11, 12 (type locality: South Atlantic Ocean, South Africa, off Cape of Good Hope, S.M.S. "Gazelle", 34°13.6'S, 15°00.7'E, 211 m).
Parapagurus brevimanus Balss, 1911: 4, fig. 5.
?*Eupagurus modicellus* Stebbing, 1914: 255, pl. 26, fig. D. (See "General distribution").
Sympagurus var. *arcuatus johnstoni* Hale, 1941: 279, fig. 13a–d.
Sympagurus var. *arcuatus mawsoni* Hale, 1941: 280, fig. 14a–c.

Material examined. *South Africa, West Coast*. WCDSS2012, AFR279: 4 males 9.5–12.0 mm, 1 ovig. female 8.1 mm, sta A32144–4116, S32°18.26', E16°18.53', 369

m, 11 Jan 2012 (SAMC MB-A066808). WCDSS2015, AND004: 1 ovig. female 9.7 mm [inside stomach of Monk fish], sta C0400–3330, S33°55.08', E17°39.26', 285 m, 20 Jan 2015 (SAMC MB-A066807); 4 males 10.0–12.0 mm, 5 ovig. females 7.7–9.1 mm, 1 female 9.4 mm, sta C0367–3336, S33°58.11', E17°52.51', 220 m, 9 Feb 2015 (SAMC MB-A066801); 1 male 7.4 mm, sta C0379-3130, S36°34.74', E20°38.10', 12 Feb 2015 (SAMC MB-A066805); 1 female 7.1 mm, sta C0458-5008, S29°57.54', E14°49.40', 448 m, 8 Mar 2015 (SAMC MB-A066803). WCDSS2016, CCH008: 1 male 7.8 mm, sta D00640, S31°28.02', E16°05.64', 470 m, 21 Feb 2016 (SAMC MB-A066806); 1 male 11.2 mm, sta D00726–2446, S32°22.98', E17°27.78', 199 m, 11 Mar 2016 (SAMC MB-A066492).

South Africa, South Coast. SCDSA 2015, AND005: 1 male 14.6 mm, sta D0520-4071, S36°27.78', E21°53.58', 401 m, 20 Apr 2015 (SAMC MB-A066839); 1 male 12.0 mm (SAMC MB-A066840), 1 male 13.2 mm (SAMC MB-A066841), sta D00521–4043, S36°25.50', E21°27.12', 192 m, 20 Apr 2015; 1 male 4.9 mm, sta D00540-6542, S35°21.30', E22°49.98', 585 m, 26 Apr 2015 (SAMC MB-A066833); 1 male 12.7 mm, sta D00561-6671, S34°05.22', E26°55.68', 466 m, 1 May 2015, (SAMC MB-A066818); 1 male 10.3 mm, sta D00565-4224, S34°10.20', E26°46.38', 425 m, 2 May 2015 (SAMC MB-A066823); 1 male 6.5 mm, 1 female 7.5 mm, sta D00582–4153, S34°54.96', E23°22.08', 210 m, 7 May 2015 (SAMC MB-A066820). SCDSA 2016, CCH009: 1 male 11.3 mm, sta D00757-4020, S36°49.19', E20°33.72', 538 m, 4 May 2016 (SAMC MB-A066802); 2 males 10.1–10.4 mm, 3 ovig. females 6.8–7.6 mm, sta D00812–4174, S34°46.80', E24°12.30', 196 m, 19 May 2015 (SAMC MB-A066804); 1 male 8.8 mm (SAMC MB-A066490), 1 ovig. female 9.4 mm (SAMC MB-A066491), sta D00819, S34°52.32', E23°35.70', 195 m, 21 May 2016.

Diagnosis, taxonomy, larval and juvenile morphology. See Lemaitre (1989; 1990; 1996; 2000; 2004b), Lemaitre and McLaughlin (1992), and Poore (2004).

Colour (in life; Fig. 7A, B). Until now, information on colour of *Sympagurus dimorphus* had been based on three published photographs taken of live specimens inside their gastropod housing (Lemaitre 2000, pl. 7; 2004b, fig. 35a; Poore 2004: pl. 17c), and formalin-preserved specimens with patterns still visible (Lemaitre 2004b). Although the basic colour pattern can be discerned in those photographs, the specimens used have only partially visible body parts, and furthermore, the exposures of the images show somewhat distorted colour tones. Herein, we present for the first time a high quality colour photograph of the entire body removed from it's housing of a freshly caught male and of an ovigerous female specimen (Fig. 7A, B), which accurately show complete colour tones and patterns. The photographs show that the background colour of the body is white, or white and light amber on the chelae. The shield has orange and reddish patches arranged more-or-less symmetrically on the calcified portions. The ocular peduncles are white, each with an orange-red stripe on the dorsal face, and a light orange ventral face. The antennular peduncles are semi-transparent. The antennal peduncles each have a light orange-red patch on the laterodistal face of the second segment, and an orange stripe on the lateral faces of the fourth and fifth segments; the flagella are semitransparent or light orange. The right cheliped has the

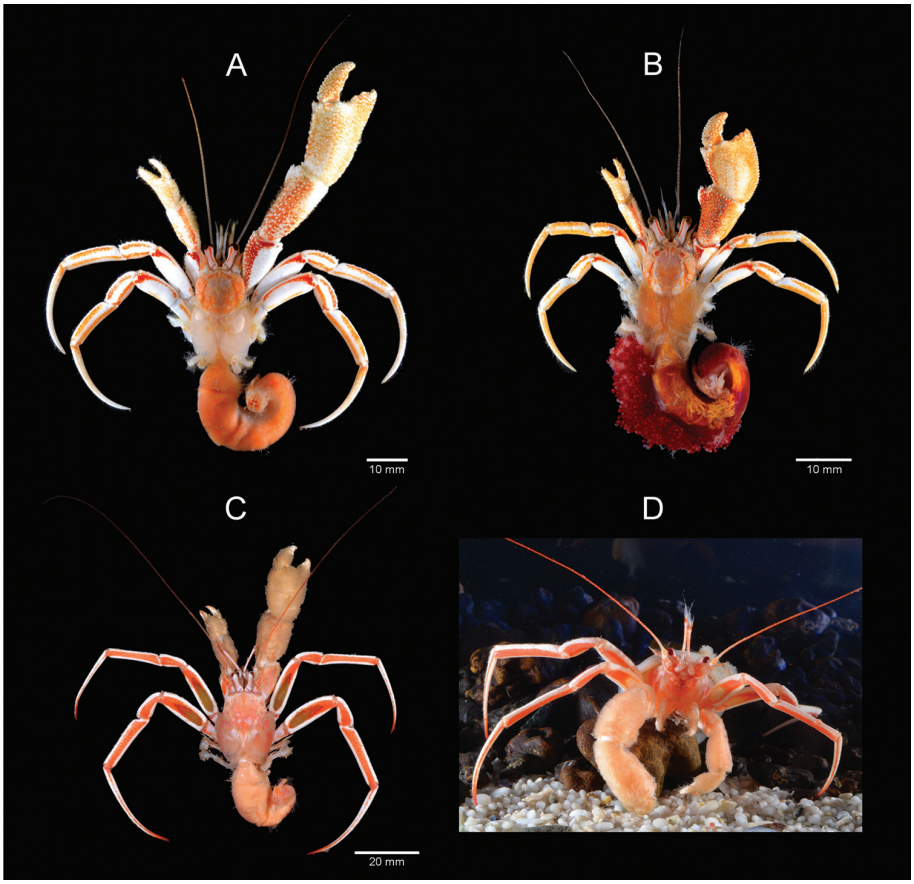

Figure 7. A, B *Sympagurus dimorphus* (Studer, 1883), South Coast **C, D** *Parapagurus bouvieri* Stebbing, 1910, West Coast (**C**), South Coast (**D**). **A** male 11.2 mm SCDSA 2016 (SAMC MB-A066492) **B** ovig. female 9.4 mm SCDSA 2016 (SAMC MB-A066491) **C** male 12.2 mm, WCDSS (SAMC MB-A066432) **D** male 10.6 mm, SCDSS2016 (SAMC MB-A066794), front view of live specimen in aquarium, using zoanthid (*Epizoanthus* sp.) carcinoecia.

chela mostly light amber with white spines or tubercles, and white patches medially; the carpus is orange dorsally, with white spines or tubercles; the merus is red dorsally, with bright white lateral and mesial faces. The colour pattern of left cheliped is similar to that of right cheliped. The ambulatory legs have dactyls mostly white except for a light orange proximally; the propodus and carpus are white except for two light orange stripes (one dorsolateral, and one ventrolateral) on the lateral face of both segments, and the mesial face of both segments are similar to the lateral face; the merus is bright white except for a dorsolateral red stripe broadening distally near the distal margin; the ischium is white with a dorsolateral light orange stripe. The pleon is orange or reddish. The uropods and telson are white with light orange.

General distribution. Reported from the Southern hemisphere from 22°S to 57°S. Depth: 91–1995 m.

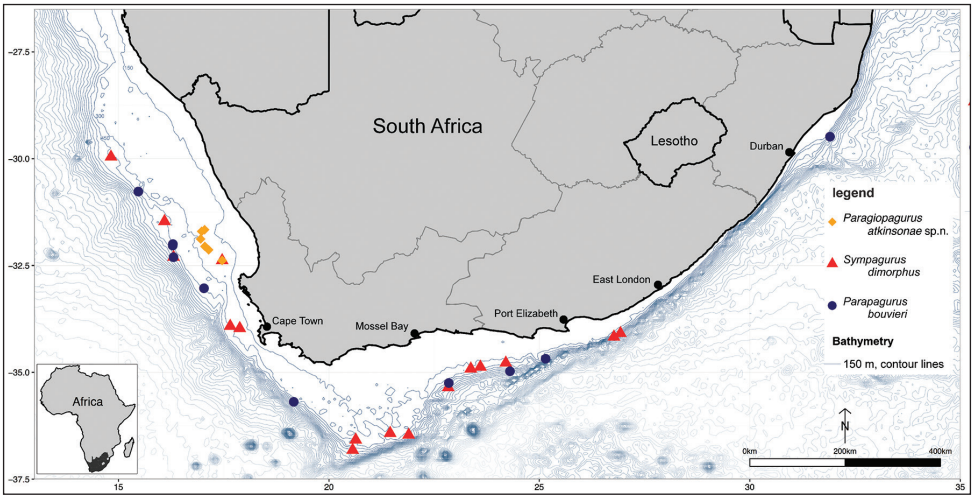

Figure 8. South African distribution of three parapagurid species based on specimens found during DAFF demersal research surveys.

As discussed by Lemaitre (2004b), *Eupagurus modicellus* Stebbing, 1914 from Ascencion Island, was believed by Manning and Chace (1990) to represent *S. dimorphus*. However, Stebbing's taxon was based on a juvenile specimen that likely does not represent *S. dimorphus*. Thus, the presence of this species as far north as Ascencion Island in the South Atlantic is considered questionable.

South African distribution (Fig. 8). Highly abundant all along the west coast, common on and along the shelf of the Agulhas Bank on the south coast, extending to offshore areas of East London; depth range of material in this study is 170–585 m.

Common names. "Monkey-nut hermit crab", "Cloaked hermit crab".

Habitat. Found living in gastropod shells, usually with actinian or zoanthid polyp attached to the shell, or in carcinoecia formed by colonies of *Epizoanthus* sp.; young have been found in scaphopod shells (Lemaitre 2004b). On the south coast of South Africa, commonly found in gastropod shells that are not covered by anthozoan symbionts.

Genetic data. Sta D0520-4071, S36°27.78', E21°53.58', 401 m, male 13.2 mm, BOLD: SEAKY876-15 (MB-A066841). Sta D0520-4071, S36°27.78', E21°53.58', 401 m, male 14.6 mm, BOLD: SEAKY962-15 (MB-A066839).

Genus *Parapagurus* Smith, 1879

Parapagurus bouvieri Stebbing, 1910

Figs 7C, D, 8

Parapagurus bouvieri Stebbing, 1910: 357, pl. 17 (Crustacea pl. 43) (type locality: South Africa, SS "Pieter Faure", sta 153, Buffalo River, NW 1/2W, 19 miles, 549 m)

Material examined. *South Africa, West Coast.* WCDSS2012, AFR279: 2 females 8.6, 11.0 mm, sta A32144-4116, S32°18.26', E16°18.529', 369 m, 11 Jan 2012 (SAMC MB-A066800); 3 males 10.4–13.1 mm, sta A32147–5079, S32°01.87', E16°17.43', 458 m, 11 Jan 2012 (SAMC MB-A066799). WCDSS2015, AND004: 8 males 7.5–14.3 mm, 3 ovig. females 9.2–11.8 mm, 1 female 8.9 mm, sta C0372–5140, S35°41.28', E19°09.82', 551 m, 11 Feb 2015 (SAMC MB-A066793); 1 female 9.4 mm, sta C0407–5104, S33°01.92', E17°01.98', 436 m, 21 Feb 2015 (SAMC MB-A066795); 2 males 6.1–12.5 mm, sta C0420–5078, S31°59.88', E16°17.64', 812 m, 27 Feb 2015 (SAMC MB-A066796). WCDSS2016, CCH008: 1 ovig. female 10.0 mm (SAMC MB-A066429), 1 male 14.0 mm (SAMC MB-A066430), 1 ovig. female 9.3 mm (SAMC MB-A066431), 1 male 12.2 mm (SAMC MB-A066432), 1 ovig. female 10.0 mm (SAMC MB-A066433), sta D00716, S30°46.14', E15°28.44', 387 m, 9 Mar 2016.

South Africa, South Coast. SCDSA 2015, AND005: 1 male 11.8, sta D00570–6628, S34°40.95', E25°09.15', 556 m, 3 May 2015 (SAMC MB-A066797); 2 males 10.0–12.7 mm, sta D00573–6592, S34°58.42', E24°18.37', 758 m, 4 May 2015 (SAMC MB-A066798). SCDSS2016, AFR289: 2 males 7.4–10.6 mm, sta A32823–96971, S35°14.95', E22°50.80', 511 m, 5 Oct 2016 (SAMC MB-A066794).

South Africa, East Coast. African Coelacanth Ecosystem Programme (no cruise name): 4 males 7.9–12.2 mm, sta ACEP 3–6, S29°29.10', E31°54.36', 563–569 m, 20 Mar 2010 (ZRC 2013.0548).

Diagnosis, taxonomy. See Lemaitre (1990; 1999; 2000), and Poore (2004).

Colour (in life; Fig. 7C, D). Until now, colour information on this species has been based only on Barnard's (1950: 451, as *Parapagurus pilosimanus*) description of specimens from South Africa, and a photograph by Poore (2004, pl. 17b) only partially showing the body of a live specimen in a zoanthid carcinoecia. Herein, we describe in detail for the first time the colouration of this species, and present colour photographs of the entire body of a fresh specimen removed from it's housing and with it's anthozoan housing (Fig. 7C, D). Shield light orange with small white patches on posterior half, and white near anterior margin. Ocular peduncles white dorsally, turning light orange on lateral faces; corneas black to dark brown. Antennules white with light orange flagella. Antennal penduncles white except for orange lateral faces of second segments, and orange acicles; flagellum light orange except for white basal portion. Colour of chelipeds hidden by dense light brown setation, surfaces white except for some orange tint distally on fingers. Ambulatory legs white with broad orange stripe on lateral faces of meri, carpi, and propodi; dactyls orange distally and with narrow orange stripe on lateral face; weakly calcified region on lateral face of meri brownish.

General distribution. Southeastern Atlantic, from Angola to South Africa, and southwestern Indian Ocean to KwaZulu-Natal (South Africa); western Pacific, from off the southern and southeastern coast of Australia, from the South Australian Bight and Queensland (Lemaitre 1999; Poore 2004). Depth: 247–990 m.

South African distribution (Fig. 8). Highly abundant on the west coast, common on the shelf of the Agulhas Bank on the south coast, and extending to the east coast off KwaZulu-Natal; depth range of material in this study from 369–812 m.

Common name. "Hairy-clawed hermit crab".

Habitat. With extremely rare exceptions, exclusively found living in carcinoecia formed by zoanthids, probably *Epizoanthus* species.

Genetic data. Sta ACEP 3–6, S29°29.10', E31°54.36', 563–569 m, male 12.2 mm, BOLD: SEAKY1174–17 (ZCR 2013.0548–2). Sta D00716, S30°46.14', E15°28.44', 387 m, male 12.2 mm, BOLD: SEAKY1169–17 (MB-A066432); ovig. female 10.0 mm, BOLD: SEAKY1167–17 (MB-A066429); ovig. female 9.3 mm, BOLD: SEAKY1168-17 (MB-A066431).

Remarks. As pointed out by Lemaitre (1990; 1999; 2000), this species is unique among species of *Parapagurus* in several characters. In *P. bouvieri* the corneas are weakly dilated, and the overall length of the ocular peduncles are atypically long, being distinctly more than half the length of the shield, whereas in other species of the genus the corneas are reduced, not wider than the distal width of the ocular peduncles, and the ocular peduncles are short, less than half the length of the shield. The most striking and distinctive character of this species is the presence of a weakly-calcified area on the lateral and mesial faces of the propodi of the ambulatory legs. In live specimens this area is brownish in colour (Fig. 7C), and that tone is similarly retained even in specimens that have been preserved for a long time.

Discussion

Sympagurus dimorphus and *Paragiopagurus atkinsonae* sp. n. are superficially similar and could be confused if the morphology is not carefully examined. Given the scarcity of taxonomic information on South African parapagurids, it is therefore not surprising that until now the latter new species has been confounded with the former. In addition, the two species co-exist and are trawled in large numbers from the same benthic environments, and both species utilize a similar housing strategy for protection, i.e., a carcinoecia formed by potentially the same species of zoanthid polyps (in South Africa, *S. dimorphus* is also often found inhabiting shells). Morphologically, both species exhibit a marked sexual dimorphism that is expressed most visibly in males by having a long and often slender right cheliped, whereas in females the right cheliped is stout, with a broad, operculate chela. The variations in males and females of *S. dimorphus* have been documented in detail by Lemaitre (1989; 1996; 2004b). The general tone of the colouration of *S. dimorphus* and *P. atkinsonae* sp. n. is also superficially similar, i.e., white in background with orange or red stripes. However, that is where the similarity ends, as the two species differ in fundamental generic characters as defined by Lemaitre (2004b) for *Sympagurus*, and Lemaitre (2013) for *Paragiopagurus*. Most significantly, species of *Sympagurus* are the only among parapagurids that posses a vestigial pleurobranch on each side of the eighth thoracic somite, above each fifth pereopod (see Lemaitre 2004b: 89, fig. 2). Furthermore, in *S. dimorphus* the gills are quadriserial, deeply divided, whereas in *P. atkinsonae* sp. n. the gills are at most weakly divided distally. In addition, the condition of pleopods in males of these two species differ drasti-

cally, the males in *S. dimorphus* having well developed, paired first and second pleopods modified as gonopods, whereas the males in *P. atkinsonae* sp. n., lack first pleopods and only have unpaired left second pleopods. Aside from fundamental generic differences, however, in the field these two species can be best identified by differences in colouration pattern (Figs 6A–D, 7A, B). In *P. atkinsonae* sp. n. the corneas are greenish (Fig. 6C), whereas in *S. dimorphus* they are dark brown or black; the general background colouration is more orange, whereas in *S. dimorphus* it is mostly white; the chelipeds are almost entirely orange with white tubercles or spines, whereas in *S. dimorphus* most of the chelae and lateral faces of carpi are white or light amber, and the meri are bright white except for a red dorsal face; the carpi, propodi and dactyls of the ambulatory legs have three orange stripes on a light orange background, whereas in *S. dimorphus* those segments have two orange stripes on often bright white background; the meri have a large white patch on the proximal half of the lateral face and a dark orange dorsal margin, whereas in *S. dimorphus* the lateral face of the merus is almost entirely bright white, except for a red-orange stripe dorsodistally.

Even without sufficient familiarity with the other taxonomic characters that define species of parapagurids, *P. bouvieri* can also be easily separated from the other two most commonly co-occurring parapagurid species encountered in the South Africa demersal surveys, by the relative length of the antennal peduncles (peduncle and acicle distinctly exceeding distal margins of the corneas), the more slender, longer, and dorsally unarmed meri and carpi of the ambulatory legs, and shape (stout propodus and short dactyl) and armature of propodus and propodal rasp (with conical scales) of the fourth pereopod, all of which can be easily compared in the publications cited herein for each of the three parapagurid species encountered in the demersal surveys. Compared to *P. atkinsonae* sp. n. and *S. dimorphus*, *P. bouvieri* inhabits different carcinoecia formed by different zoanthid species. Whereas the carcinoecia is firm, rigid, stabilized by imbedded grains of sand, and usually dark brown in the former two species, the carcinoecia inhabited by *P. bouvieri* is softer and gelatinous, grey to rosy in colour and almost neutrally buoyant in sea water. Additionally, the colour photographs (Figs 4C, D, 6A–C, 7A–D) presented for *P. bouvieri*, *Sympagurus dimorphus*, and *Paragiopagurus atkinsonae* sp. n., complete the set of morphological comparisons that should enable biologists to identify these three species.

Despite the considerable sampling effort along the entire extent of the South African offshore demersal survey grounds, *P. atkinsonae* sp. n. was confined to a small area on the West Coast, where it appears to be common. The distribution, being restricted to an area of only 43 nautical miles in the north-south, and only 25 nautical miles in the east-west direction, is unusual for any parapagurid species, which normally have wide-spread distributions (e.g. Lemaitre 1999; 2004b; 2013; 2014)). For example, in the South African benthic abundance surveys, the distributions of *S. dimorphus* and *P. bouvieri* extend from the westernmost fishing grounds from the Namibian boarder to the easternmost sites west of Port Elisabeth. Using the newly provided identification information, future studies should monitor the occurrence of *P. atkinsonae* sp. n. in the demersal abundance surveys. Should it be confirmed that *P. atkinsonae* occurs

exclusively in the small area of the South African West Coast then this area should be given more research attention. The area does not obviously appear oceanographically or biologically distinct, but more detailed sampling of the benthic invertebrate community and ecosystem might reveal that it provides specific habitat conditions that could be important to both study and protect from future anthropogenic impacts.

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RESEARCH ARTICLE

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

Chia-Hsuan Wei[1], David J. Lohman[2,3,4], Djunijanti Peggie[5], Shen-Horn Yen[1]

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.

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Keywords
Batesian mimicry, convergent evolution, Elymniini, 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)) (Fruhstorfer 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 (Fruhstorfer 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*

(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 hypermenstra* (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 between 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

ECMP	Entomology Collection, Bureau of Science, Manila, Philippines
FMNH	Field Museum of Natural History, Chicago, USA
HPC	Hiroto Hanafusa Private Collection, Japan
HSPC	Hiroyuki Soeda Personal Collection, Japan
IM	Indian Museum, Calcutta, India
IPC	Yutaka Inayoshi Private Collection, Chiang Mai, Thailand
JPC	Julian Jumalon Private Collection, Cebu City, Philippines
KMSPC	Kazu-Michi Suzuki Private Collection, Japan
KUTH	Department of Entomology, Kasetsart University, Thailand
LSL	Linnaean Society of London, London, London, UK
MCZ	Museum of Comparative Zoology, Harvard University, USA
MEPR	Museo Entomologico Pietro Rossi, Duino, Italy
NODAI	Tokyo University of Agriculture, Tokyo, Japan
MUS	Malaysia Universiti Sarawak, Kota Samarahan, Malaysia
NBC	National Biodiversity Center, Leiden, Netherlands
NHM	The National History Museum, London, UK
NHMT	The National History Museum at Tring, Tring, UK
NHMW	Vienna Museum of Natural History, Vienna, Austria
NMNH	National Museum of Natural History, USA
NRM	Naturhistoriska Riksmuseet, Stockholm, Sweden
NSYSU	National Sun Yat-Sen University, Kaohsiung, Taiwan
NWSUAF	Northwest A & F University, Shaanxi, China
OMPC	Kikumaro Okano Private Collection, Japan
OPC	Kiyoshi Okubo Private Collection, Japan
PNM	National Museum of the Philippines, Manila, Philippines
SMFD	Naturmuseum Senckenberg, Frankfurt am Main, Germany
SMK	Sarawak Museum Kuching, Sarawak, Malaysia
SMTD	Staatliches Museum für Tierkunde, Dresden, Germany
SPC	Kotaro Saito Private Collection, Japan
TME	Toyosato Museum of Entomology, Tsukuba, Japan
TPC	Tsukada Private Collection, Japan
UPC	Yoshinobu Uémura Private Collection, Japan
ZMHB	Museum für Naturkunde, Berlin, Germany
ZMUC	Zoological Museum University of Copenhagen, Copenhagen, Denmark

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 reproductively 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 mimetic butterfly taxa (Punnett 1915), we adopted the following procedures for evaluating 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 taxonomic 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*, *hypermnestra*, *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 morphological 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 applied 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 species groups. They have been circumscribed based on relatedness as inferred by a multilocus molecular phylogeny.

Distribution maps and type localities

A variety of sources were used to infer the distribution maps that we provide, including 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)[1]
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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[1] 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)[2]
Lepidoptera Indica 2 (18): 165–168.
Elymniopsis Fruhstorfer, 1907 (Type species: *Papilio phegea* Fabricius, 1793)[3]
Dt. ent. Z. Iris 20 (3): 173–174.

***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.

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

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.

Elymniopsis 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] *Elymniopsis* 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 *Elymniopsis*.

Elymniopsis 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, 1869[4]

Elymnias papua Wallace, 1869. **TL**: New Guinea[5]. **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, Koofbivak, 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 *bivitatta* 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)**[6]

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 Mountains[7] (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.

ssp. *borneensis* Wallace, 1869[8]

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)[9]

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. *maheswara* Fruhstorfer, 1894

Elymnias (*Dyctis*) *maheswara* 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. *splendida* Tateishi, 2001

Elymnias esaca splendida 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* Teteishi, 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**[10]

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 thycana 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

[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 Dinstant & 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**: ZMHB *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**: ZMHB. *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

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[11] Staudinger (1889) described *albofasciata* based on specimens from Palawan. However, the locality of a "type specimen" deposited in ZMHB 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. Witley* 1 (1): 173.

Melanyias 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)**[13]

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 kuenstleri 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[14]

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.**[15]

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. *nigritia* 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)**[16]

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.

Melaninis mehida Hewitson, 1863. **TL**: Singapore. **TS**: NHM. *Ill. exot. Butts.* [4] (*Melanitis*): [69], pl. [36], figs 2–3.

Elymnias abrisa 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 *Elymnnias borneensis* Wallace 1869)

Elymnias penanga trepsichroides 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]

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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 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)[19]

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: Sarawak, 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.[20]

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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[19] 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.

[20] 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.

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, 1878[22]

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, 1882[23]

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. genutia*), 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 km^2) 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[19]

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[19]

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 *bea-*

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* Fruhsorfer, 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, 1907[25]

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 & Uémura, 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.

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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**[26]

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[27]

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[28]

Distribution: Fig. 43

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

nepheronides-group

***nepheronides* Fruhstorfer, 1907**[29]

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

ssp. *nepheronides* Fruhstoerfer, 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**[30]

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 *hewitsoni* 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 haterti [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[31]

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)[32]

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. *mimus* Wood-Mason & de Nicéville, 1881

Elymnias mimus Wood-Mason & de Nicéville, 1881. **TL**: Nicobar Islands (India: Nicobar Islands). **TS**: uknown. *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], [Banka] (Indonesia: Banka-Belitung Province, Banka Island). **TS**: NHM. *Berl. ent. Zs.* 49: 188.

Elymnias defasciata Fruhstorfer, 1911, **syn. n. TL**: Borneo. **TS**: **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

Elymnais 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[35]

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.

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[35] Having examined the type material described by Fruhstorder 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:** Phillipines: 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, 1869[37]

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.

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.[41]

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.

ssp. *praetextata* Fruhstorfer, 1896

Elymnias casiphone praetextata Fruhstorfer, 1896. **TL:** Lombok (Indonesia: West Nusa Tenggara, Lombok). **TS**: NHM. *Soc. Ent.* 11 (17): 140.[42]

Elymnias kamara lombokiana Fruhstorfer, 1911. **syn. n. TL:** Lombok Island (Indonesia: West Nusa Tenggara, Lombok). **TS**: NHM. *Gross-Schmett. Erde* 9: 383.[38]

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.[43]

Elymnias casiphone djilantik Martin, 1909, **syn. n. TL:** Bali (Indonesia: Bali). **TS**: NHMT. *Dt. ent. Z. Iris* 22 (1): 49.[41]

ssp. *alumna* Fruhstorfer, 1907

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.

[41] 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.

[42] 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.

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

[44] 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

Elymnias 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

Elymnias 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

Elymnias 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)**[48]

Specimens: Fig. 15A–D; Male Genitalia: Fig. 25C; Distribution: Fig. 61

ssp. *melias* (C. & R. Felder, 1863)

Melanitis 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

Elymnias melias malis Semper, 1887**. TL**: Casiguran (Philippines: Central Luzon, Aurora, Casiguran). **TS**: SMFD. *Reisen Philipp.* (2): 62, pl. 12, figs 2–3.

Elymnias palmifolia Schultze, 1908. **TL:** Cagayang (Philippines: Northern Luzon, Cagayan). **TS:** ECMP. *Philipp. J. Sci* 3 (1): 27, pl. 1, fig. 1.

***beza* (Hewitson, 1877)**

Specimens: Fig. 15E–F; Male Genitalia: Fig. 25D; Distribution: Fig. 62.

ssp. *beza* (Hewitson, 1877)

Melanitis 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. *Dt. 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. *Dt. 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.

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[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)**[50]

Specimens: Figs 16A–H, 17A–I, 18A–M, 19A–M; Male Genitalia: Fig. 25H–N; Distribution: Fig. 66

ssp. *agondas* (Boisduval, 1832)[51]

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 melantho 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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[50] 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.

[51] 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 Fruhsforfer, 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.

ssp. *thryallis* Kirsch, 1876. comb. n.[48]

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. *pseudosalpinx* 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**: Halmaheira (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*.

***cumaea* (C. & R. Felder, [1867])**[54]

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

ssp. *cumaea* (C. & R. Felder, [1867])[55]

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.[56]

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

ssp. *toliana* Fruhstorfer, 1899[57]

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

Elymnias pseudeuploea Fruhstorfer, 1911. **unavailable name. TL**: Sulawesi (Indonesia: Sulawesi). **TS**: NHM. *Gross-Schmett. Erde* 9: 385.

***hewitsoni* Wallace, 1869**

Specimens: Fig. 20I–J; Male Genitalia: Fig. 26C; Distribution: Fig. 69

ssp. *hewitsoni* Wallace, 1869

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

Elymnias hewitsoni hewitsoni f. *sumptuosa* Fruhstorfer, 1907. **TL**: Tanetta (Indonesia: Central Sulawesi, Poso Regency, Tentena). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 237.

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] Nominotypical *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: Southeast Sulawesi). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 239, pl. 7, fig. 5.

***hicetas* Wallace, 1869**

Specimens: Fig. 20O–P; Male Genitalia: Figs 26E–F; Distribution: Fig. 71

ssp. *hicetas* Wallace, 1869

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

Elymnias hicetas bonthainensis Fruhstorfer, 1899. **syn. n. TL**: Bua Kraeng (Indonesia: South Sulawesi, Mt. Bawakaraeng). **TS**: NHM. *Berl. ent. Zs.* 44 (1/2): 55.[58]

ssp. *hicetina* Fruhstorfer, 1904

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

ssp. *butona* Fruhstorfer, 1904

Elymnais hicetas butona Fruhstorfer, 1904. **TL**: North Buton (Indonesia: Southeast Sulawesi, Buton). **TS**: NHM. *Soc. Ent.* 19 (7): 53.

ssp. *rarior* Martin, 1929[59]

Elymnias hicetas 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.

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

[59] Martin described *rarior* as a subspecies of *hicetas* without a clear indication of its type locality in Sulawesi. In our phylogenetic study, two specimens identified as *rarior* are paraphyletic with regard to *hicetas* and *butona*. Since the type locality of *rarior* is unclear, we retain *rarior* as a subspecies of *hicetas*.

***bornemanni* Ribbe, 1889. stat. n.**[60]

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.**[61]

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.**[62]

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.**[63]

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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[60] 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.

[61] *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.

[62] *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.

[63] Martin (1929) placed *resplendens* with *cumaea*, but our analysis suggests that *resplendens* is closely related to *hewitsoni* and deserves full species status.

Species not placed in any group[64]

***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 popuations. 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

[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 *Elymias* 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 delimitating 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, 1886)

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 vacudera [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 ternatana 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 leucocyma 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.

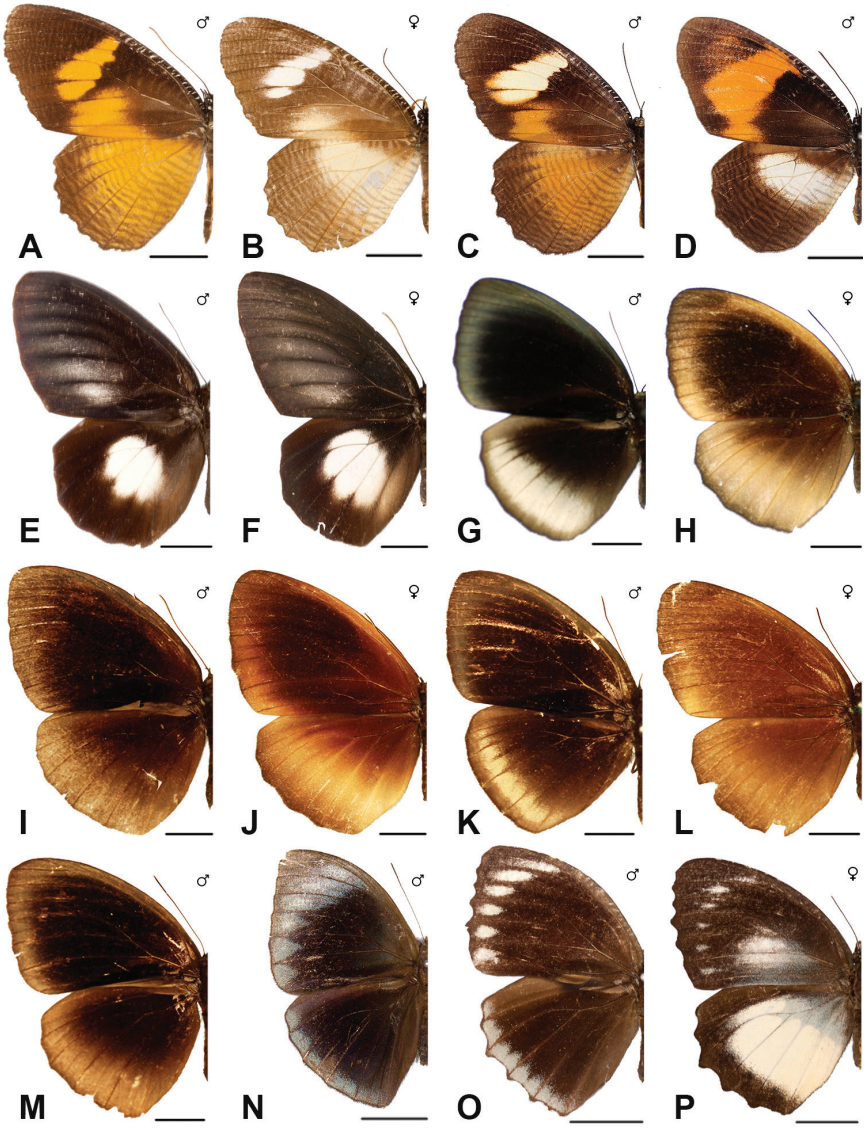

Figure 1. A *bammakoo bammakoo* ♂ D NHM central Africa **B** *bammakoo bammakoo* ♀ D NHM collection locality unknown **C** *bammakoo bammakoo* ♂ D NMNH Central African Republic: Bangui **D** *bammakoo rattrayi* ♂ D NMNH Uganda: Bwamba **E** *paradoxa* ♂ D NHM Indonesia: Papua, Weyland Mountains **F** *paradoxa* ♀ D NHM Indonesia: Papua, Weyland Mountains **G** *papua papua* ♂ D NHM Indonesia: Papua, Yos Sudarso Bay; Syntype of *Elymnias papua viridescens* **H** *papua papua* ♀ D NHM Indonesia: Papua, Yos 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.

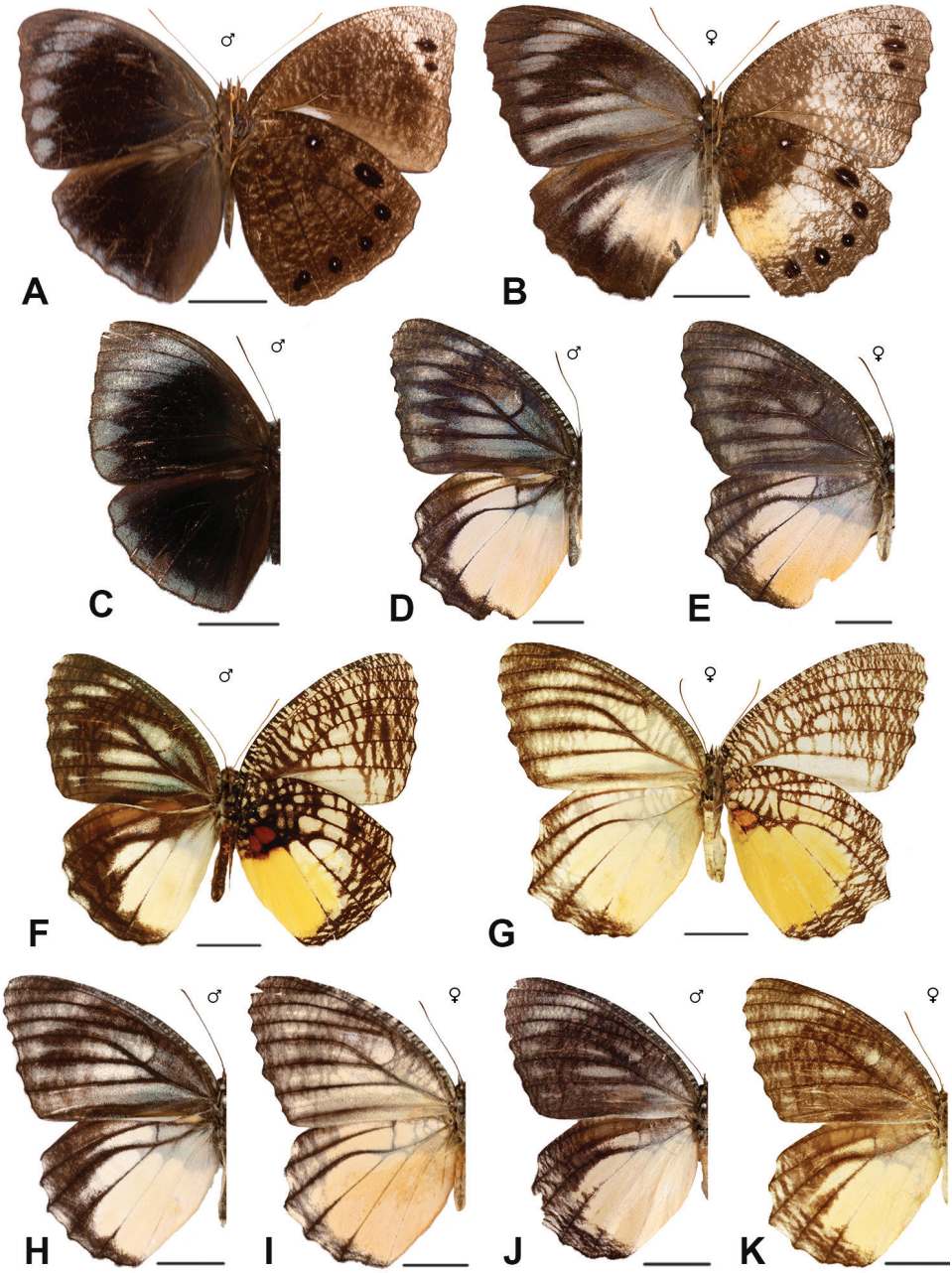

Figure 2. A *esaca leontina* ♂ D+V NHM Indonesia: North Sumatra, Nias **B** *esaca leontina* ♀ D+V NHM Indonesia: North Sumatra, Nias **C** *esaca esaca* ♂ D KUTH Thailand: Yala, Than To **D** *vasudeva* ♂ D KUTH Thailand: Kanchanburi, Sri Sawat **E** *vasudeva* ♀ D KUTH Thailand: Chaiyaphum, Phu Khieo **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.

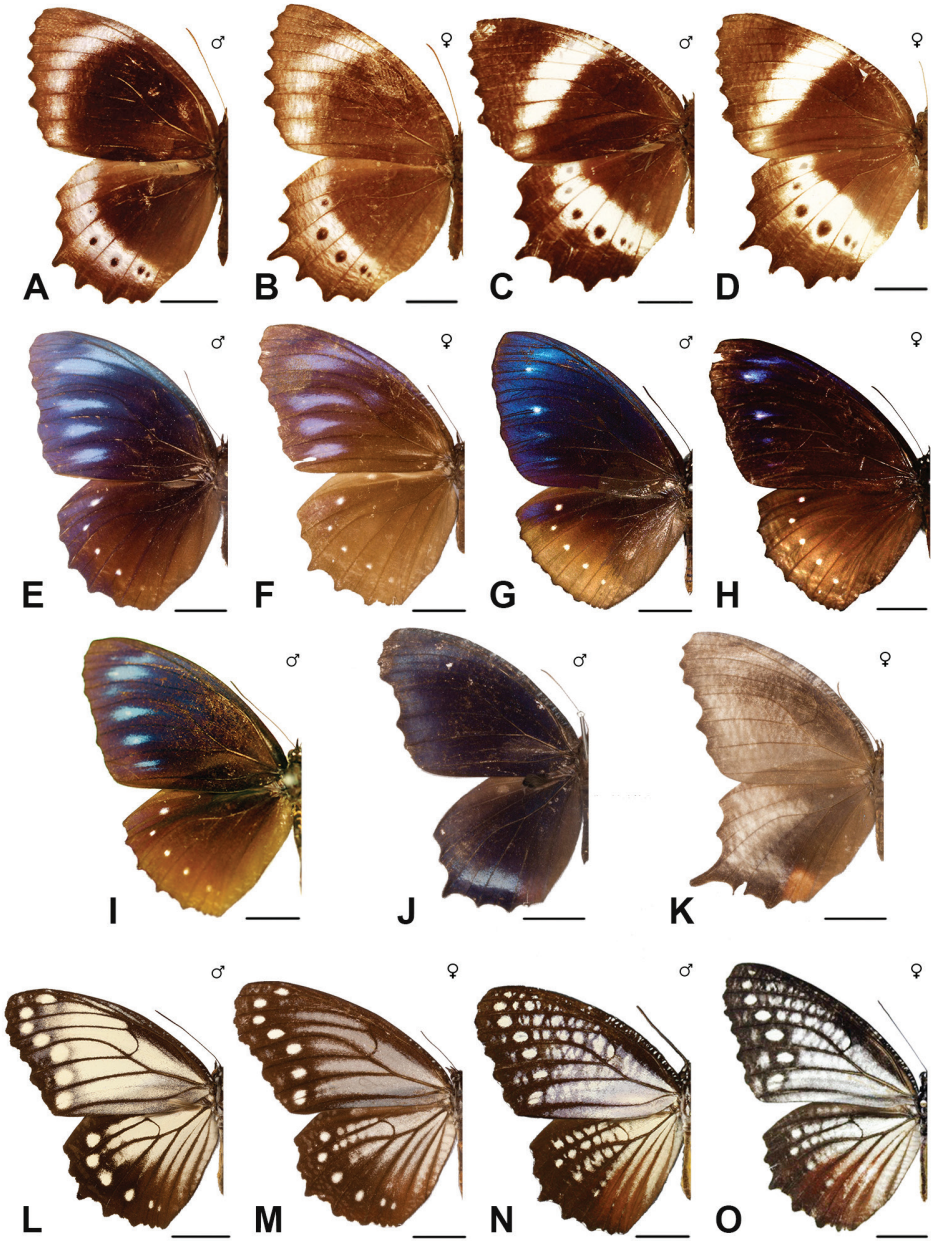

Figure 3. A *dara bengena* ♂ D NHM Indonesia: West Java **B** *dara bengena* ♀ D NHM Indonesia: West Java **C** *dara daedalion* ♂ D NHM Myanmar **D** *dara daedalion* ♀ D NHM Myanmar **E** *patna patna* ♂ D NHM India: Sikkim **F** *patna patna* ♀ D NHM India: West Bengal, Darjeeling, Pedong **G** *patna* "*inayoshii*" (nomem 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.

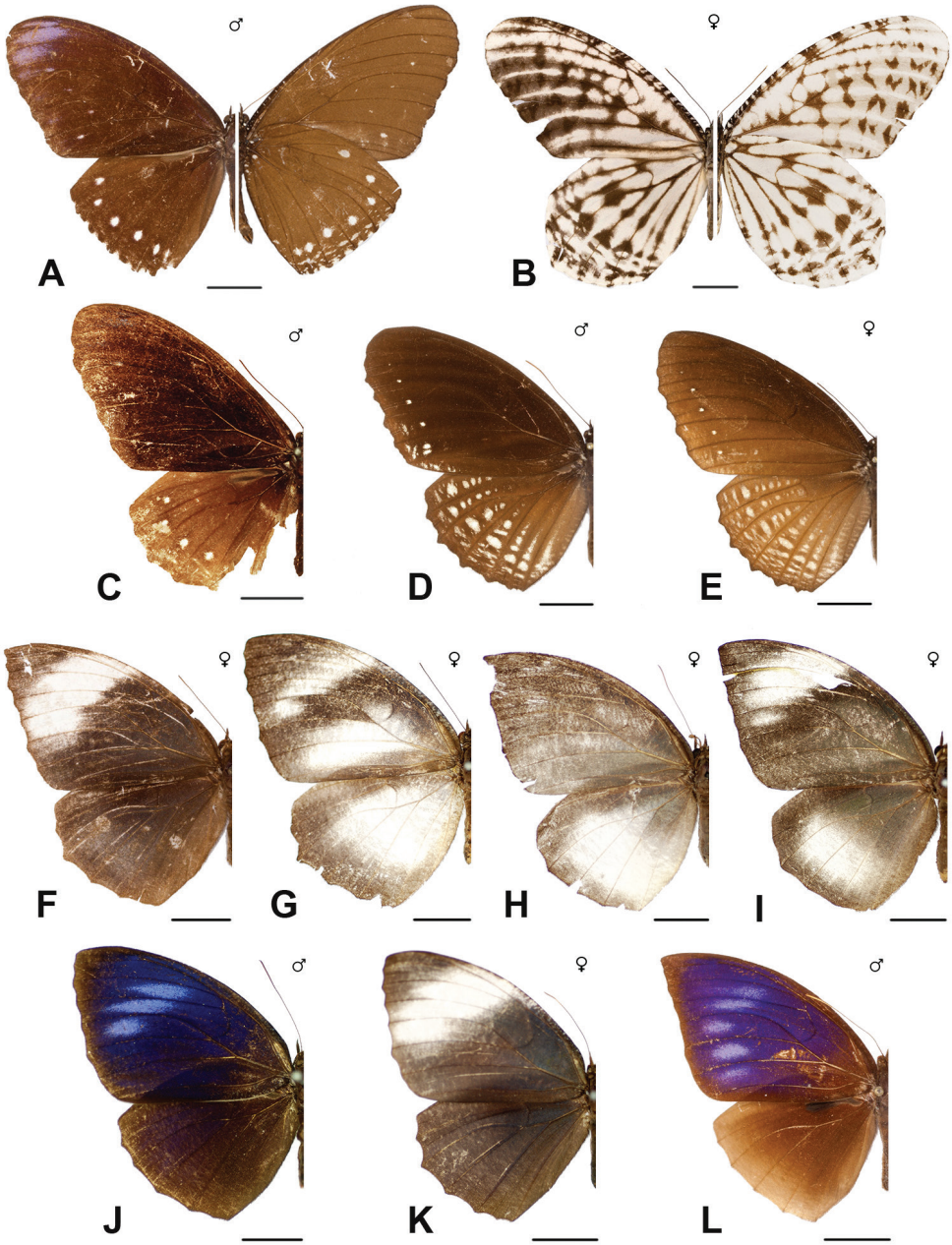

Figure 4. A *kuenstleri kuenstleri* ♂ D+V NHM Specimen locality unknown **B** *kuenstleri kuenstleri* ♀ D+V NHM Peninsular Malaysia: Selangor, Bukit Kutu **C** *kuenstleri rileyi* ♂ D NHM Borneo **D** *pellucida* ♂ D NHM Malaysia: Sabah, Mt. Kinabalu **E** *pellucida* ♀ D NHM Malaysia: Sabah, Mt. Kinabalu **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* f. *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 chelensis* ♂ D NHM Thailand: Ranong.

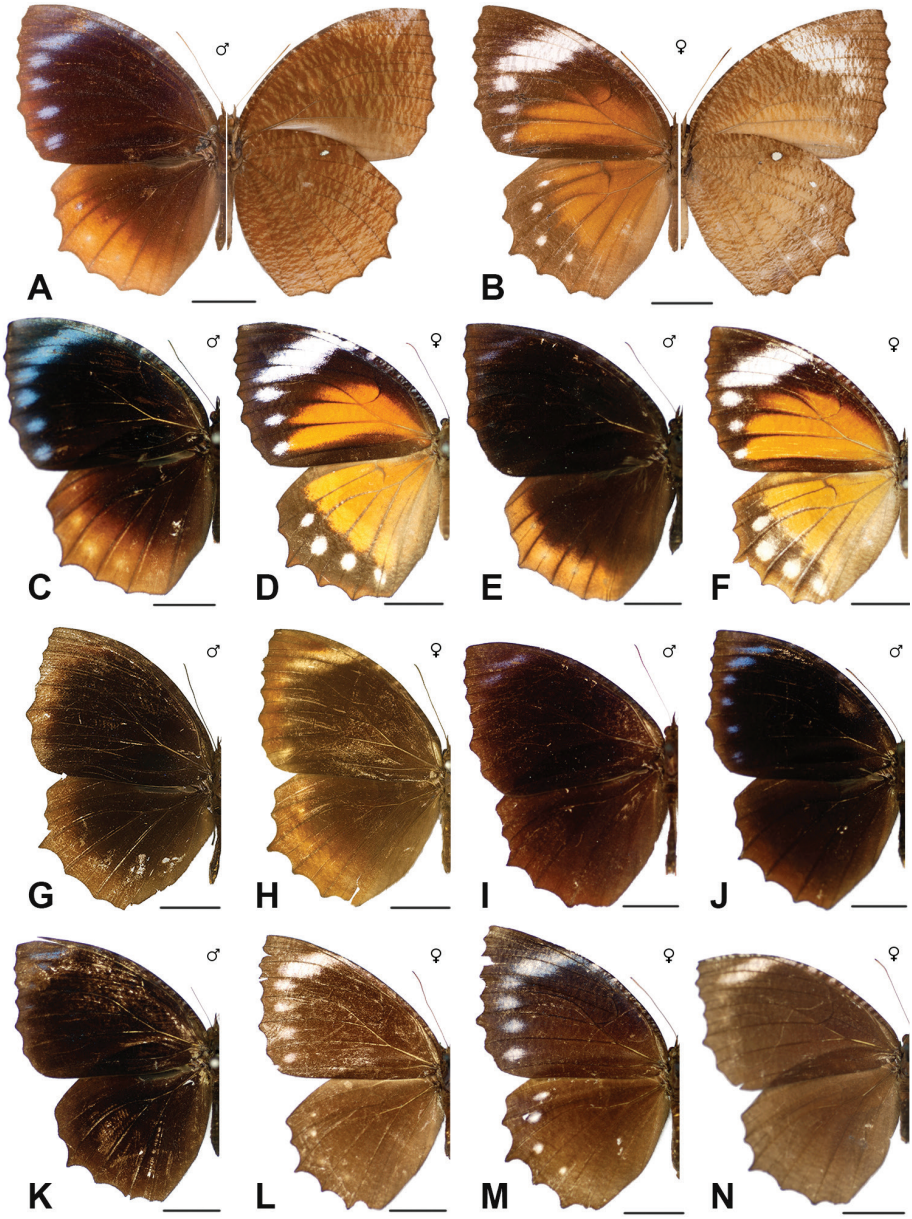

Figure 5. A *hypermnestra hypermnestra* ♂ D+V NHM Indonesia: Java, Bogor **B** *hypermnestra hypermnestra* ♀ D+V NHM Indonesia: Java, Bogor **C** *hypermnestra undularis* ♂ D NHM India: Assam **D** *hypermnestra undularis* ♀ D NHM India: Sikkim **E** *hypermnestra fraterna* ♂ D NHM Sri Lanka **F** *hypermnestra 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.

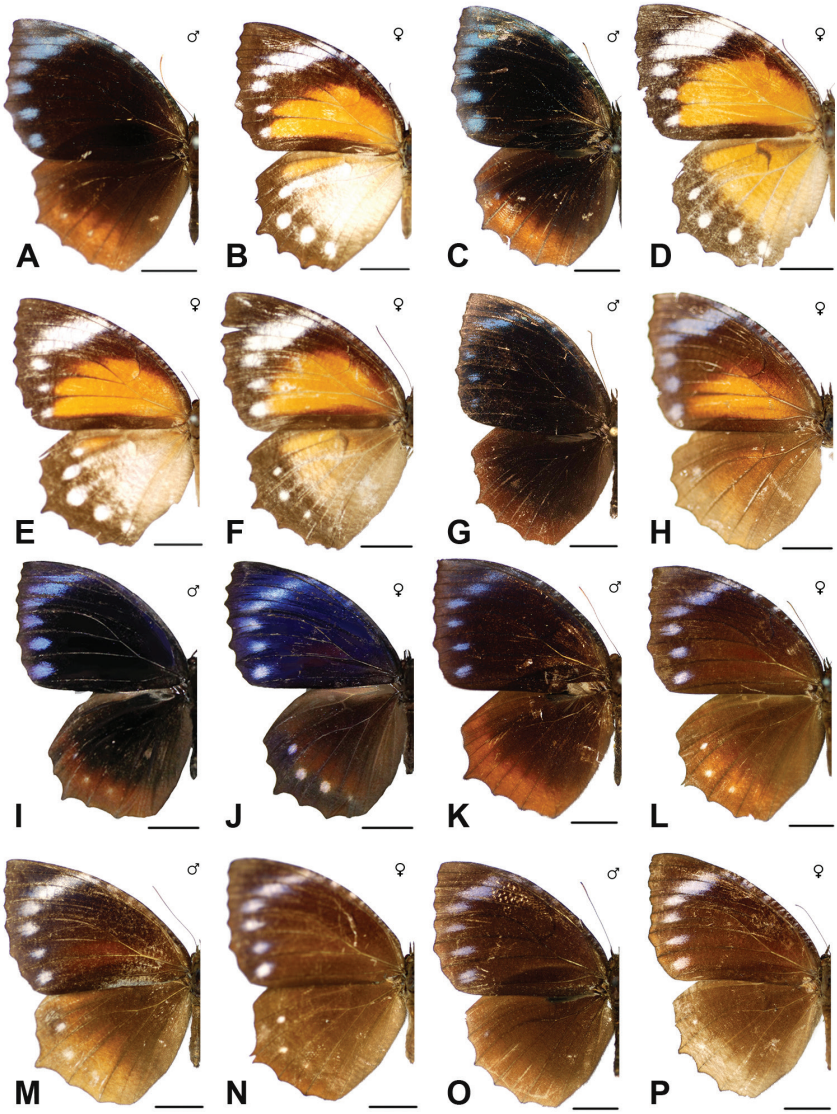

Figure 6. A *hypermnestra tinctoria* ♂ D NHM Myanmar: Bago **B** *hypermnestra tinctoria* ♀ D NHM Myanmar: Ayeyarwady, Pathein **C** *hypermnestrta tinctoria* ♂ D NHM Thailand: Bangkok **D** *hypermnestra tinctoria* ♀ D NHM Thailand: Bangkok **E** *hypermnestra tinctoria* ♀ D NHM Myanmar: Tanintharyi; 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.

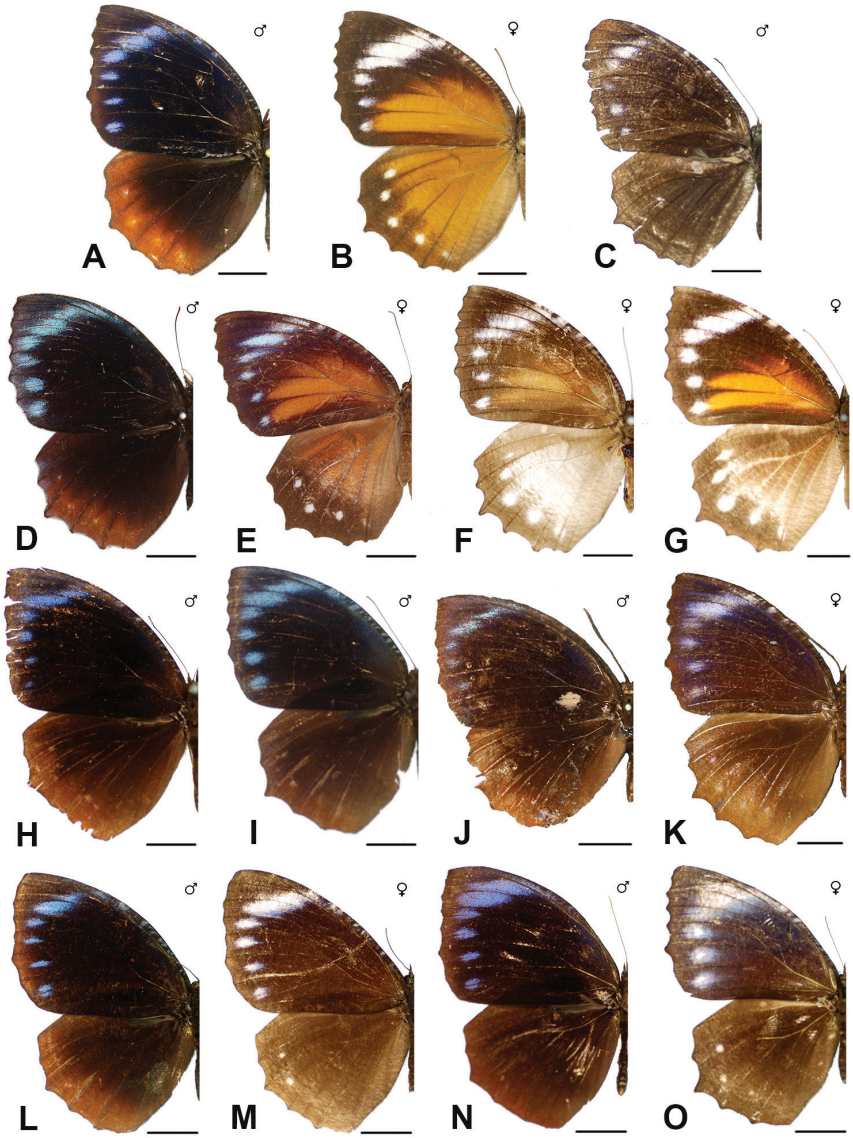

Figure 7. A *hypermnestra baliensis* ♂ D NHM Indonesia: Bali **B** *hypernmestra baliensis* ♀ D NHM Indonesia: Bali **C** *hypermnestra baliensis* ♂ D NHM Indonesia: Bali; Holotype of *Elymnias nigrescens bulelenga* **D** *hypermnestra tinctoria* ♂ D KUTH Thailand: Chiang Mai **E** *hypermnestra tinctoria* ♀ 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; **Holoype** of *Elymnias meridionalis* 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 sumbana* ♂ D NHM Indonesia: East Nusa Tenggara, Sumba **M** *hypermnestra sumbana* ♀ D NHM Indonesia: East Nusa Tenggara, Sumba **N** *hypermnestra decolorata* ♂ D NHM Indonesia: Sumatra **O** *hypermnestra decolorata* ♀ D NHM Indonesia: Sumatra.

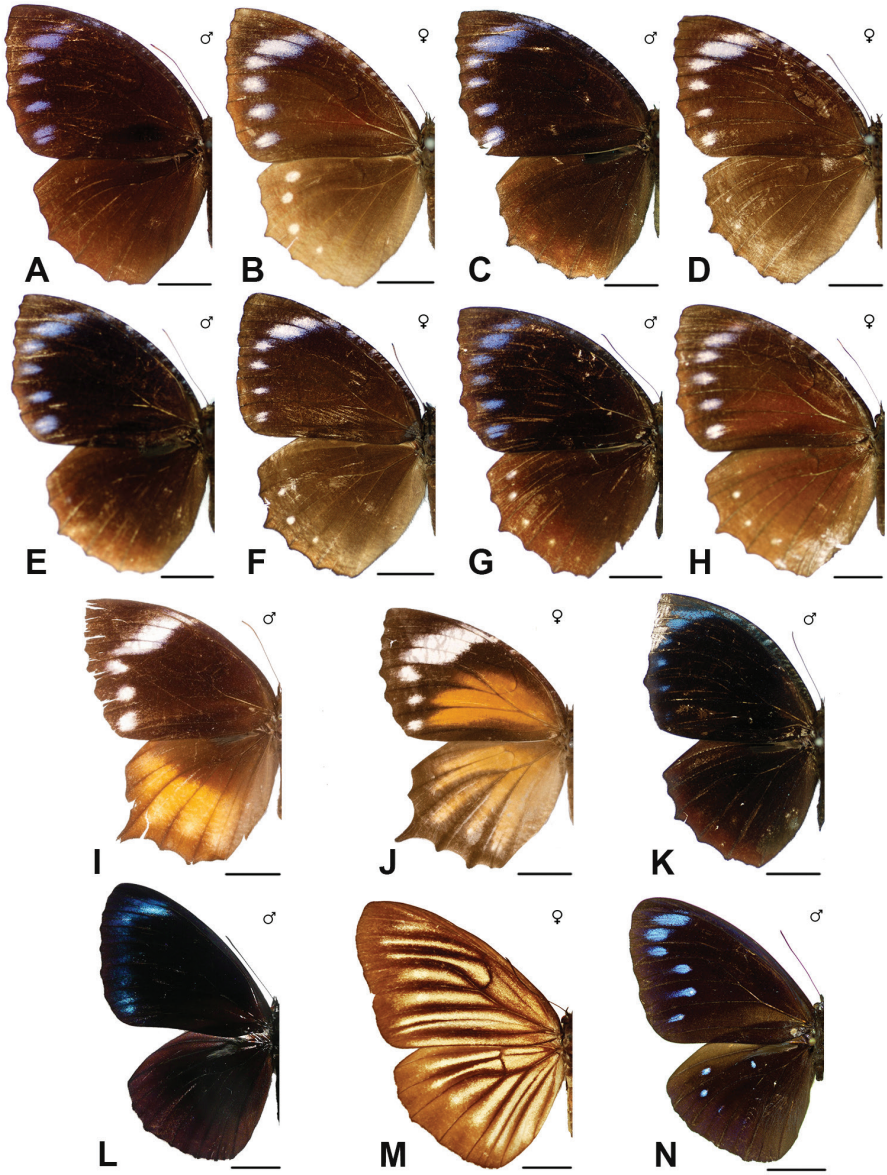

Figure 8. A *hypermnestra sumbawana* ♂ D NHM Indonesia: West Nusa Tenggara, Sumbawa **B** *hypermnestra sumbawana* ♀ D NHM Indonesia: West Nusa Tenggara, Sumbawa **C** *hypermnestra timorensis* ♂ D NHM East Timor: Dili **D** *hypermnestra timorensis* ♀ D NHM East Timor: Dili **E** *hypermnestra alorensis* ♂ 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.

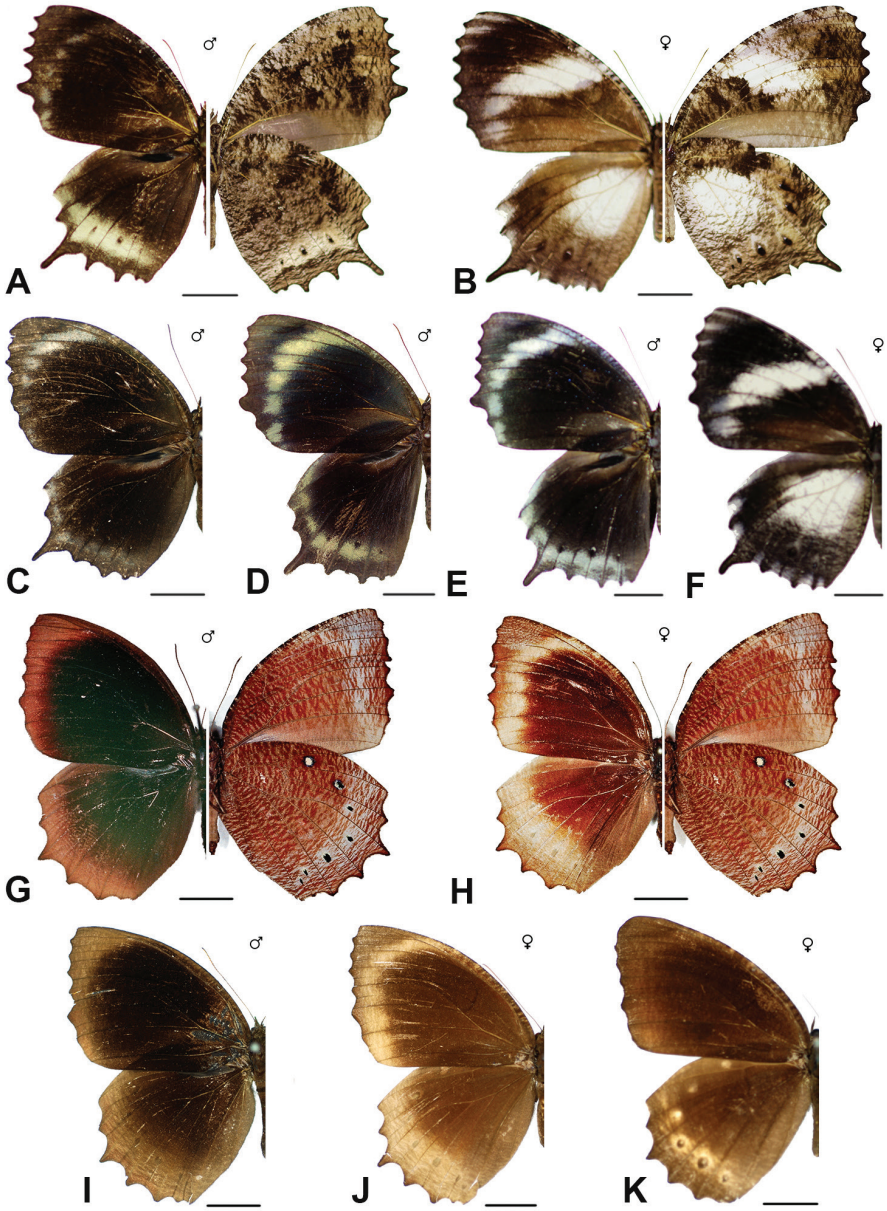

Figure 9. A *harterti harterti* ♂ D+V OPC Malaysia: Perak, Batang Padang, Tapah **B** *harterti harterti* ♀ D+V OPC Malaysia: Perak, Batang Padang, Tapah **C** *harterti brookei* ♂ D NHM collection locality unknown **D** *harterti lautensis* ♂ D OPC Indonesia: South Kalimantan, Laut Island; Holotype **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.

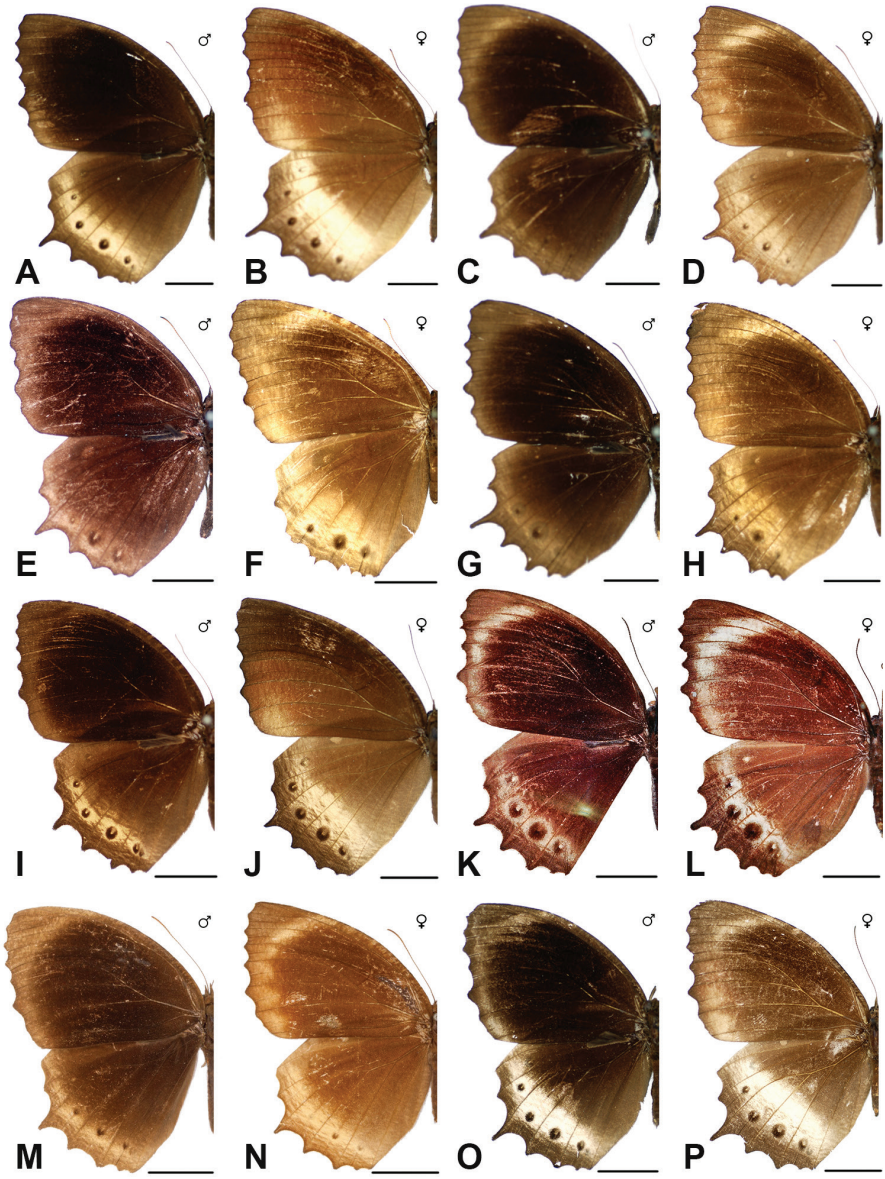

Figure 10. A *panthera panthera* ♂ D NHM Peninsular Malaysia **B** *panthera panthera* ♀ D NHM Peninsular Malaysia **C** *panthera dusara* ♂ D NHM Indonesia: Java **D** *panthera dusara* ♀ D NHM Indonesia: Java **E** *panthera mimus* ♂ D NHM India: Nicobar Islands **F** *panthera mimus* ♀ D NHM India: 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.

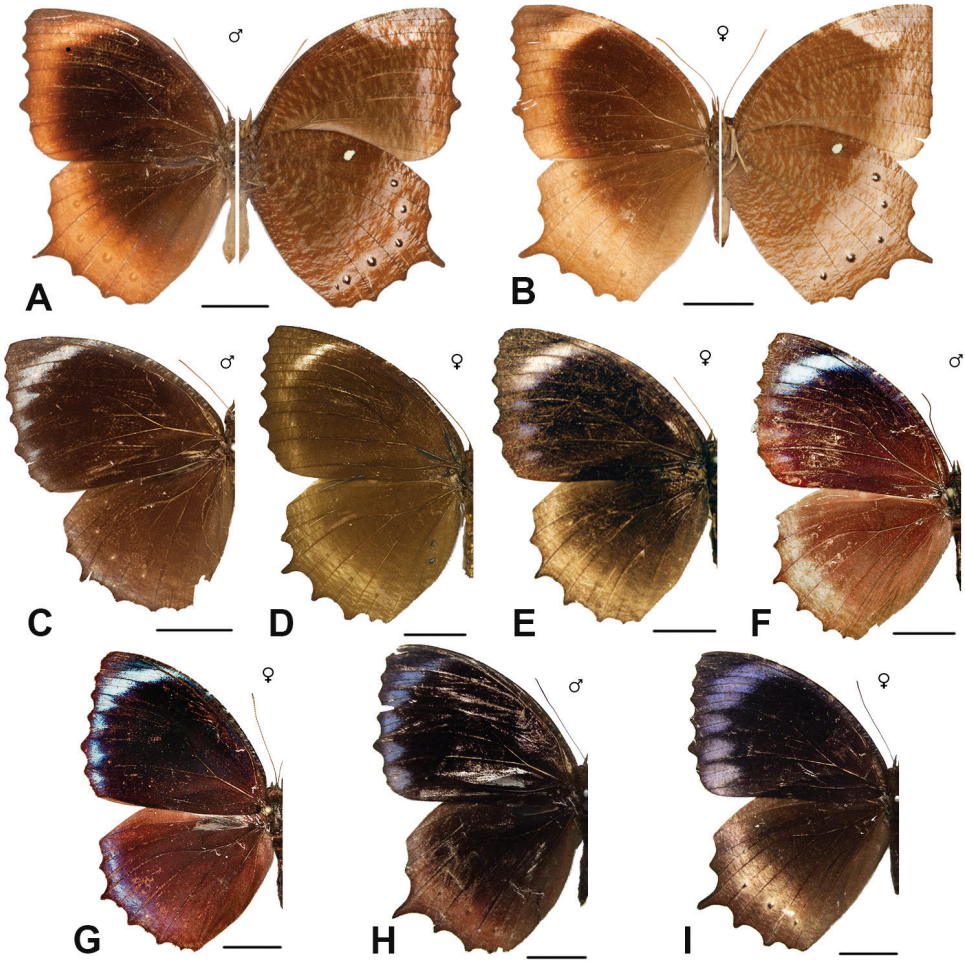

Figure 11. A *obnubila* ♂ D+V NHM Malaysia: Perak **B** *obnubila* ♀ D+V NHM Thailand: Ranong **C** *congruens congruens* ♂ D NHM Philippines: Cebu, Camotes Island **D** *congruens subcongruens* ♀ D NHM Philippines: Mindoro **E** *congruens endida* ♂ D SMFD Philippines: Bohol **F** *congruens endida* ♀ 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.

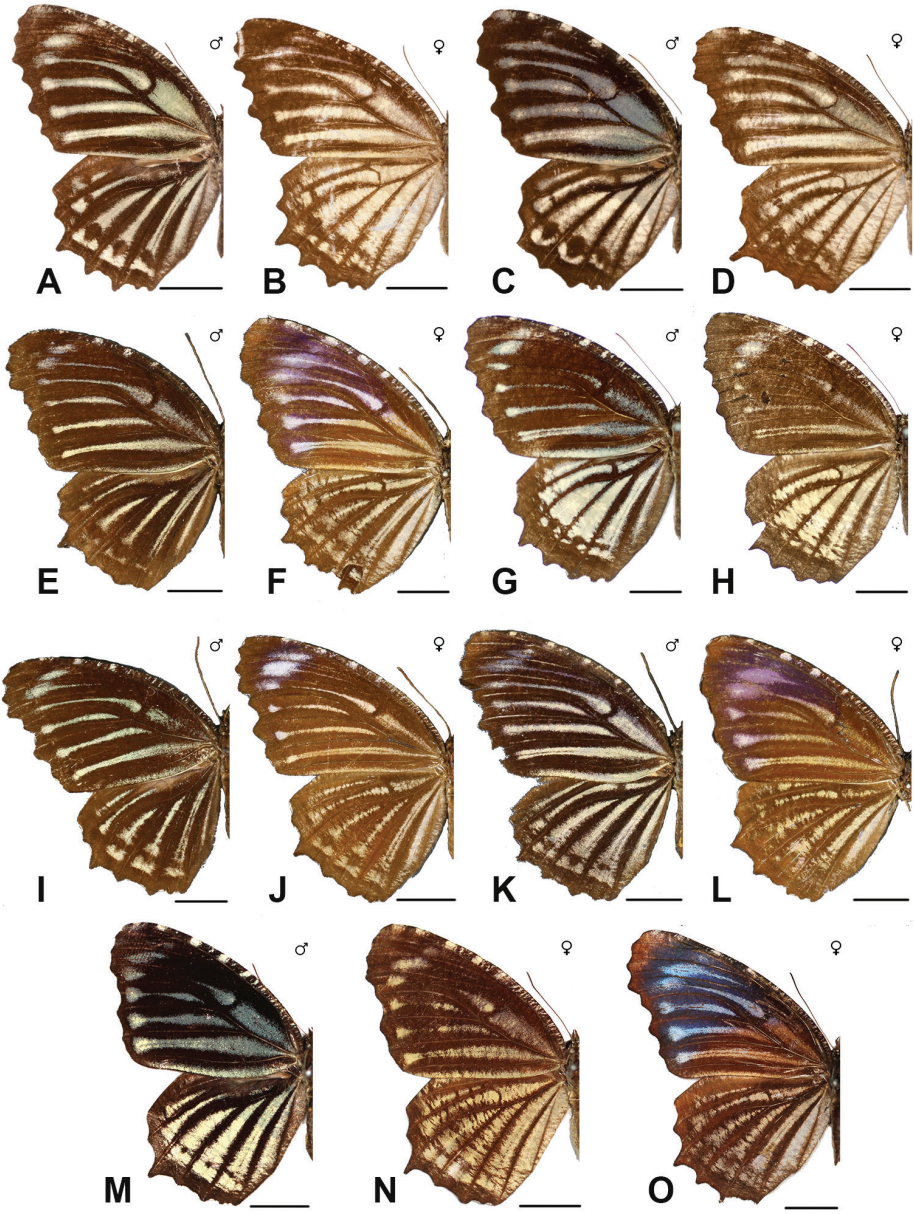

Figure 12. A *nesaea nesaea* ♂ D NHM Indonesia: Java **B** *nesaea nesaea* ♀ D NHM Indonesia: Java **C** *nesaea timandra* ♂ D NHM India: Meghalaya, Khasi Hills **D** *nesaea timandra* ♀ D NHM India: Meghalaya, Khasi Hills **E** *nesaea laisidis* ♂ D MCZ Indonesia: Sumatra **F** *nesaea laisidis* ♀ D MCZ Indonesia: West Sumatra, Padang **G** *nesaea baweana* ♂ 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.

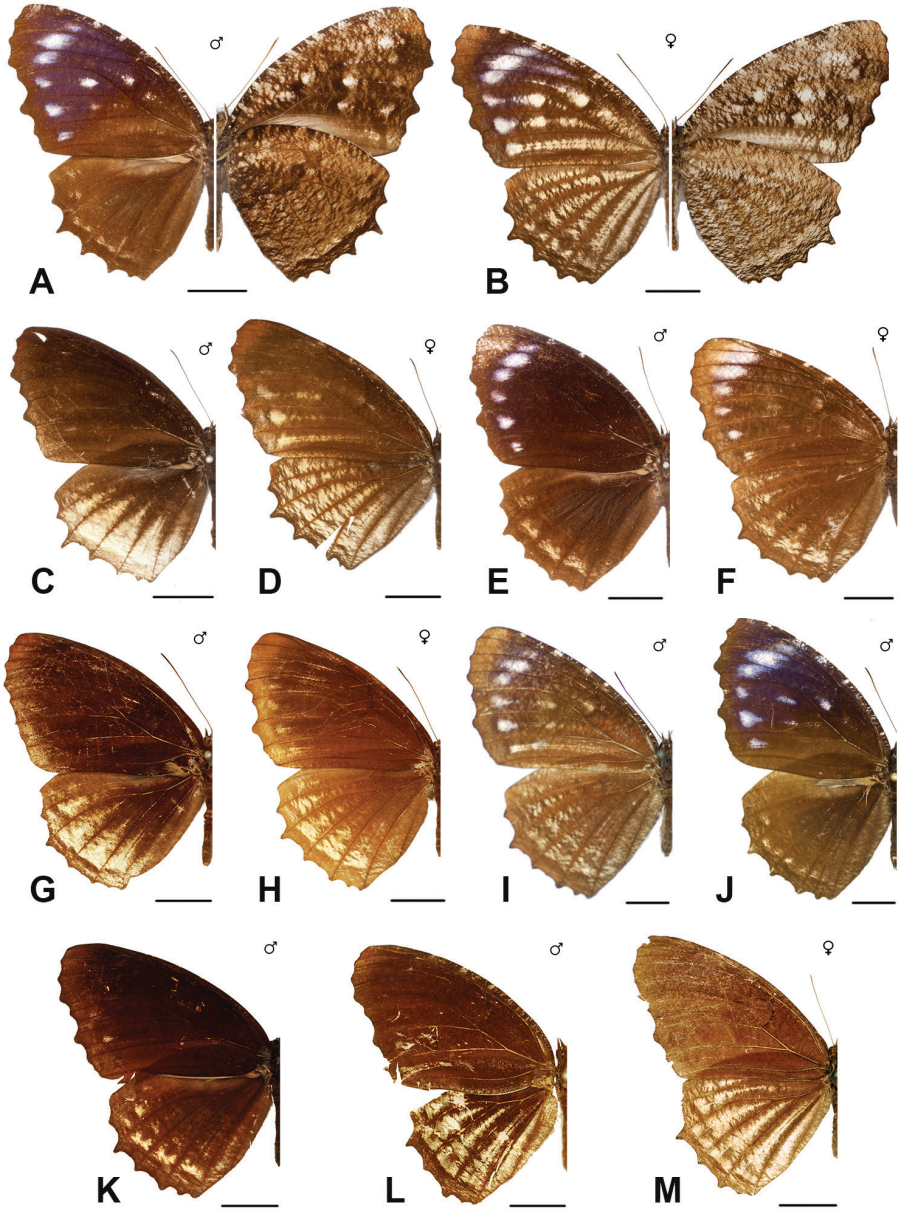

Figure 13. A *casiphone casiphone* ♂ D+V NHM Indonesia: Java **B** *casiphone casiphone* ♀ D+V NHM Indonesia: Java **C** *casiphone kamara* ♂ D NHM Indonesia: Java **D** *casiphone kamara* ♀ D NHM Indonesia: Java **E** *casiphone praetextata* ♂ D NHM Indonesia: West Nusa Tenggara, Lombok **F** *casiphone 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.

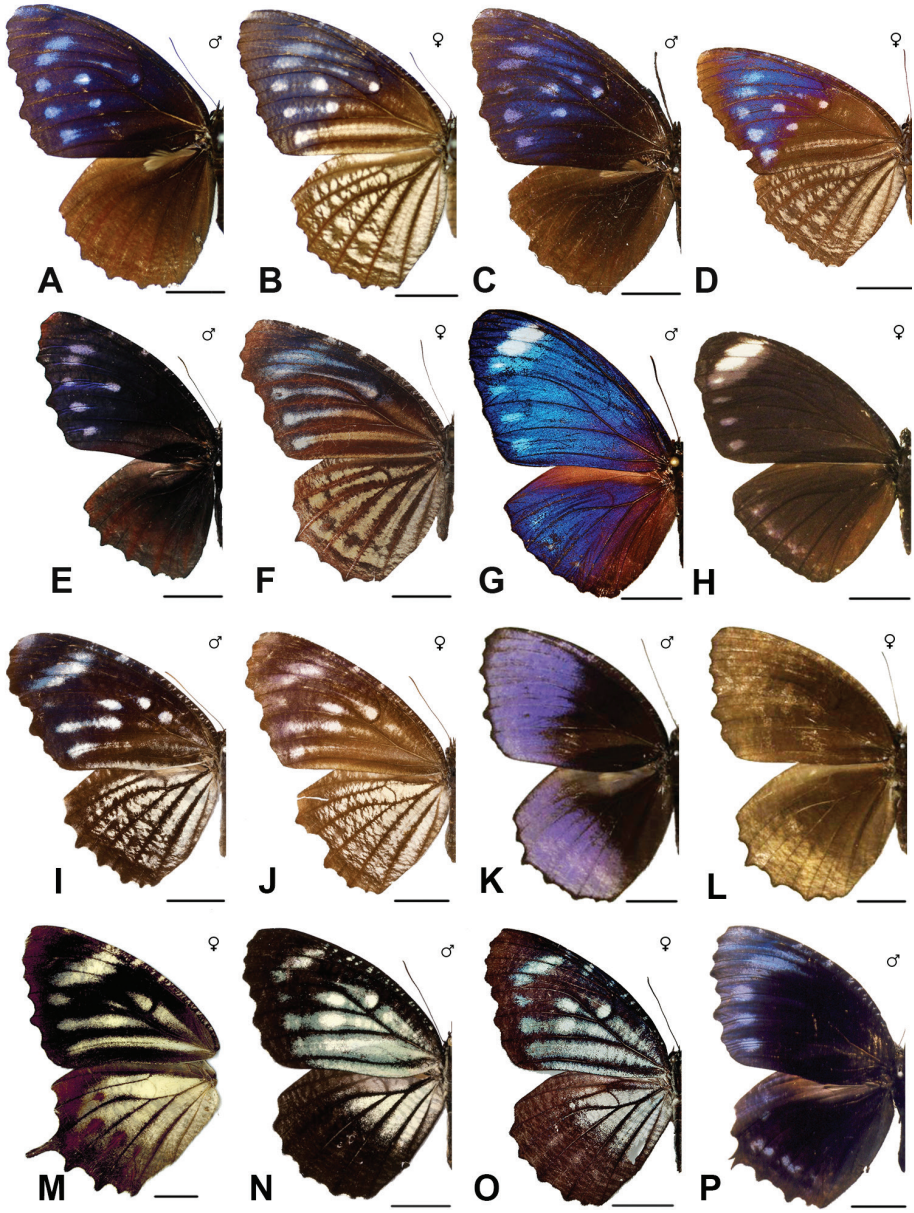

Figure 14. A *malelas* ♂ D NHM India: Sikkim **B** *malelas* ♀ D NHM India: Sikkim **C** *malelas* ♂ D MCZ Vietnam **D** *malelas* ♀ D KUTH Thailand: Chiang Mai **E** *saueri* ♂ D IPC Thailand: Phetchabun **F** *saueri* ♀ D NMNH Malaysia: Johor, Mersing to Kluang **G** *kochi* ♂ D SMFD Philippines: Luzon, 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.

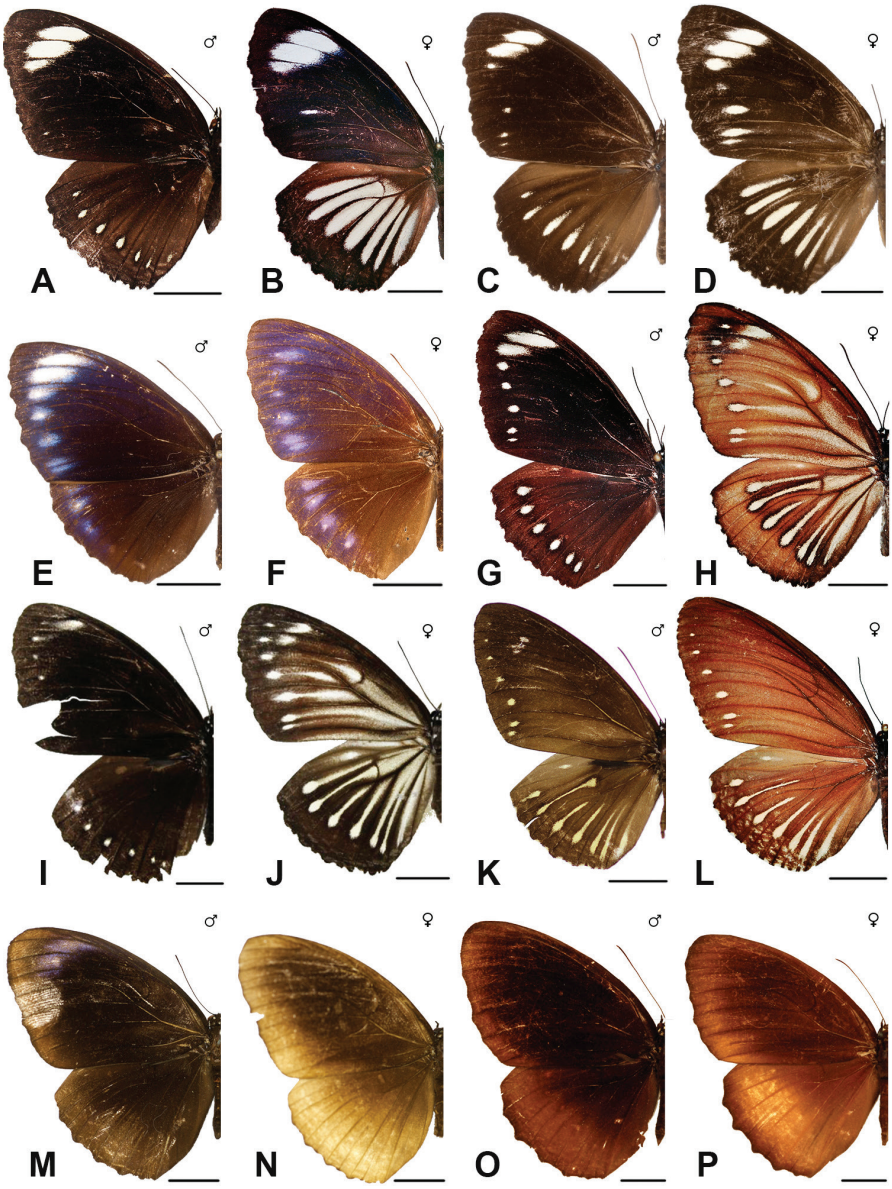

Figure 15. A *melias melias* ♂ D NMNH Philippines: Luzon, Cavite, Puerto Azul **B** *melias melias* ♀ D SMFD Philippines: Luzon, Sierre Madre Mountains **C** *melias malis* ♂ D NHM Philippines: Quezon, Polillo Island **D** *melias malis* ♀ D NHM Philippines: Luzon, Los Baños **E** *beza beza* ♂ D NHM 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, Penangudltan, 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.

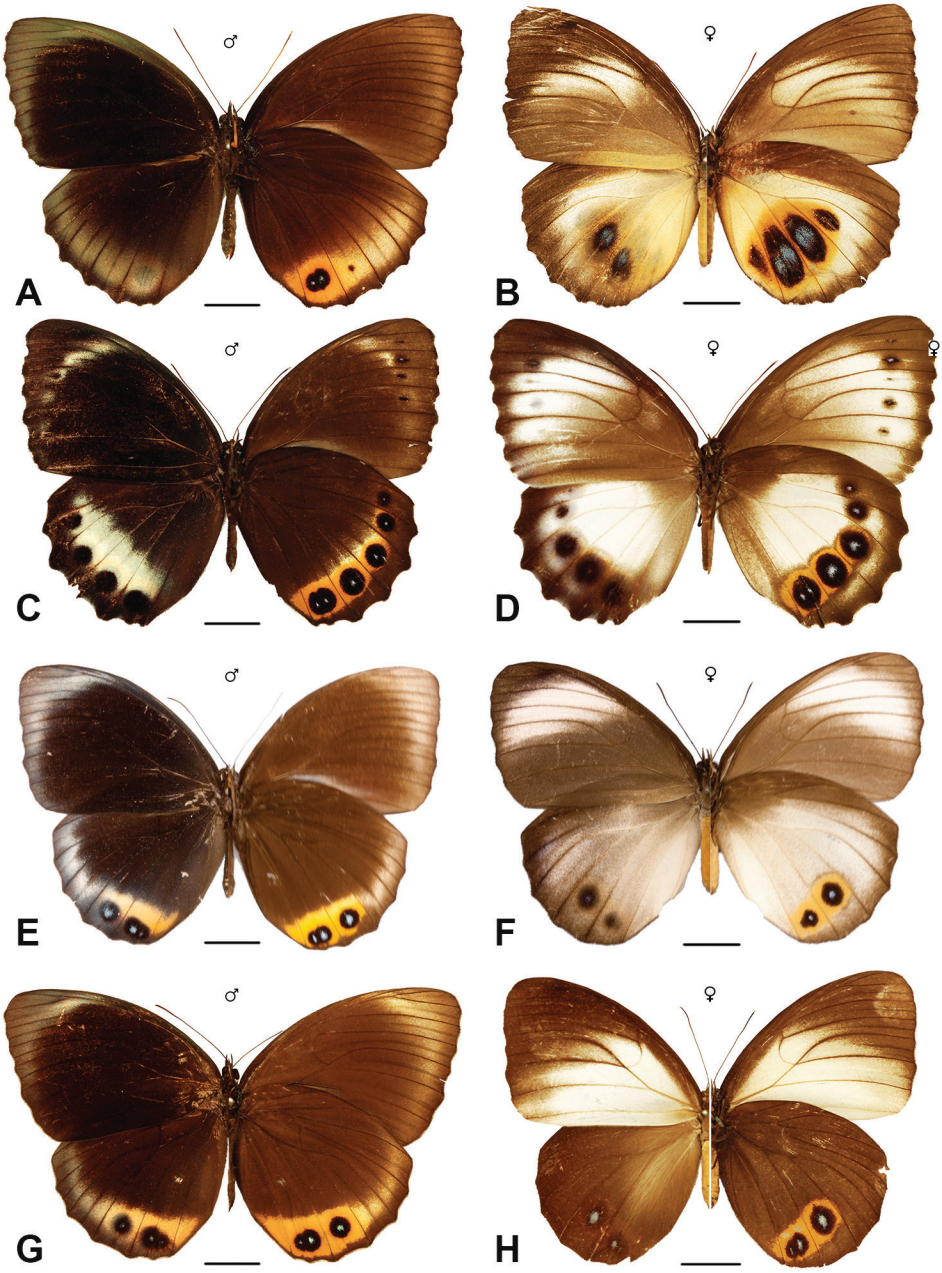

Figure 16. A *agondas agondas* ♂ D+V NHM Indonesia: West Papua **B** *agondas agondas* ♀ D+V NHM Indonesia: West Papua **C** *agondas melane* ♂ D+V NHM Indonesia: Maluku, Kei Island **D** *agondas melane* ♀ D+V NHM Indonesia: Maluku, Kei Island **E** *agondas glaucopis* ♂ D+V NHM Papua New Guinea: Oro 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.

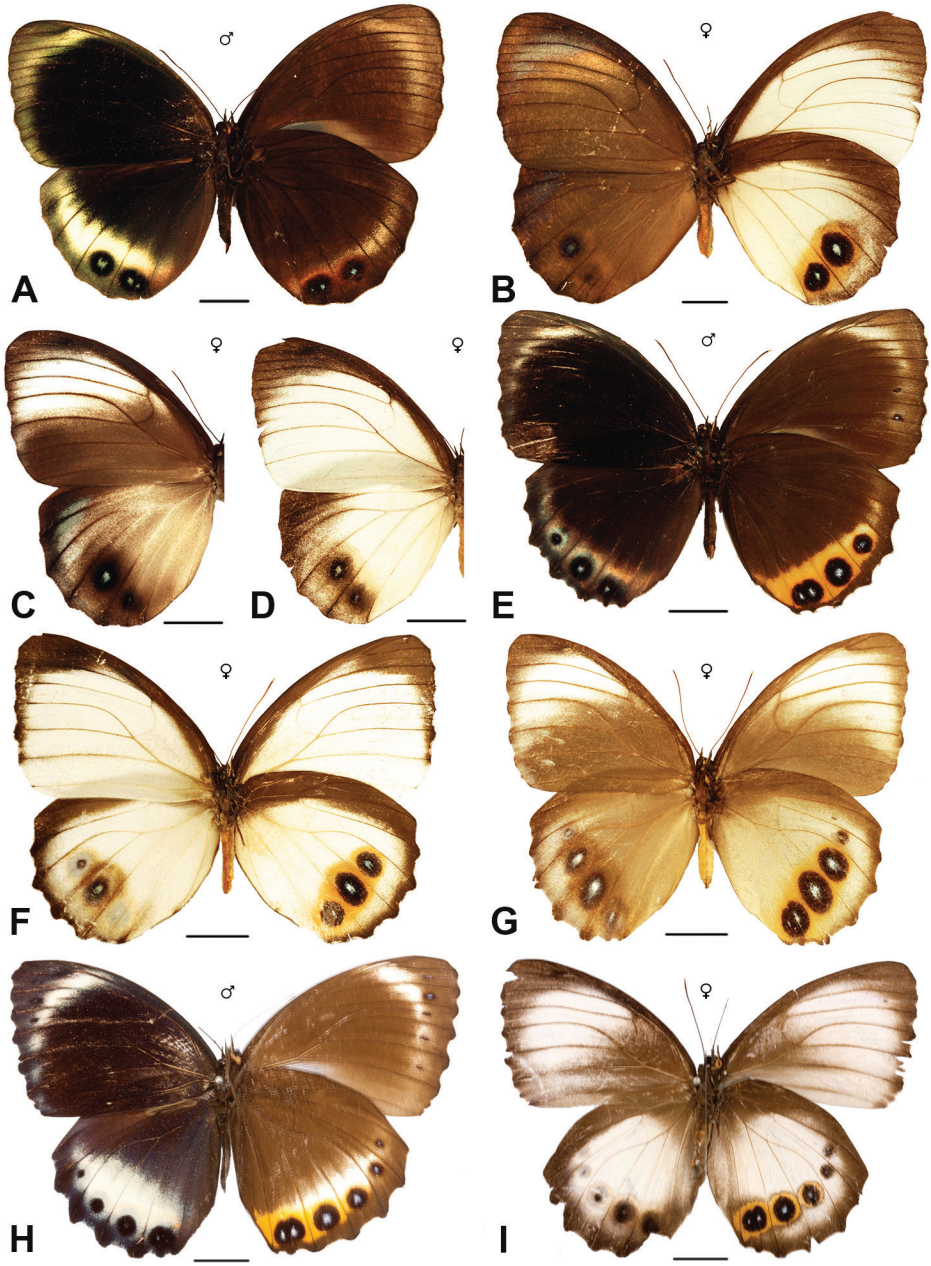

Figure 17. A *agondas melanthes* ♂ D+V NHM Papua New Guinea: Milne Bay, Woodlark Island **B** *agondas melanthes* ♀ D+V NHM Papua New Guinea: Milne Bay, Woodlark Island **C** *agondas melanthes* ♀ D NHM Papua New Guinea: Milne Bay, Woodlark Island **D** *agondas melanthes* ♀ D NHM Papua New Guinea: Milne 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.

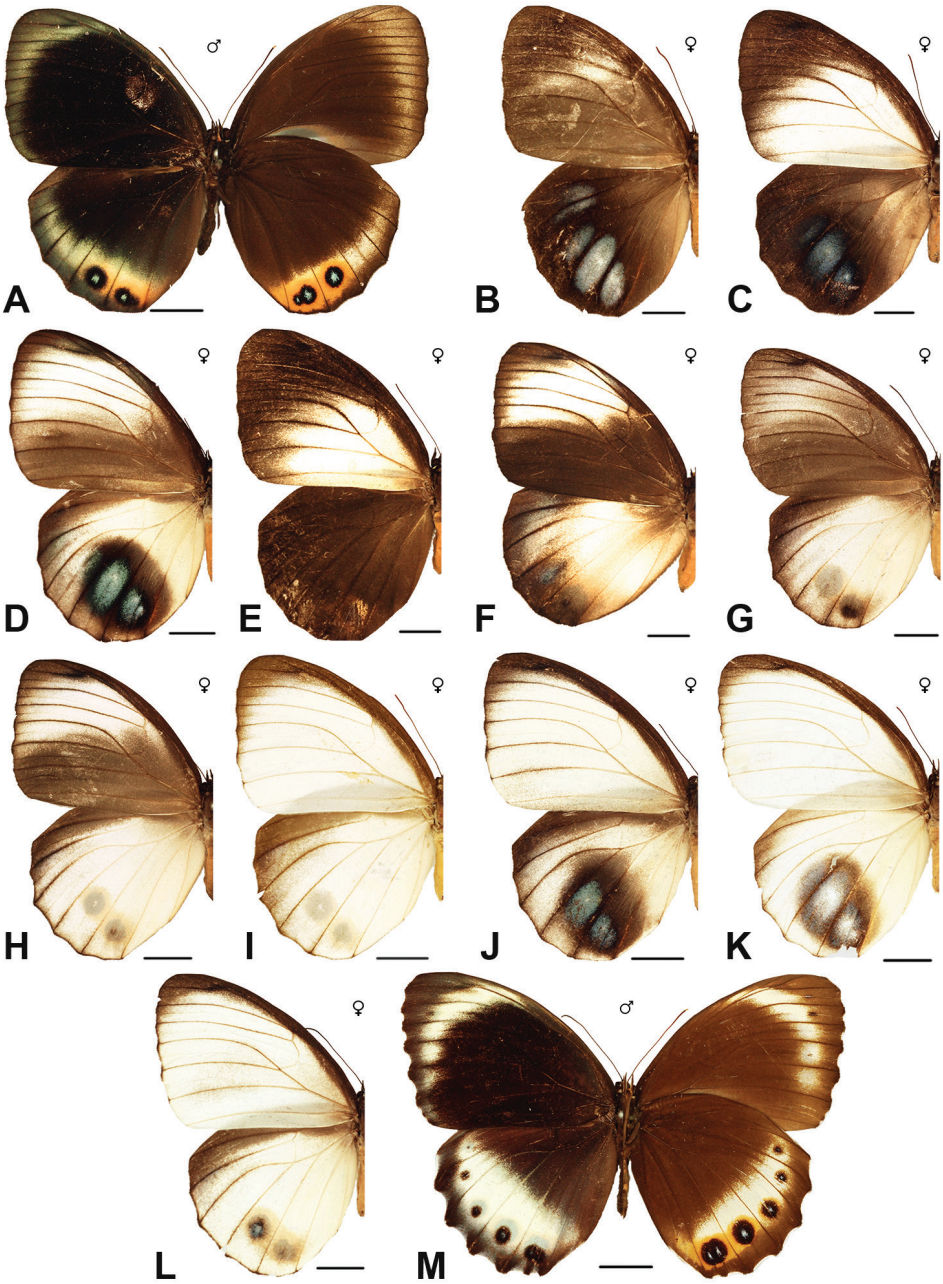

Figure 18. A *agondas melagondas* ♂ D+V NHM New Guinea **B** *agondas melagondas* ♀ D NHM New Guinea **C** *agondas melagondas* ♀ D NHM New Guinea **D** *agondas melagondas* ♀ D NHM New Guinea **E** *agondas melagondas* ♀ D NHM New Guinea **F** *agondas melagondas* ♀ D NHM New Guinea **G** *agondas melagondas* ♀ 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.

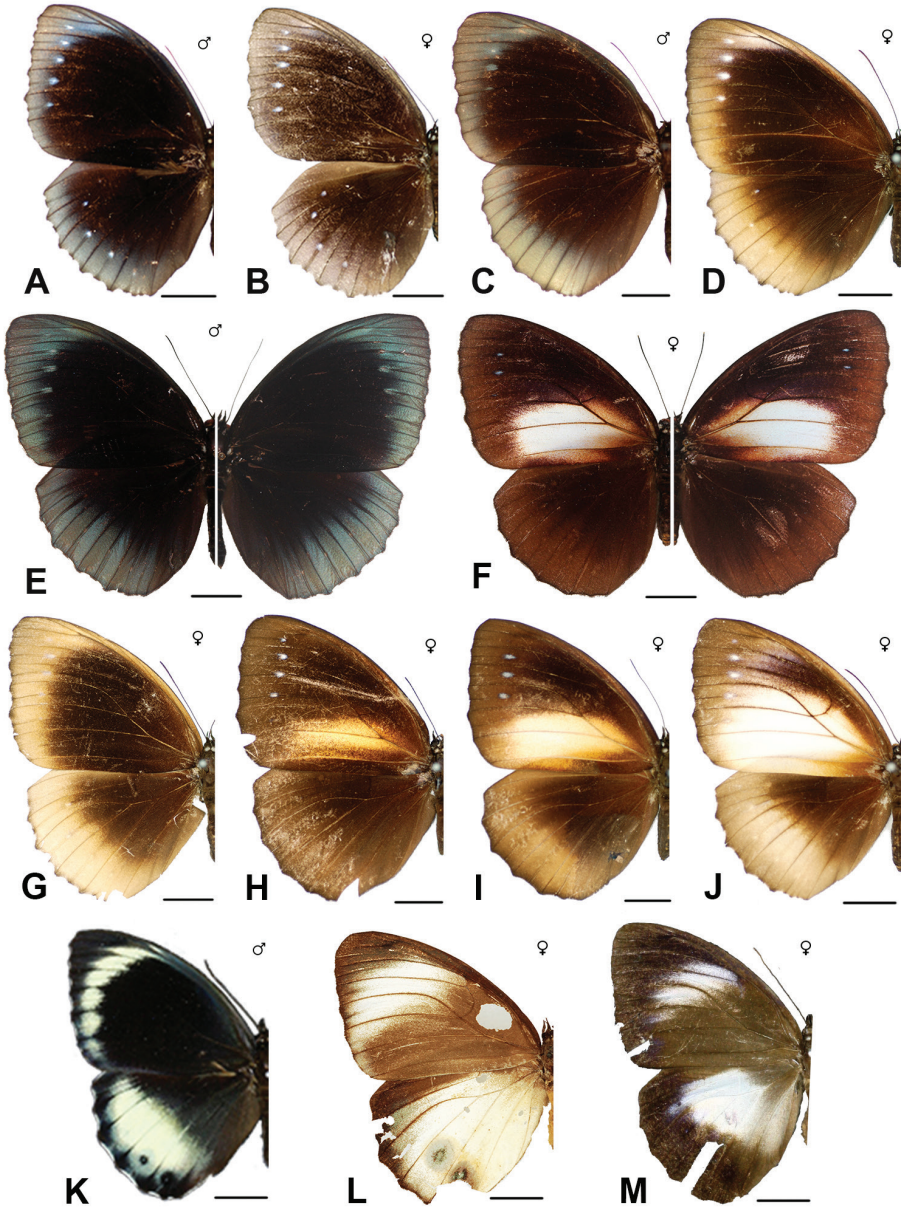

Figure 19. A *agondas dampierensis* ♂ D NHM Papua New Guinea: Madang, Karkar Island; Syntype **B** *agondas dampierensis* ♀ D NHM Papua New Guinea: Madang, Karkar Island **C** *agondas thryallis* ♂ D NHM Papua New Guinea **D** *agondas thryallis* ♀ D NHM Papua New Guinea **E** *agondas thryallis* ♂ D+V 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 thryallis* ♀ D NHM Indonesia: Papua, Yos Sudarso Bay **K** *agondas australiana* ♂ D MCZ Australia: Queensland, Claudie River **L** *agondas australiana* ♀ D NHM Australia: Queensland **M** *agondas australiana* ♀ D MCZ Australia: Queensland, West Claudie River.

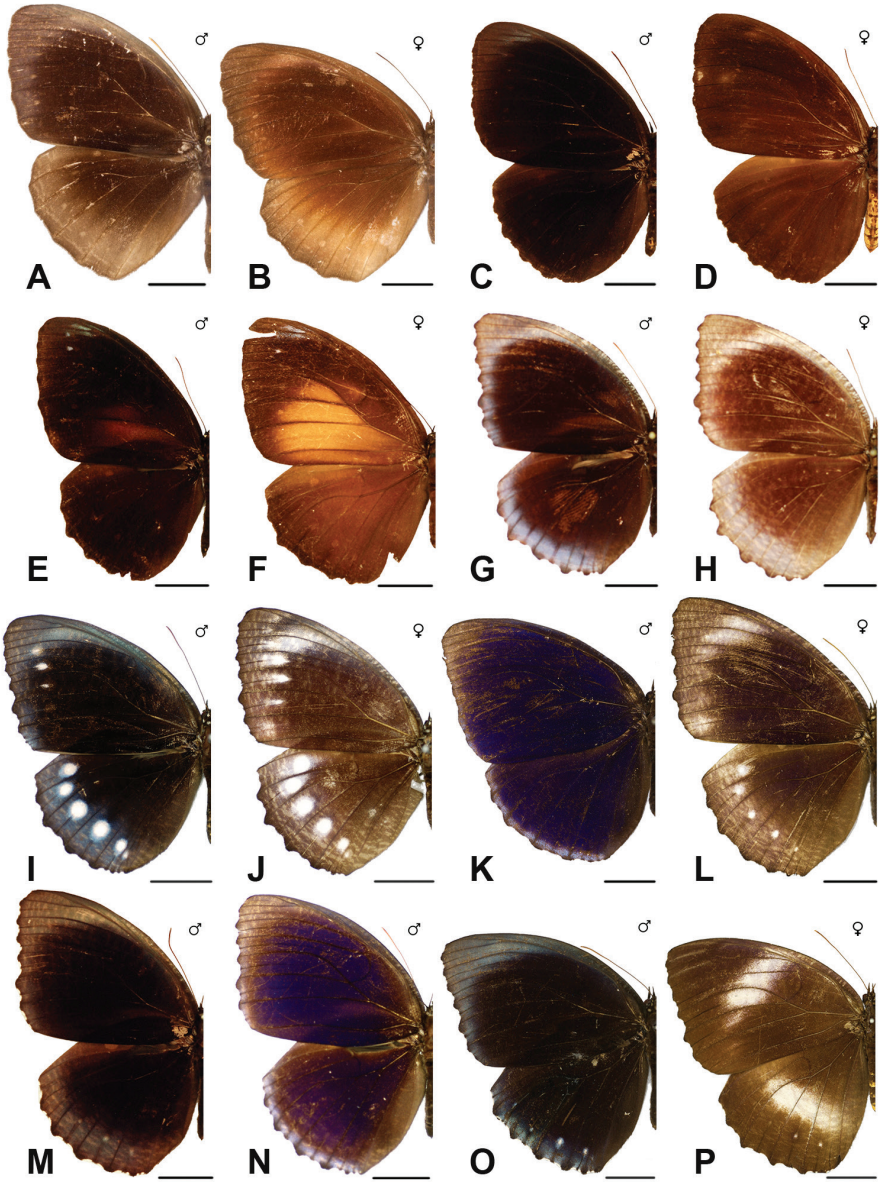

Figure 20. A *cybele cybele* ♂ D NHM Indonesia: North Maluku, Halmahera **B** *cybele cybele* ♀ D NHM Indonesia: North Maluku, Halmahera **C** *cybele cybele* ♂ D NHM Indonesia: North Maluku, Bacan **D** *cybele cybele* ♀ D NHM Indonesia: North Maluku, Bacan **E** *cybele obiana* ♂ D NHM Indonesia: North 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: North 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: Sulawesi **P** *hicetas hicetas* ♀ D NHM Indonesia: South Sulawesi.

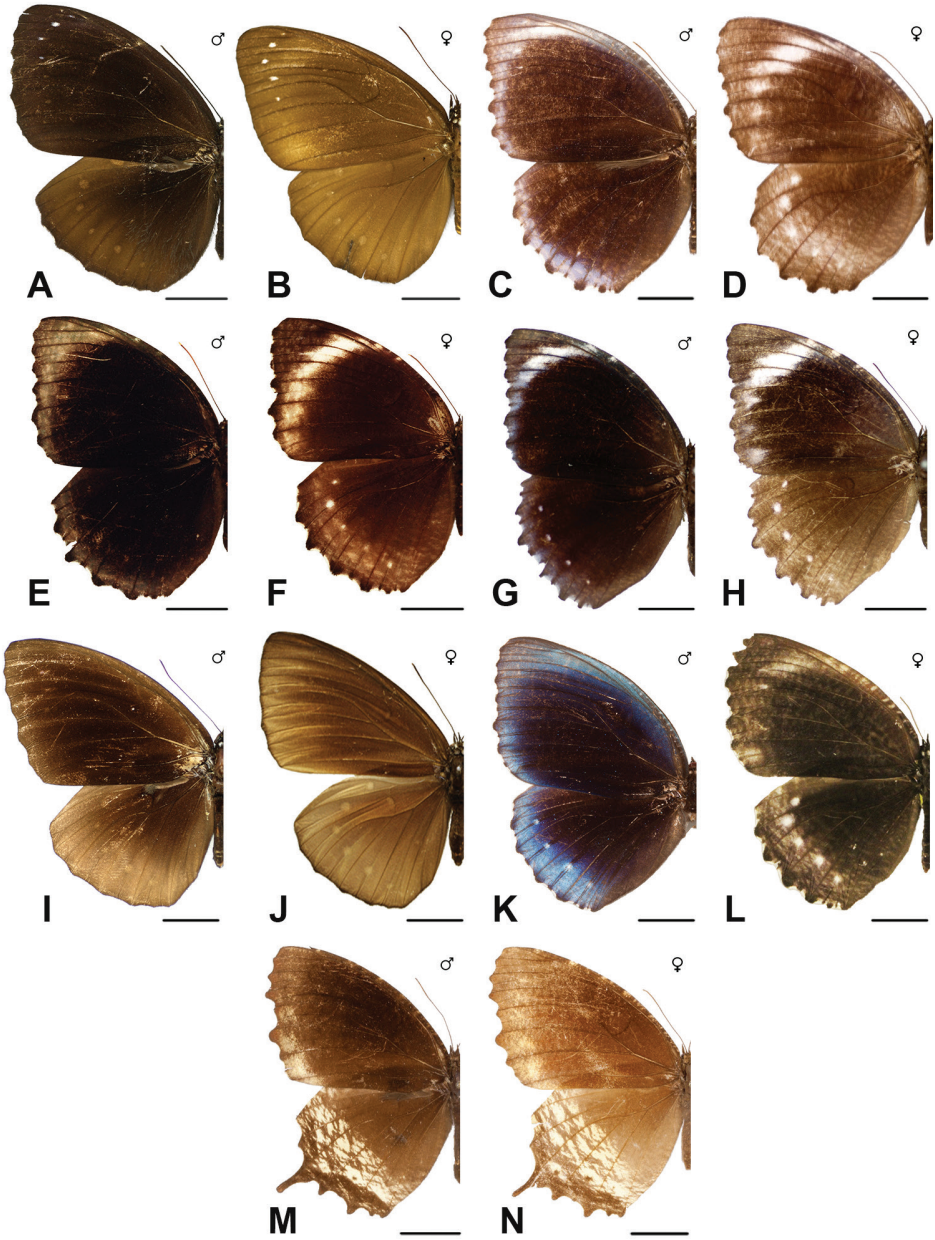

Figure 21. A *holofernes* ♂ D NHM Papua New Guinea: New Britain **B** *holofernes* ♀ D NHM Papua New Guinea: New Britain **C** *bornemanni* ♂ D NHM Indonesia: Central Sulawesi, Banggai **D** *bornemanni* ♀ D NHM Indonesia: Central Sulawesi, Banggai **E** *phrikonis* ♂ D NHM Indonesia: Sula Archipelago **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.

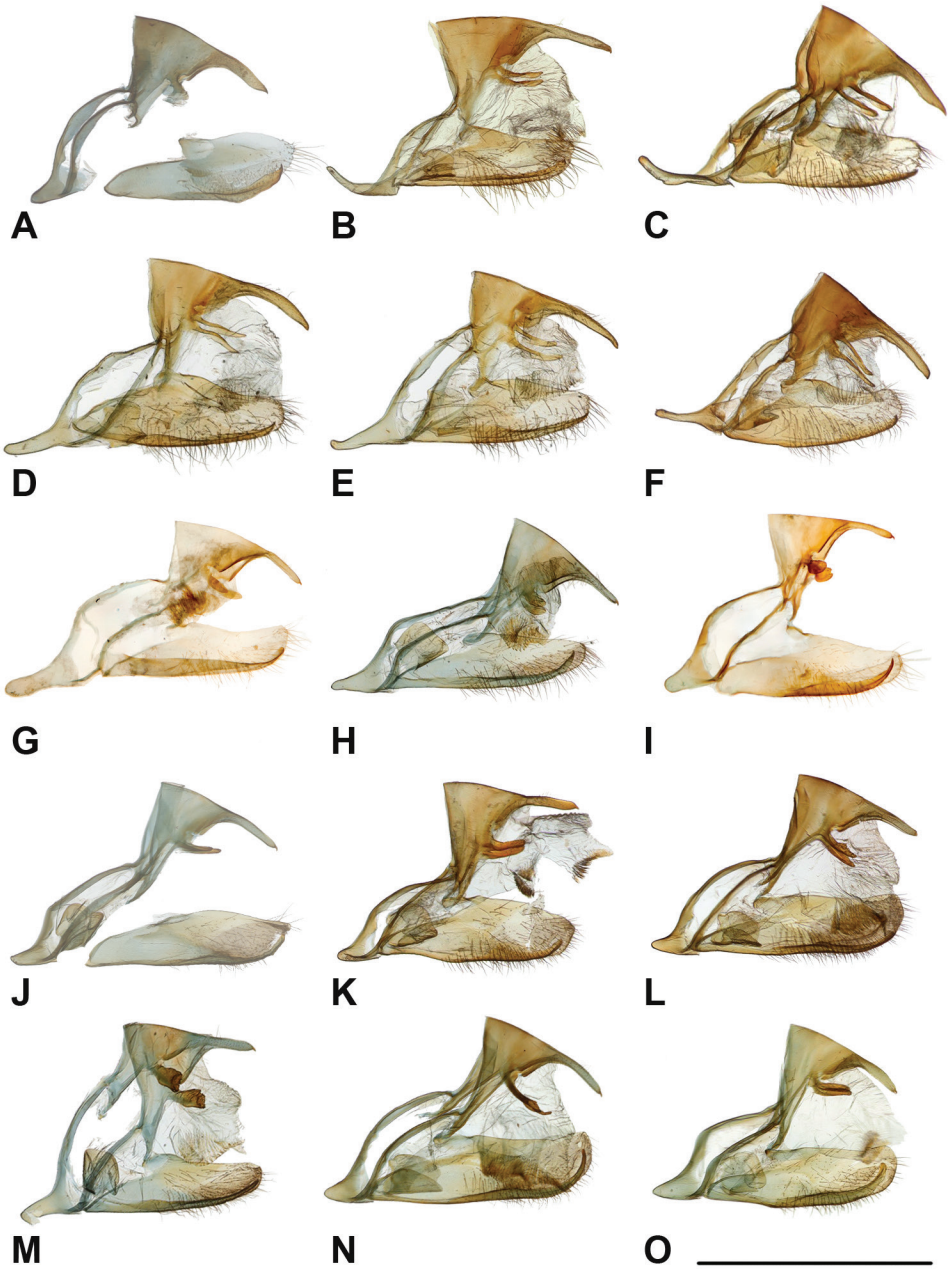

Figure 22. A *bammakoo bammakoo* NHM Central Africa **B** *paradoxa* NHM Indonesia: Papua, Weyland Mountains **C** *papua cinereomargo* NHM Indonesia: Papua, Biak **D** *esaca maheswara* NHM Indonesia: Java **E** *esaca leontina* NHM Indonesia: North Sumatra, Nias **F** *vasudeva* NHM India: Meghalaya, 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** *ceryx* NHM Indonesia: Java **M** *kuenstleri* NHM collection locality unknown **N** *pellucida* NHM East Malaysia: Sabah, Mt. Kinabalu **O** *penanga chelensis* NHM Thailand: Ranong.

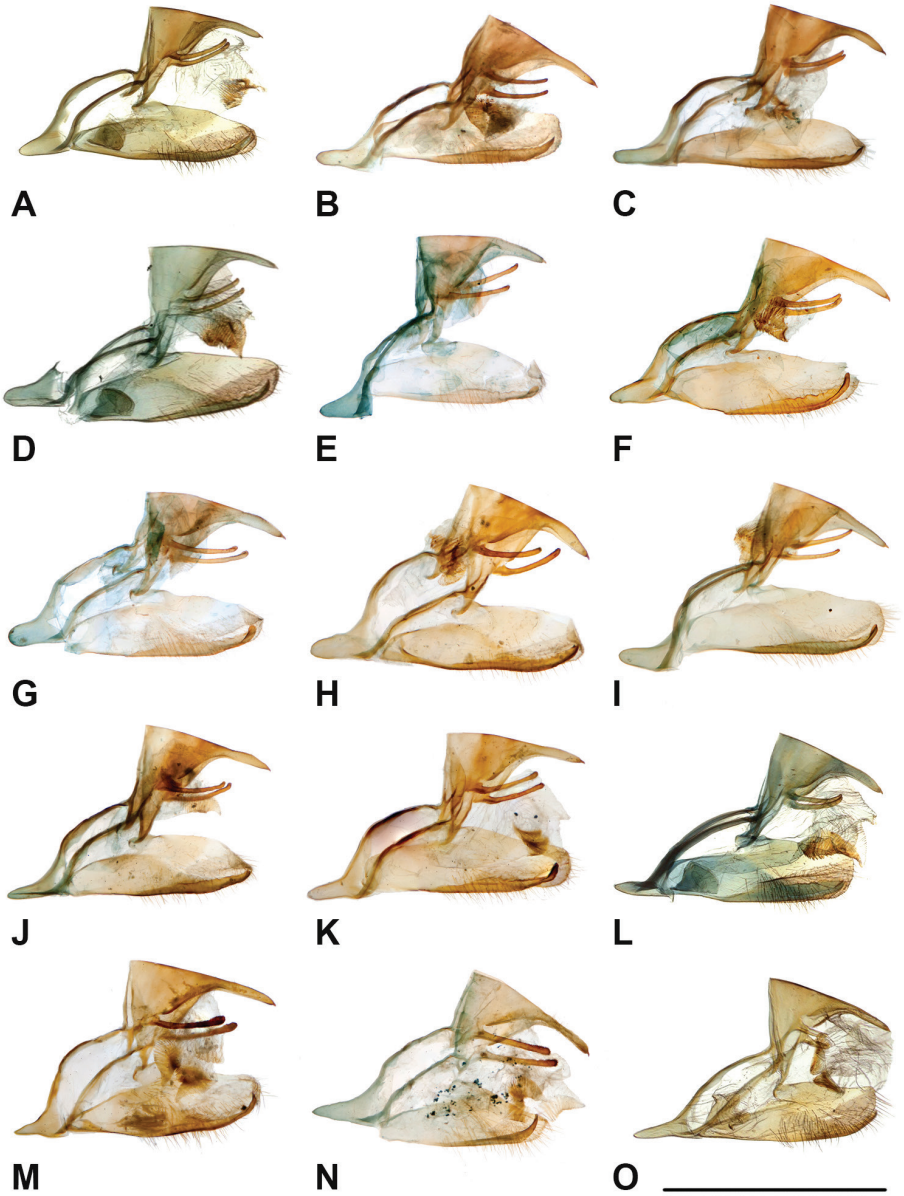

Figure 23. A *hypermnestra hypermnestra* NHM Indonesia: West Java, Bogor **B** *hypermnestra hypermnestra* MCZ Indonesia: Maluku, Seram **C** *hypermnestra fraterna* MCZ Sri Lanka: Western Province **D** *hypermnestra cottonis* NHM India: Andaman Islands **E** *hypermnestra tinctoria* NSYSU Thailand: 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.

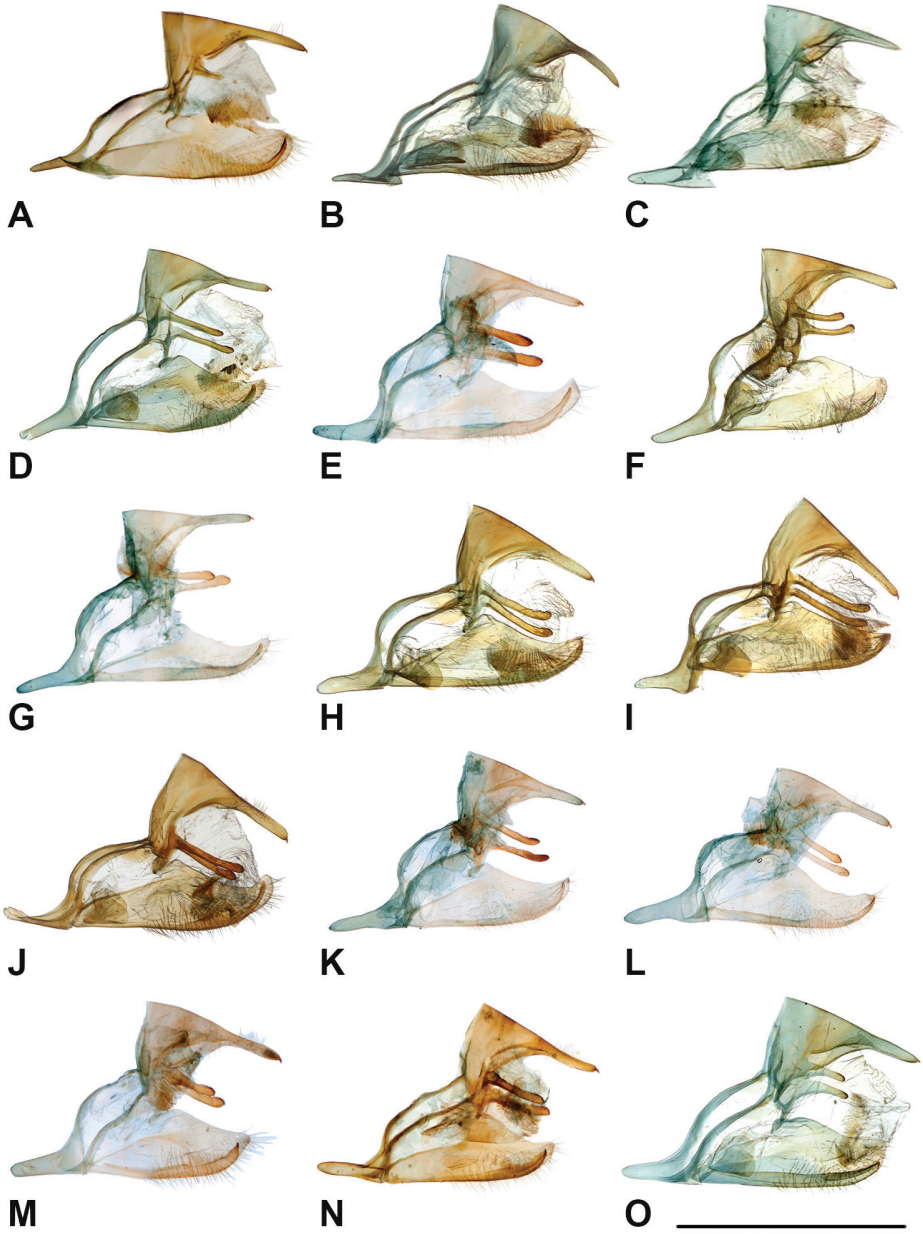

Figure 24. A *panthera balina* MCZ Indonesia: Bali **B** *obnubila* NHM Peninsular Malaysia: Perak **C** *congruens congruens* NHM Philippines: Cebu, Camotes Island **D** *nesaea nesaea* NHM Indonesia: Java **E** *nesaea nesaea* NSYSU Indonesia: Bali **F** *nesaea timandra* NHM India: Meghalaya, Khasi Hills **G** *nesaea 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

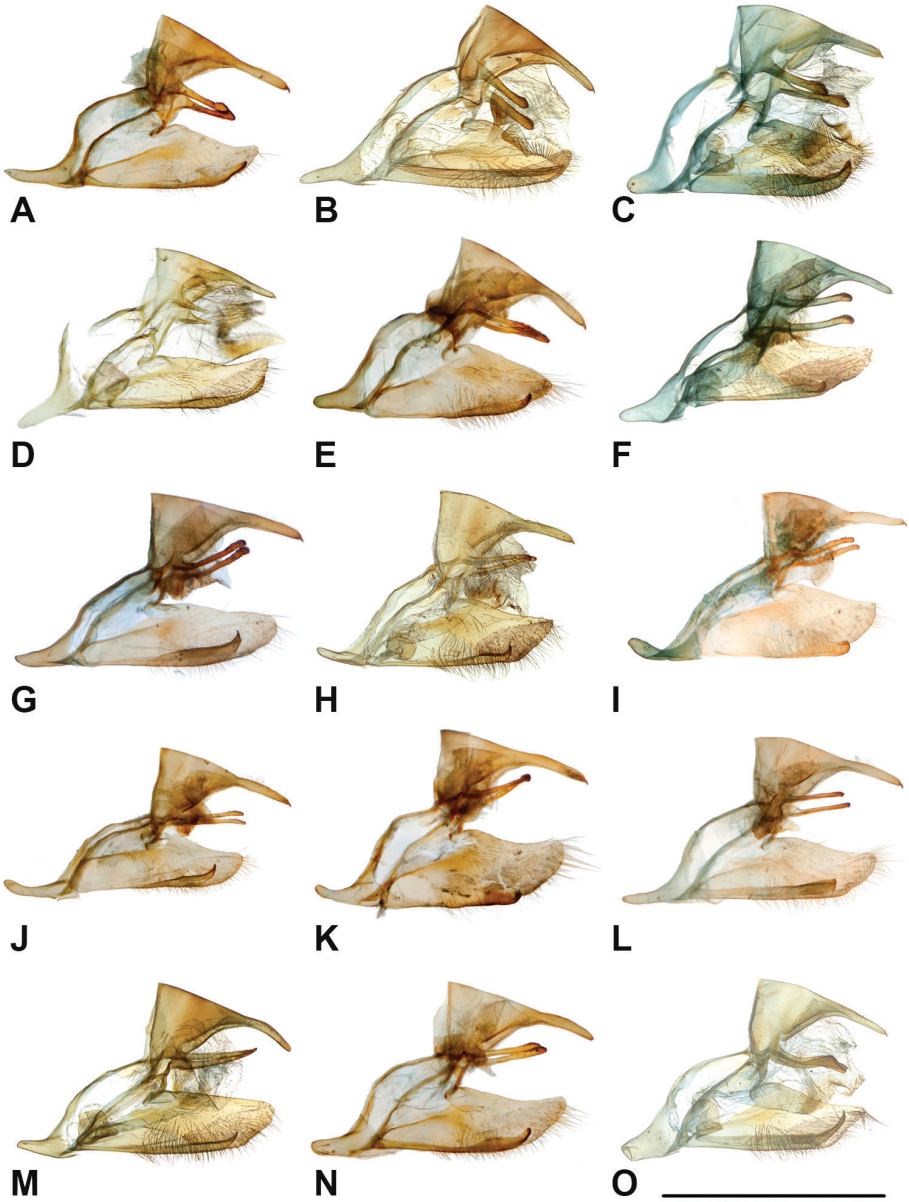

Figure 25. A *nelsoni* MCZ Indonesia: West Sumatra, Pagai Island **B** *kanekoi* NHM Philippines: Negros **C** *melias malis* NHM Philippines: Quezon, Polillo Island **D** *beza beza* NHM Philippines: Mindanao **E** *sansoni aklanensis* MCZ Philippines: Panay, Aklan, Mt. Madiaas **F** *vitellia vitellia* 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.

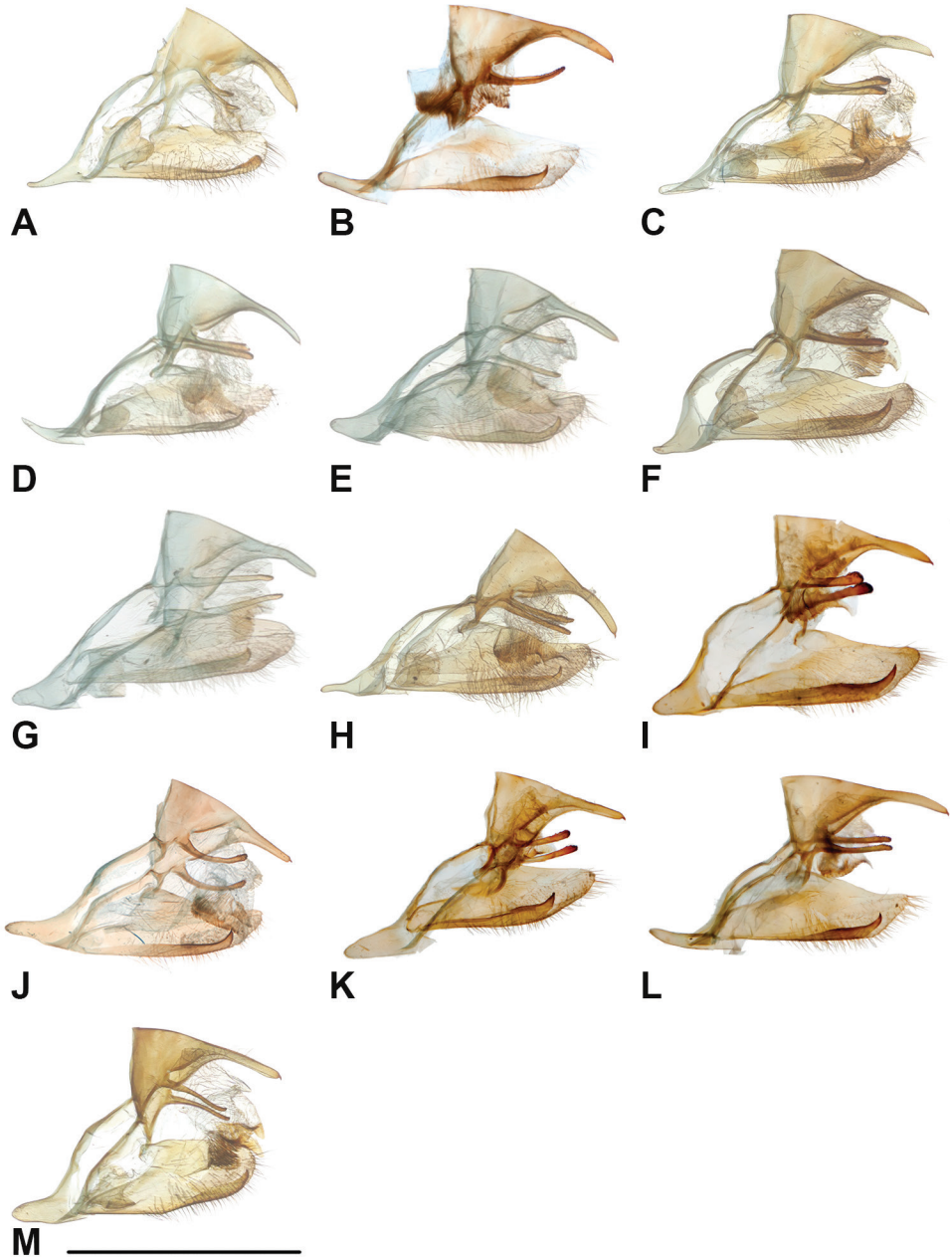

Figure 26. A *cybele cybele* NHM Indonesia: North Maluku, Halmahera **B** *cumaea toliana* MCZ Indonesia: North Sulawesi **C** *hewitsoni meliophila* NHM Indonesia: Maluku, Kisar **D** *mimalon mimalon* NHM Indonesia: Sulawesi **E** *hicetas hicetas* NHM Indonesia: Sulawesi **F** *hicetas hicetina* NHM Indonesia: Sulawesi **G** *holofernes* NHM Papua New Guinea: New Britain **H** *bornemanni* 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

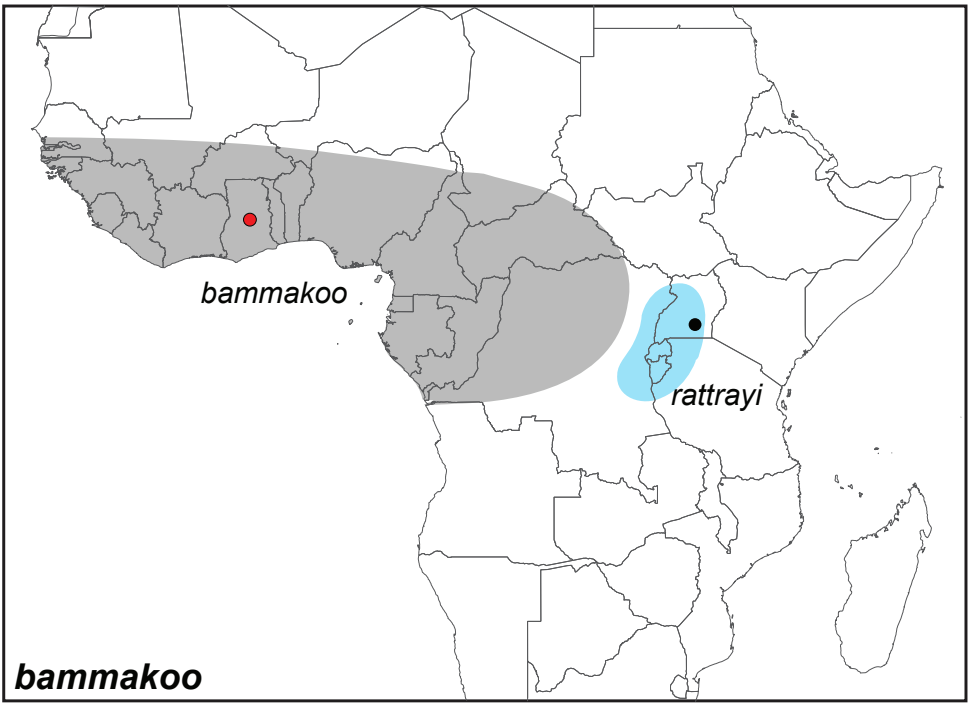

Figure 27. Distribution map of *Elymnias bammakoo*.

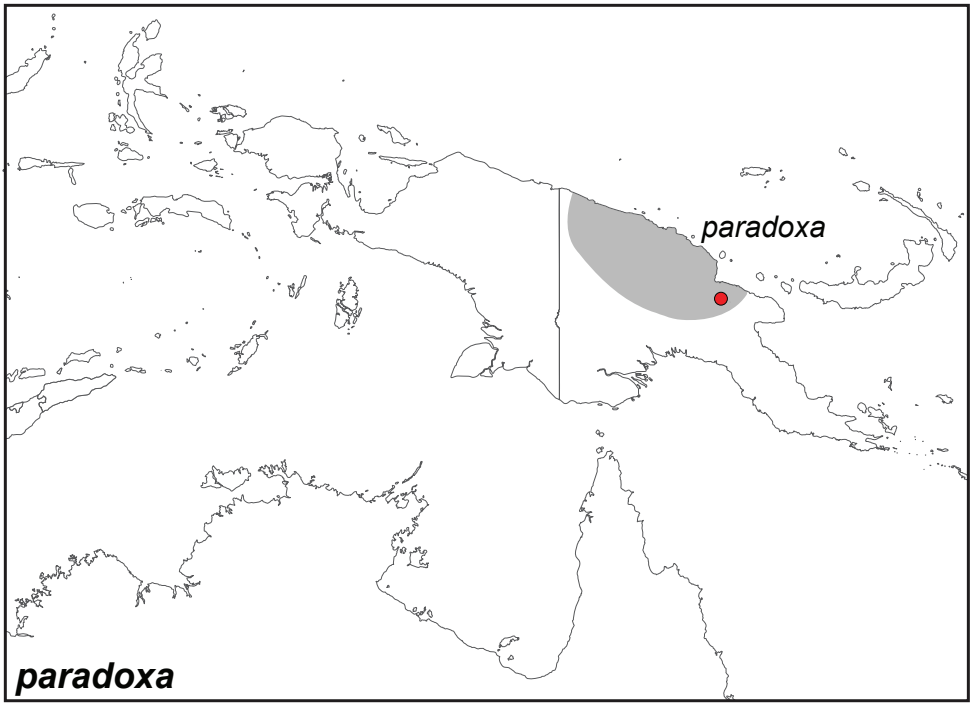

Figure 28. Distribution map of *Elymnias paradoxa*.

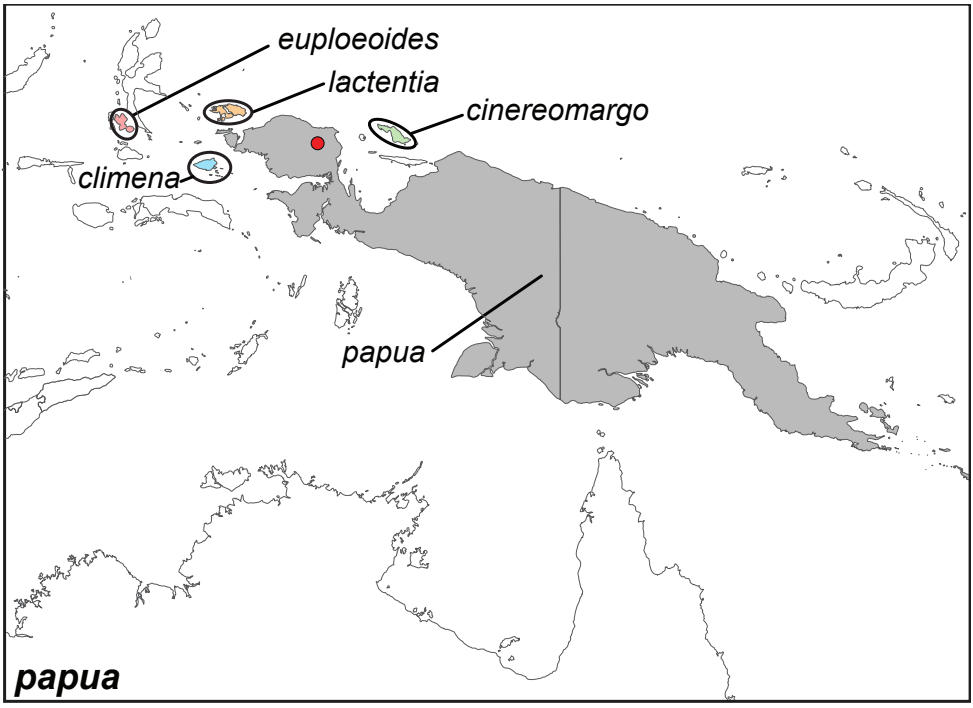

Figure 29. Distribution map of *Elymnias papua.*

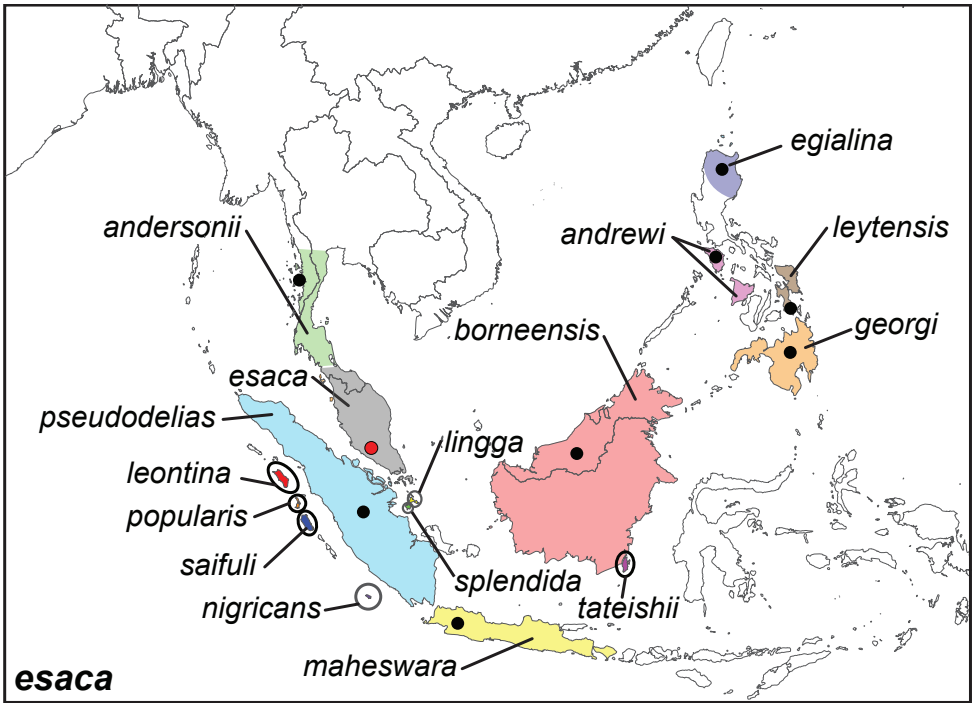

Figure 30. Distribution map of *Elymnias esaca.*

Figure 31. Distribution map of *Elymnias vasudeva.*

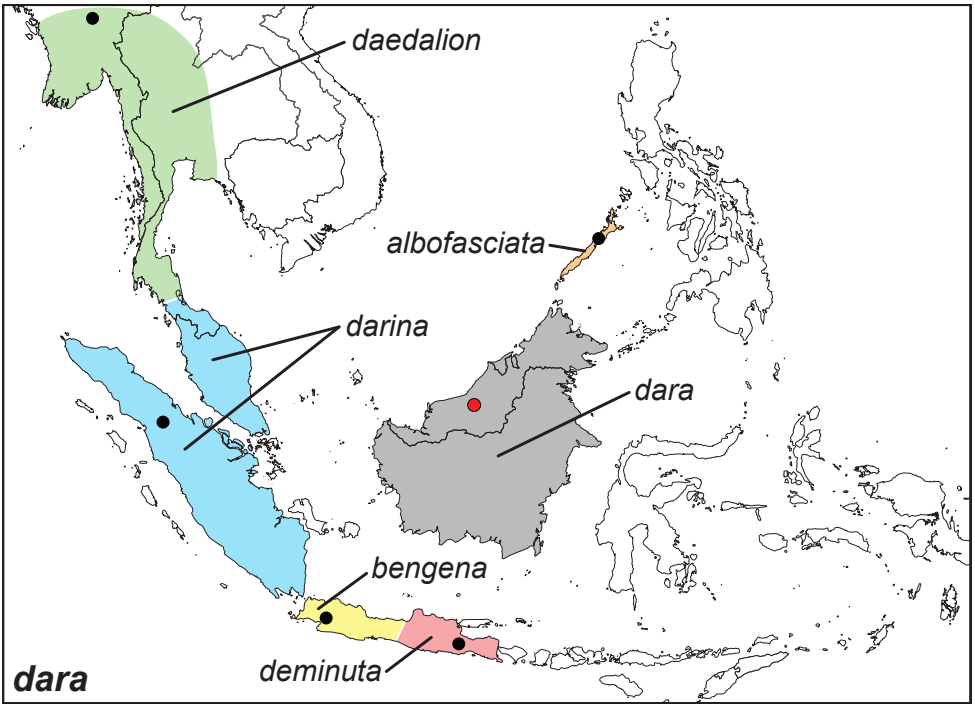

Figure 32. Distribution map of *Elymnias dara*.

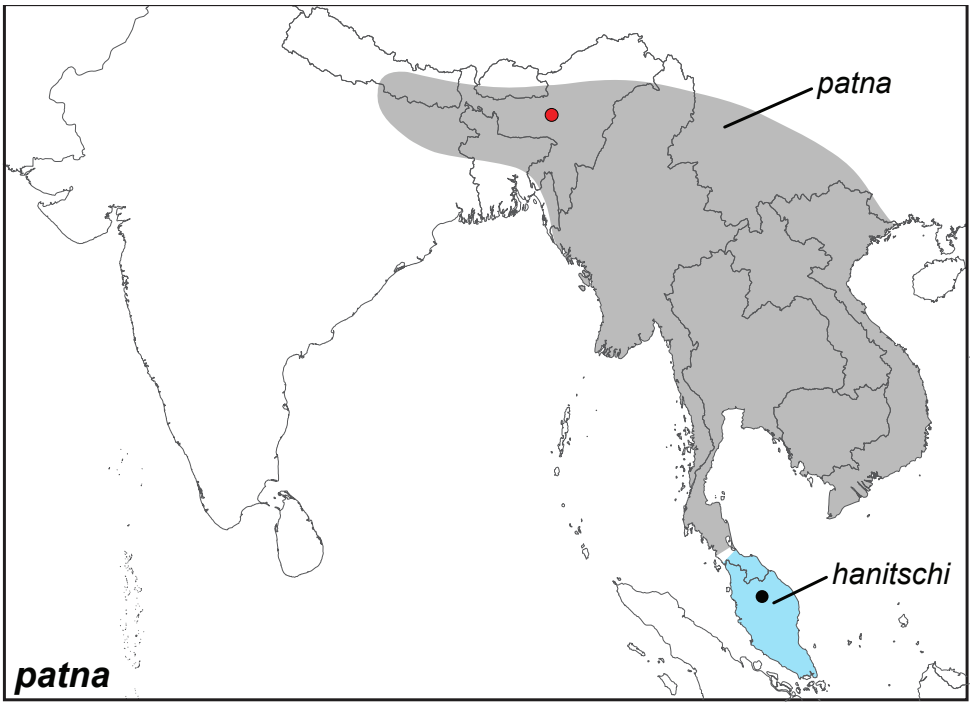

Figure 33. Distribution map of *Elymnias patna*.

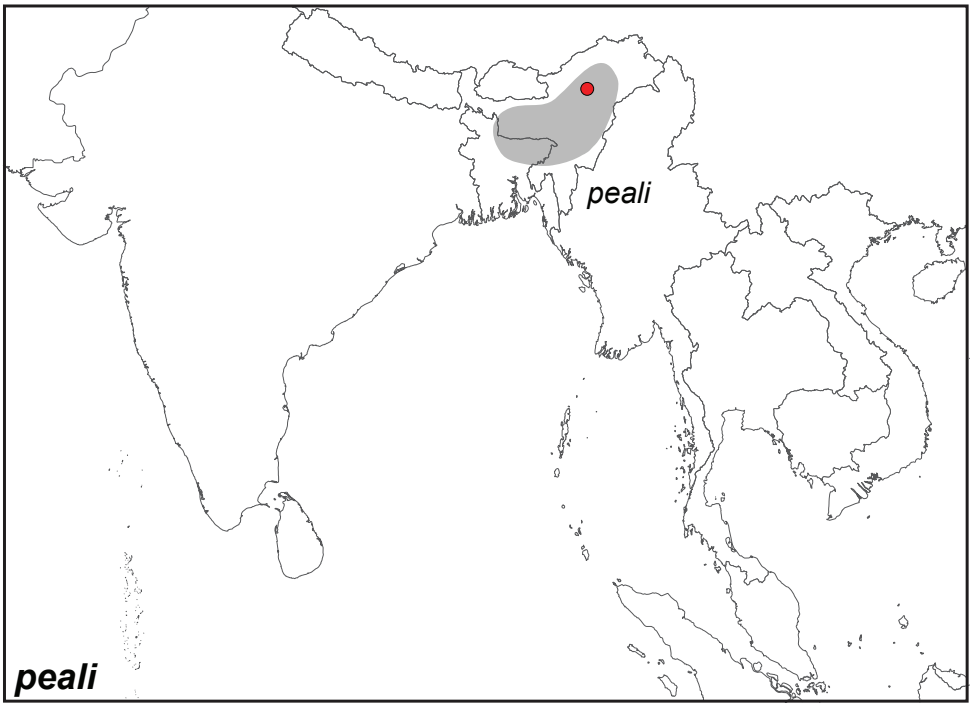

Figure 34. Distribution map of *Elymnias peali*.

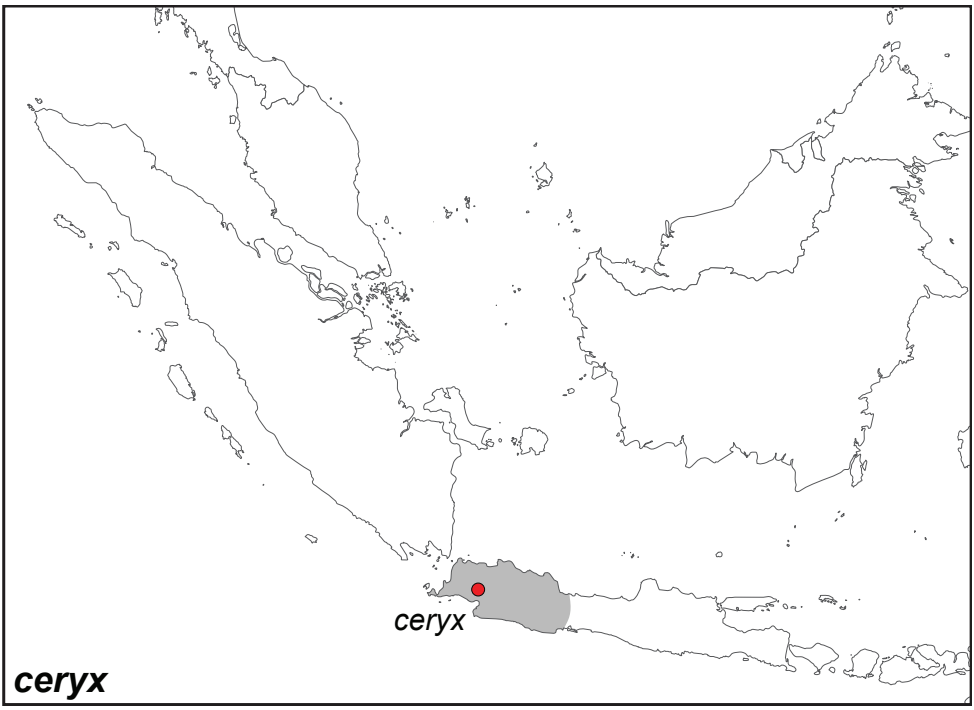

Figure 35. Distribution map of *Elymnias ceryx*.

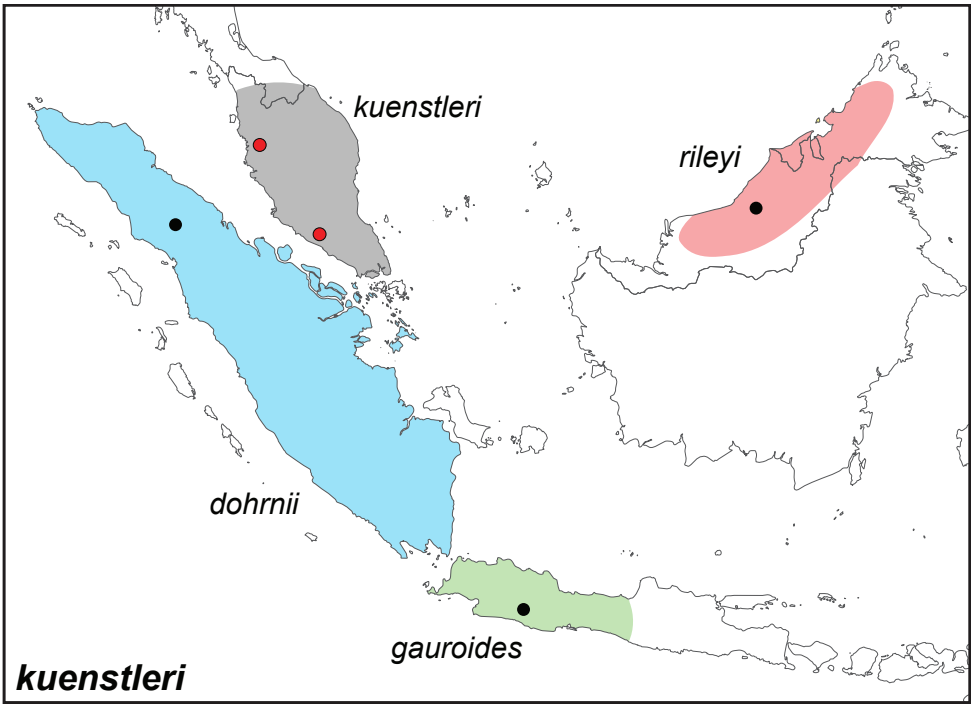

Figure 36. Distribution map of *Elymnias kuenstleri*.

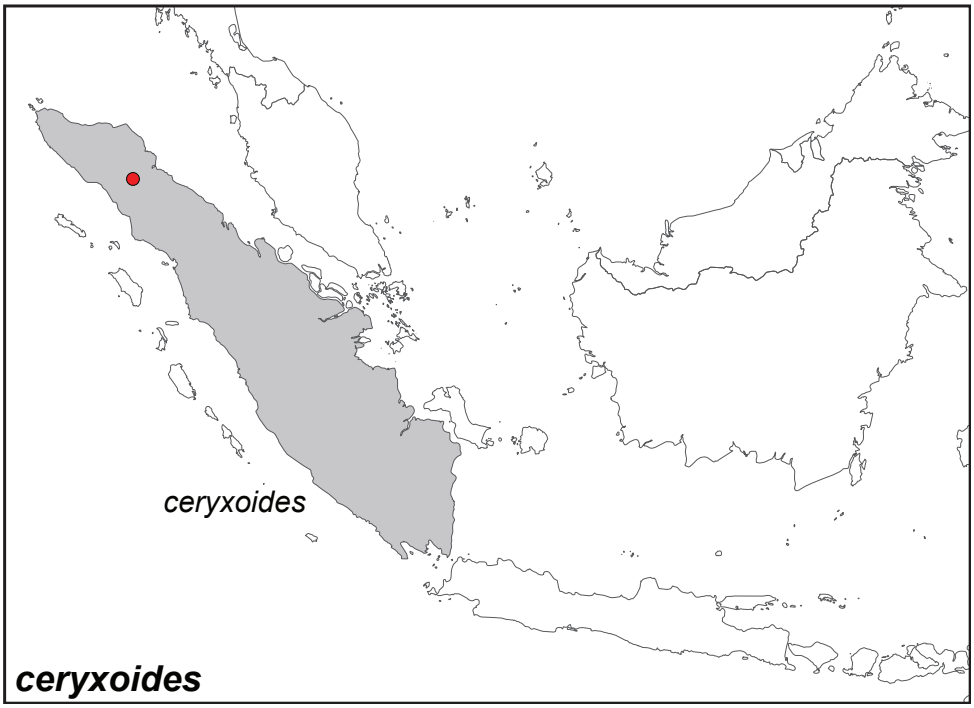

Figure 37. Distribution map of *Elymnias ceryxoides*.

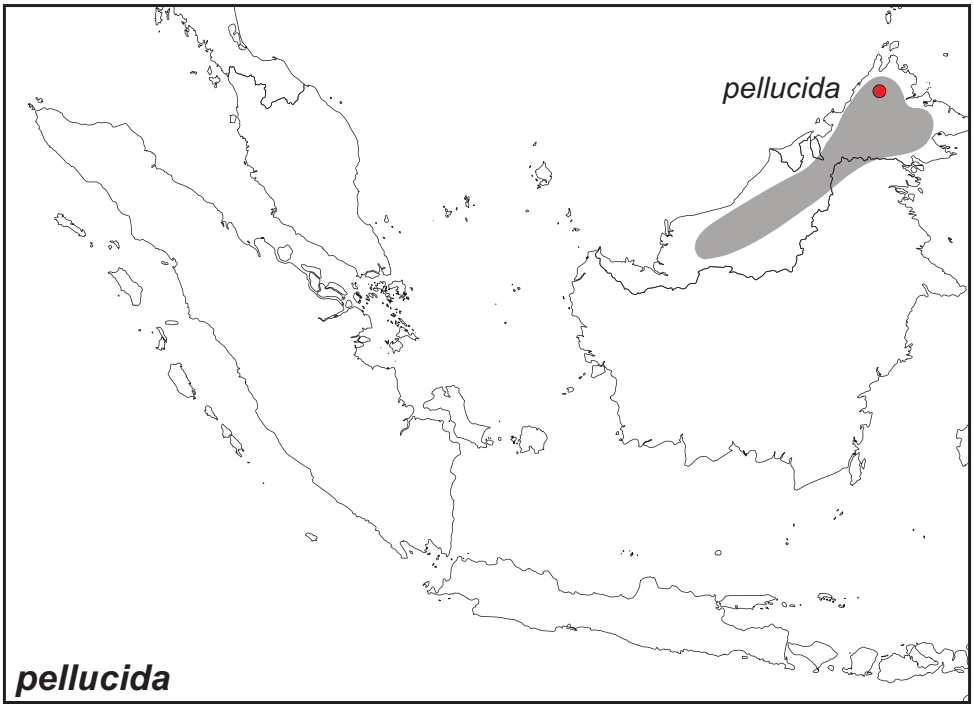

Figure 38. Distribution map of *Elymnias pellucida*.

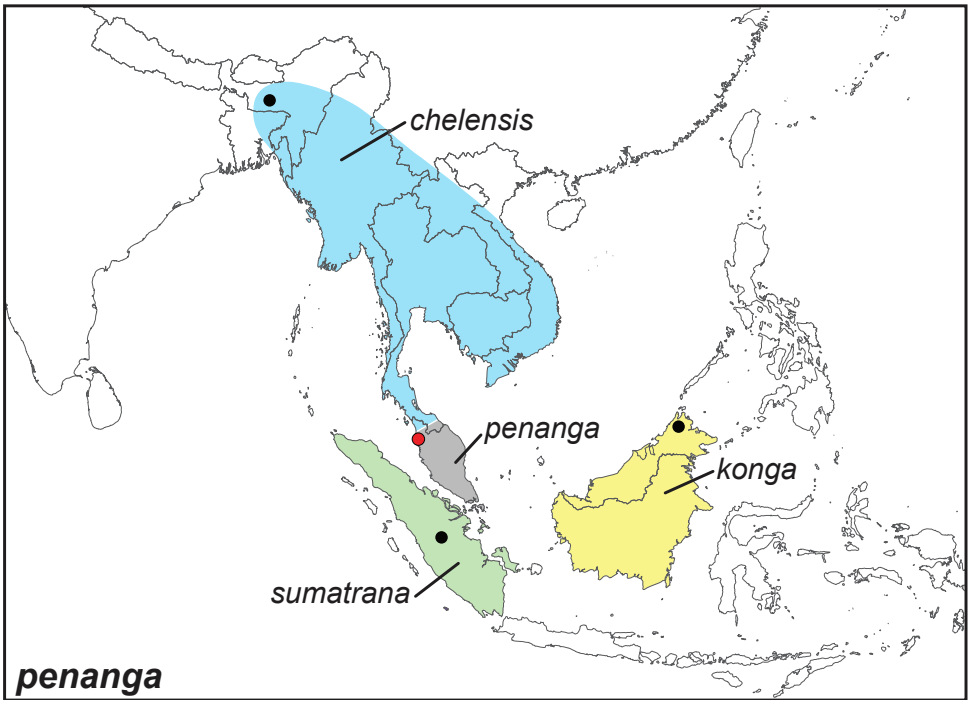

Figure 39. Distribution map of *Elymnias penanga*.

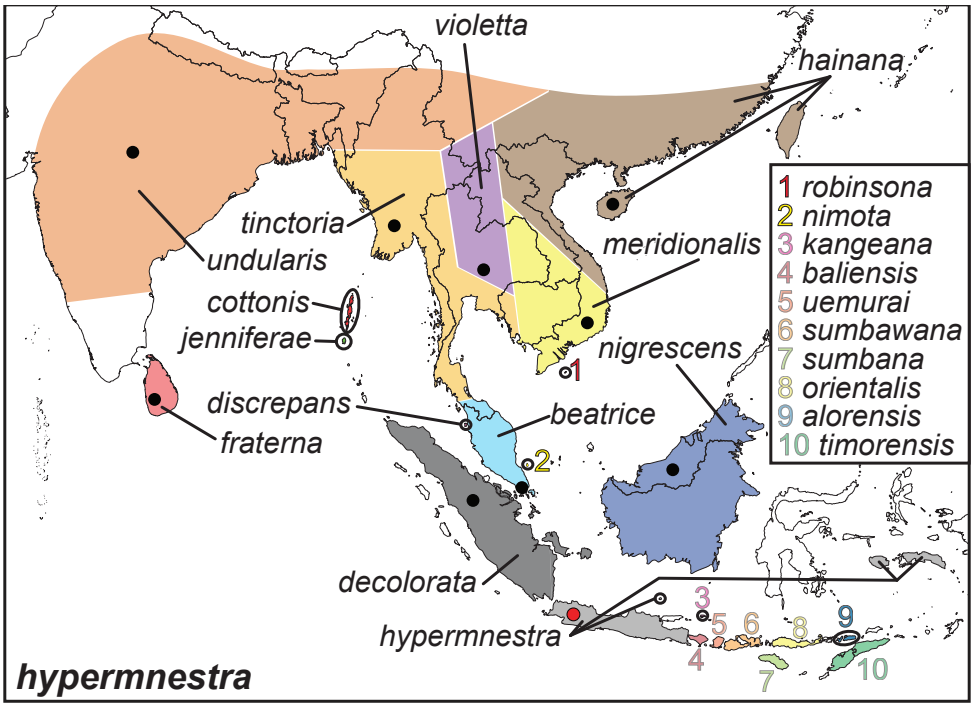

Figure 40. Distribution map of *Elymnias hypermnestra*.

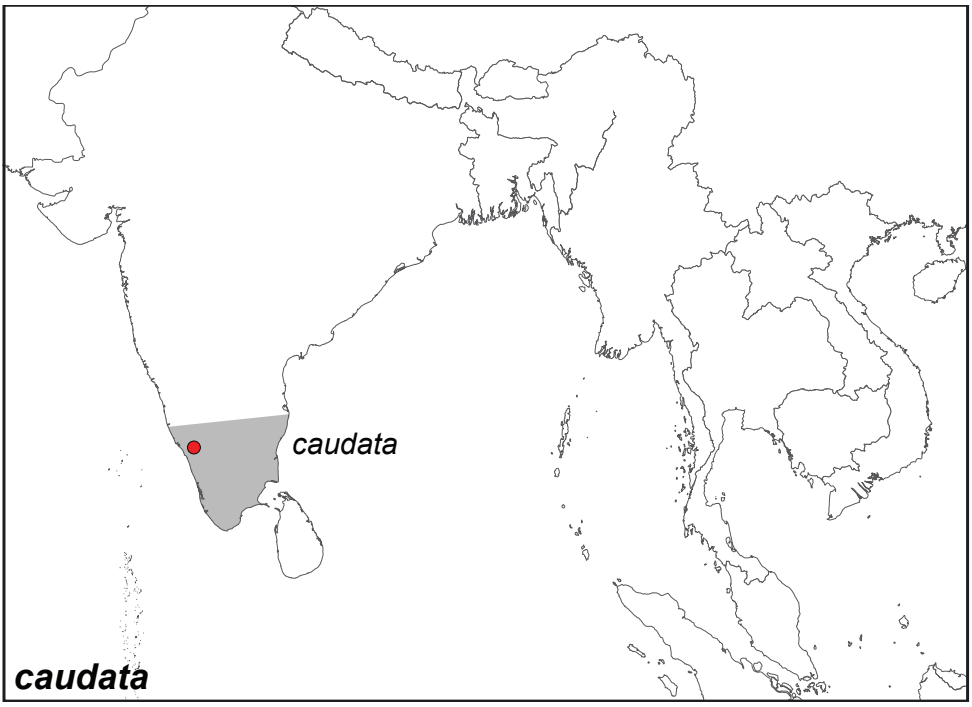

Figure 41. Distribution map of *Elymnias caudata*.

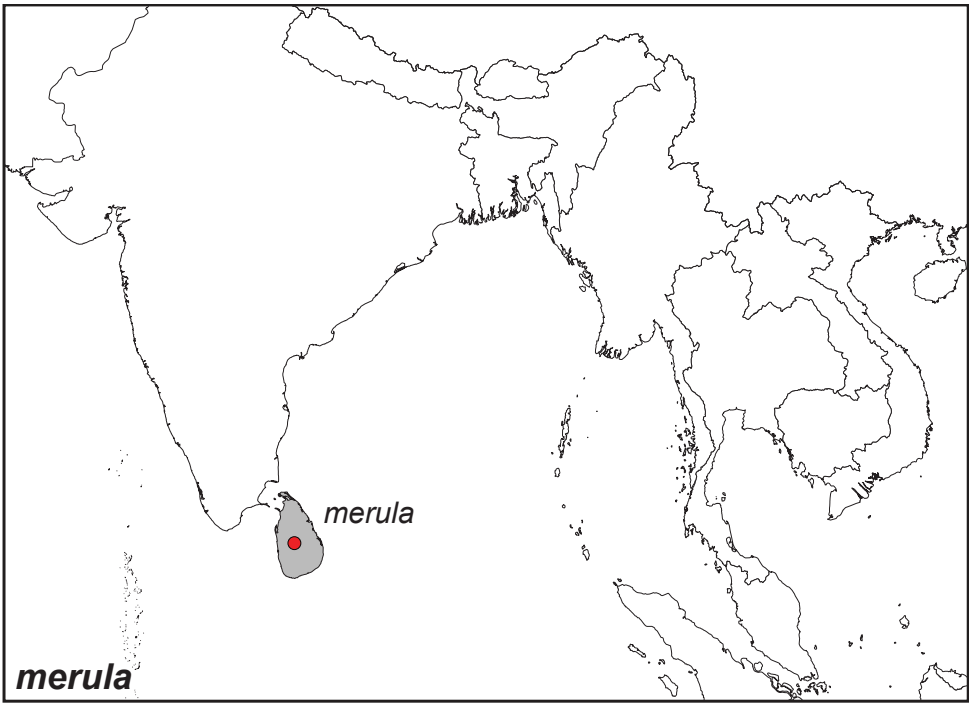

Figure 42. Distribution map of *Elymnias merula*.

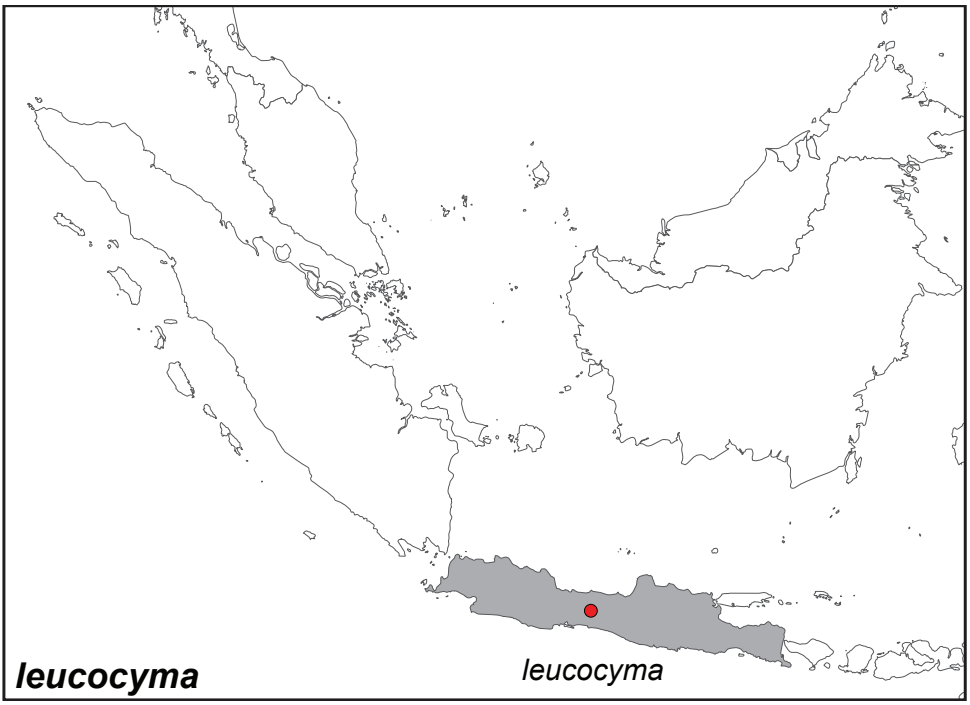

Figure 43. Distribution map of *Elymnias leucocyma*.

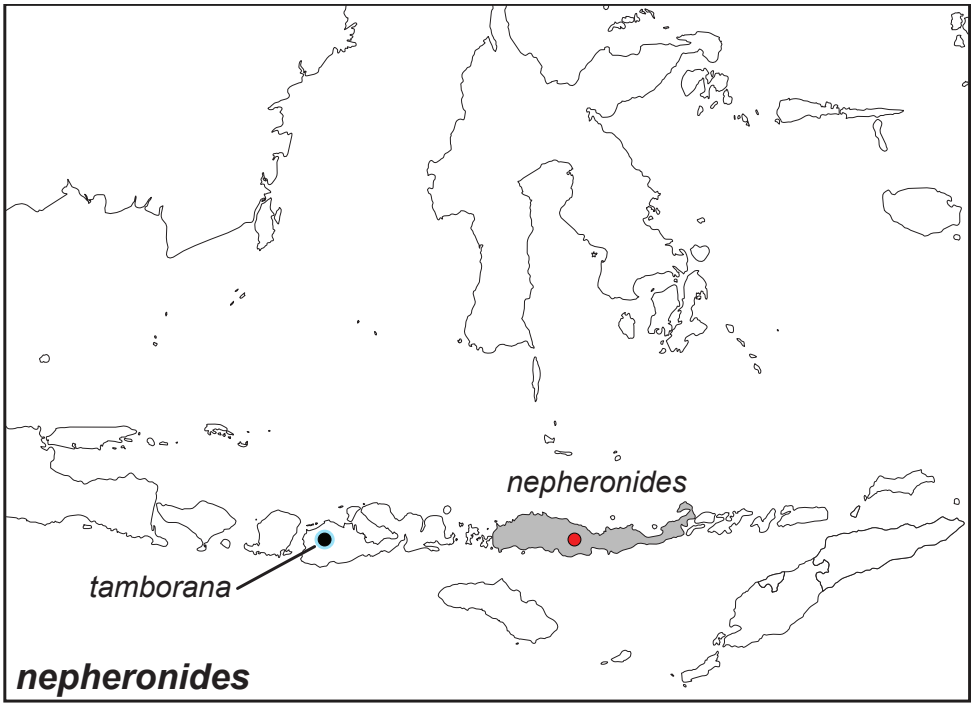

Figure 44. Distribution map of *Elymnias nepheronides*.

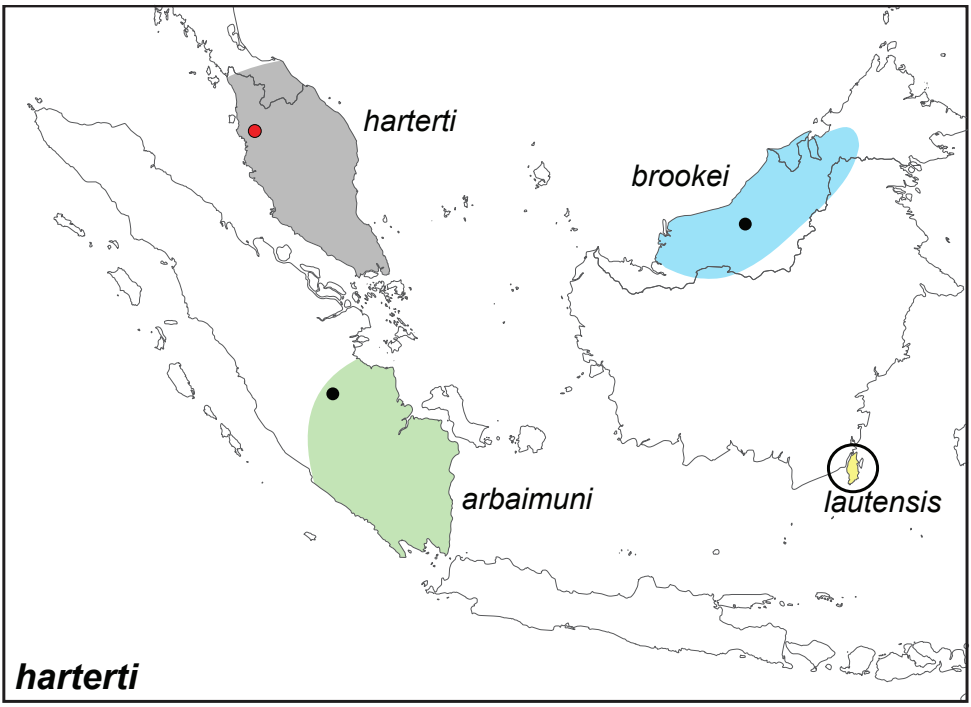

Figure 45. Distribution map of *Elymnias harterti*.

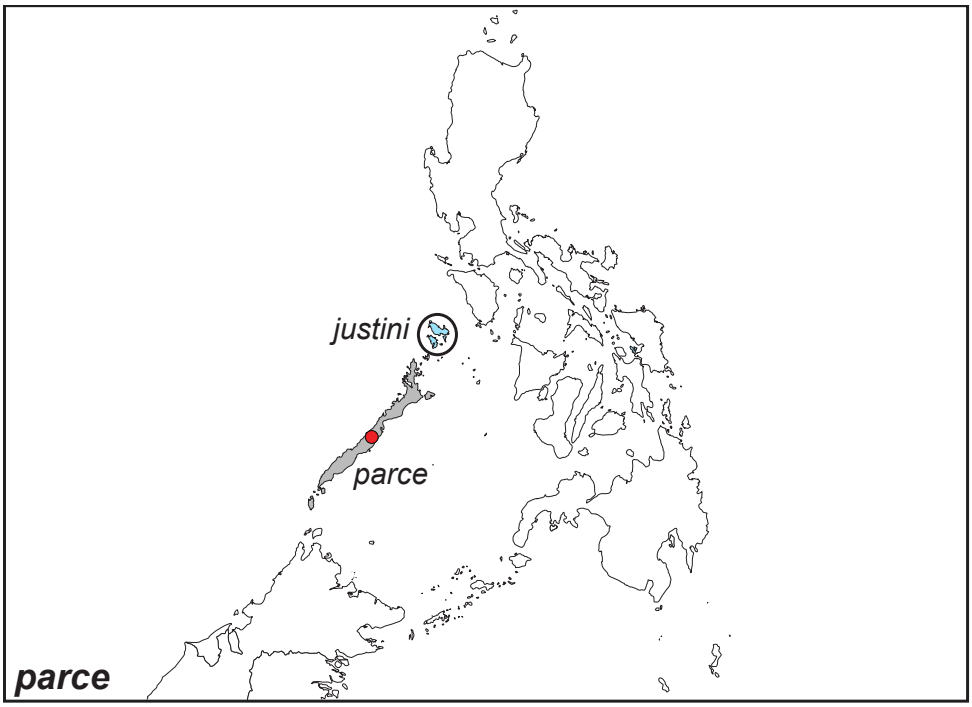

Figure 46. Distribution map of *Elymnias parce*.

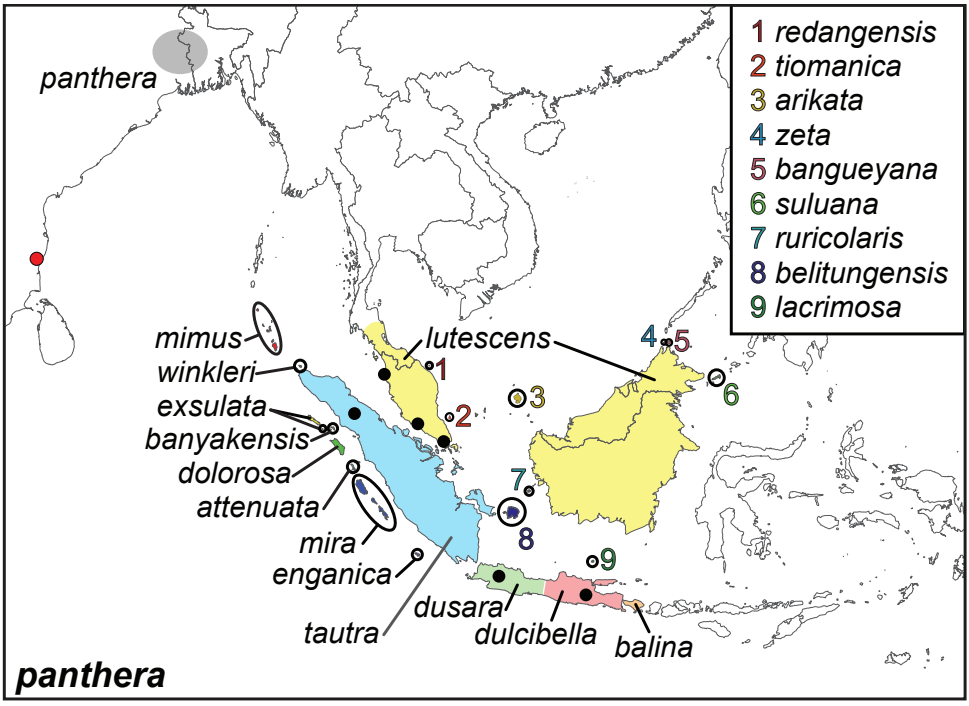

Figure 47. Distribution map of *Elymnias panthera*.

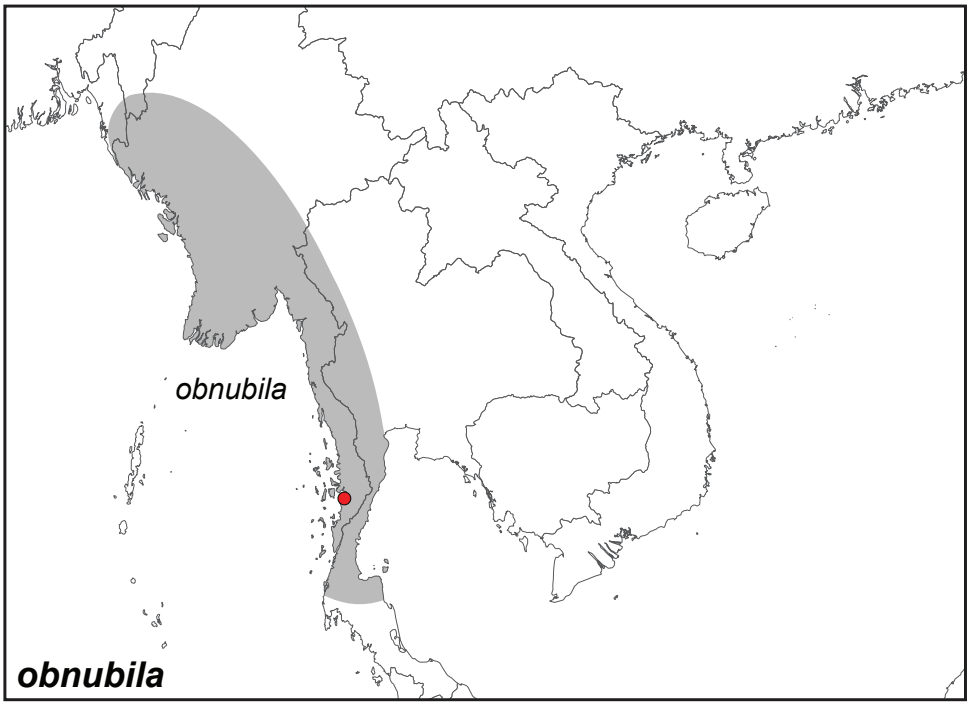

Figure 48. Distribution map of *Elymnias obnubila*.

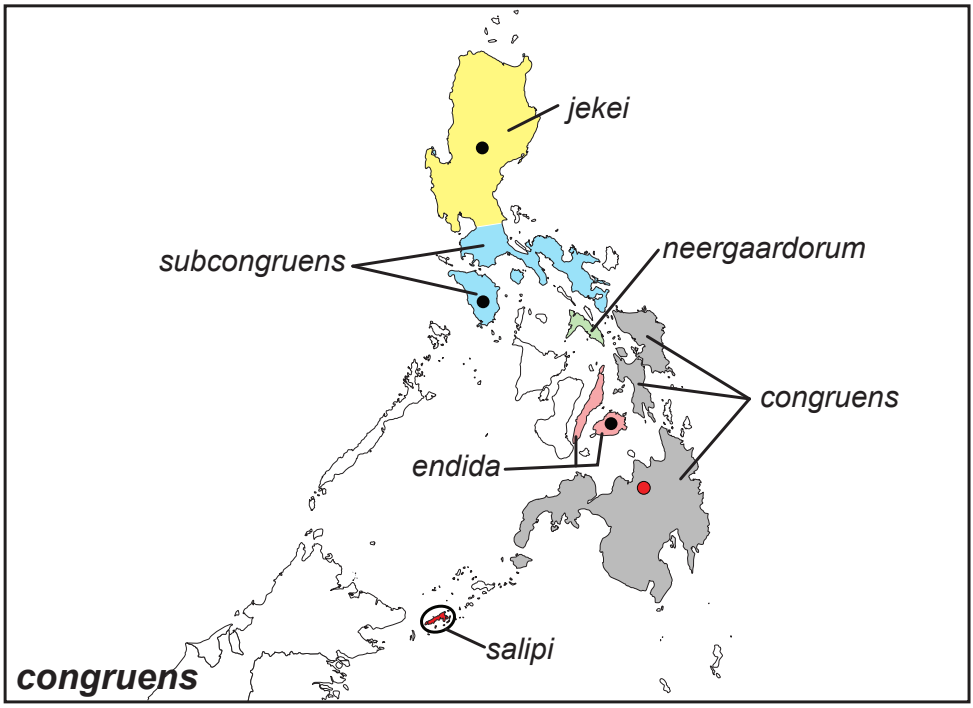

Figure 49. Distribution map of *Elymnias congruens*.

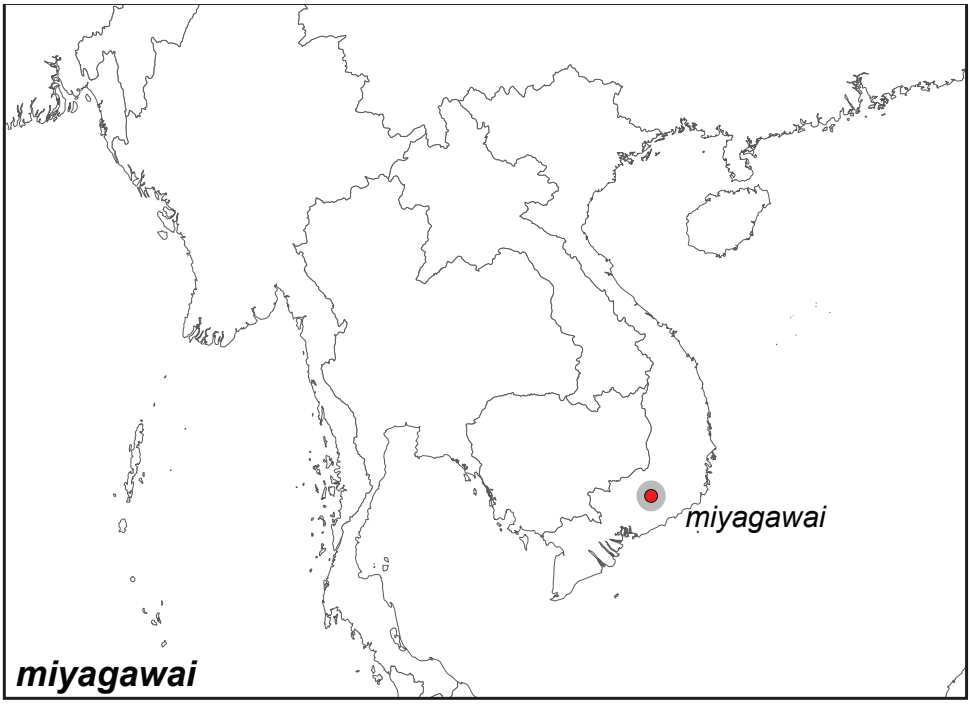

Figure 50. Distribution map of *Elymnias miyagawai*.

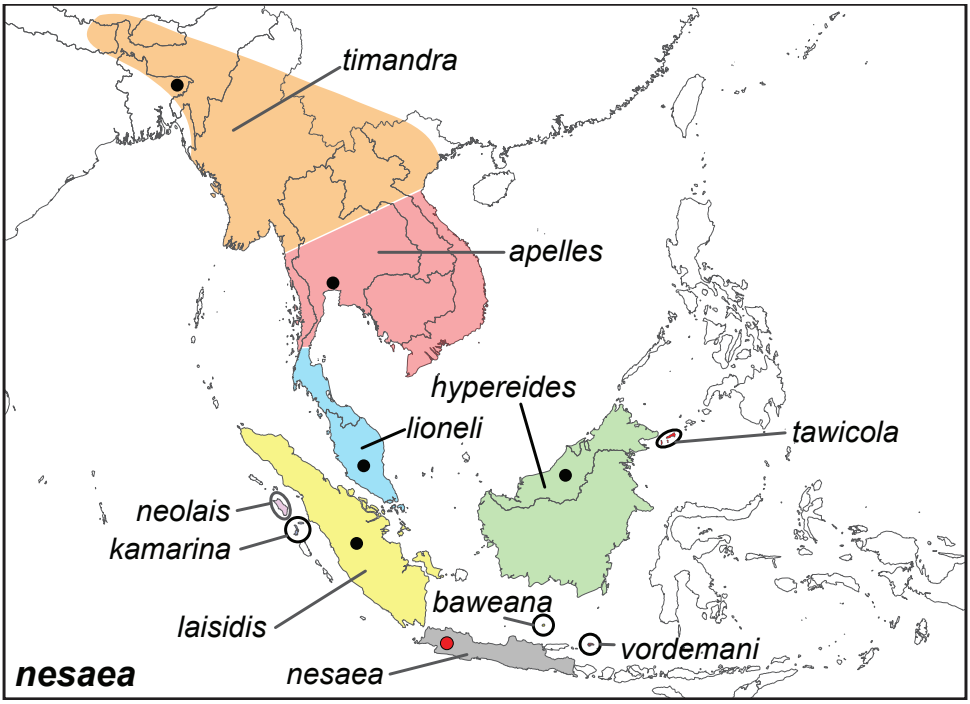

Figure 51. Distribution map of *Elymnias nesaea*.

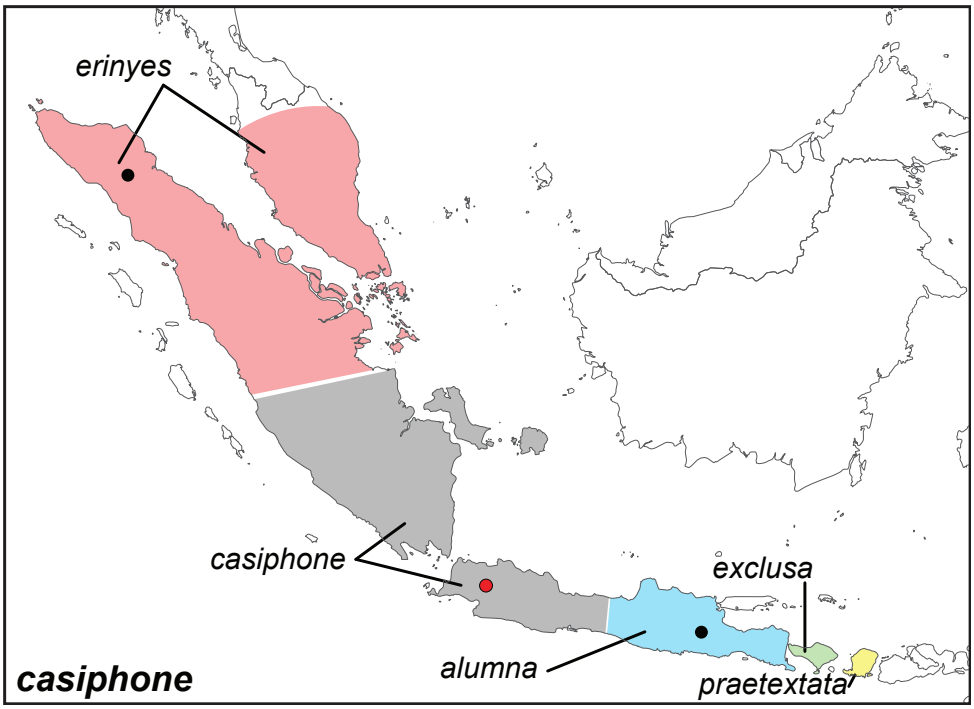

Figure 52. Distribution map of *Elymnias casiphone*.

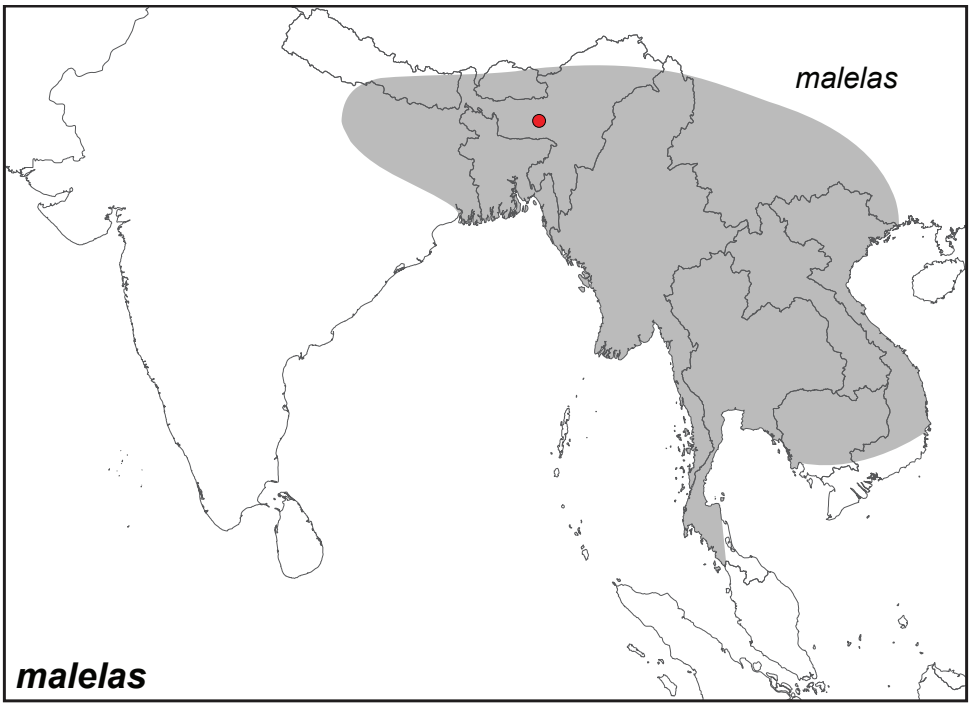

Figure 53. Distribution map of *Elymnias malelas*.

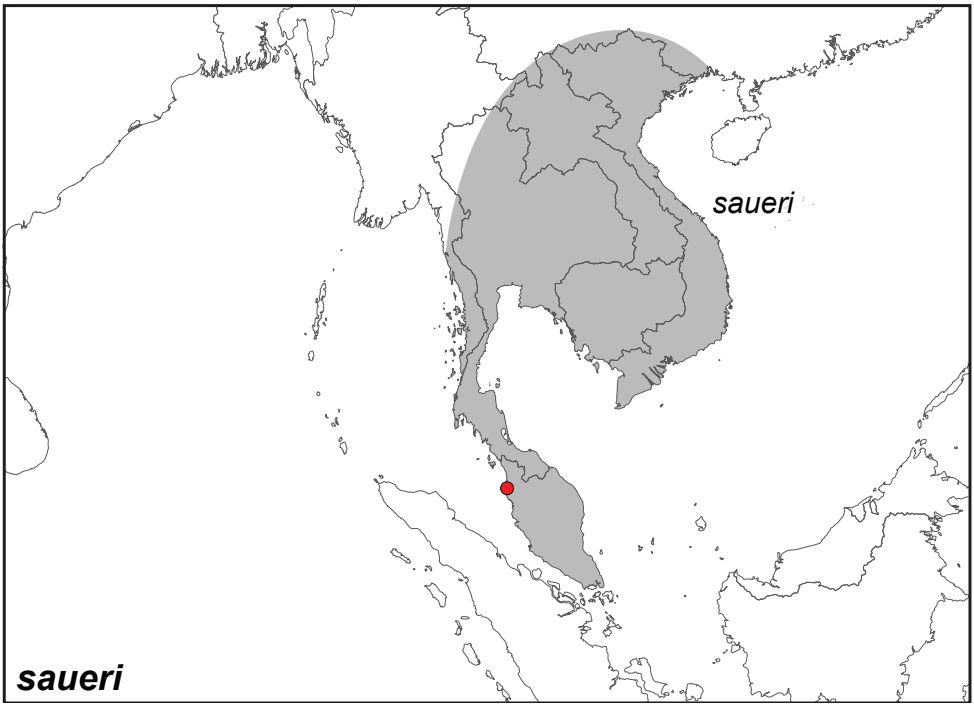

Figure 54. Distribution map of *Elymnias saueri*.

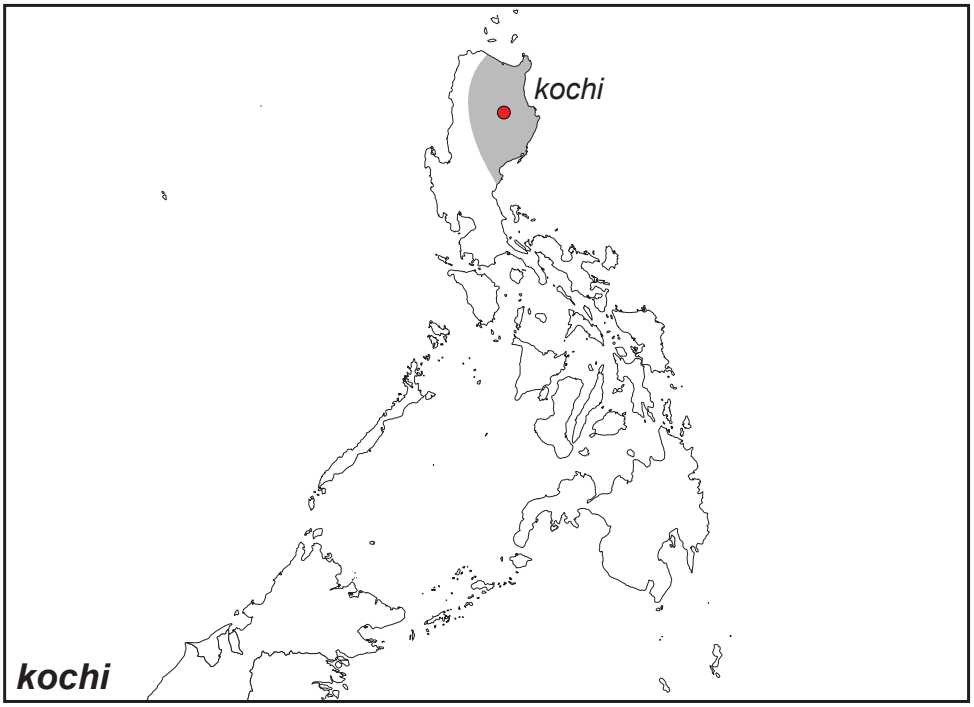

Figure 55. Distribution map of *Elymnias kochi*.

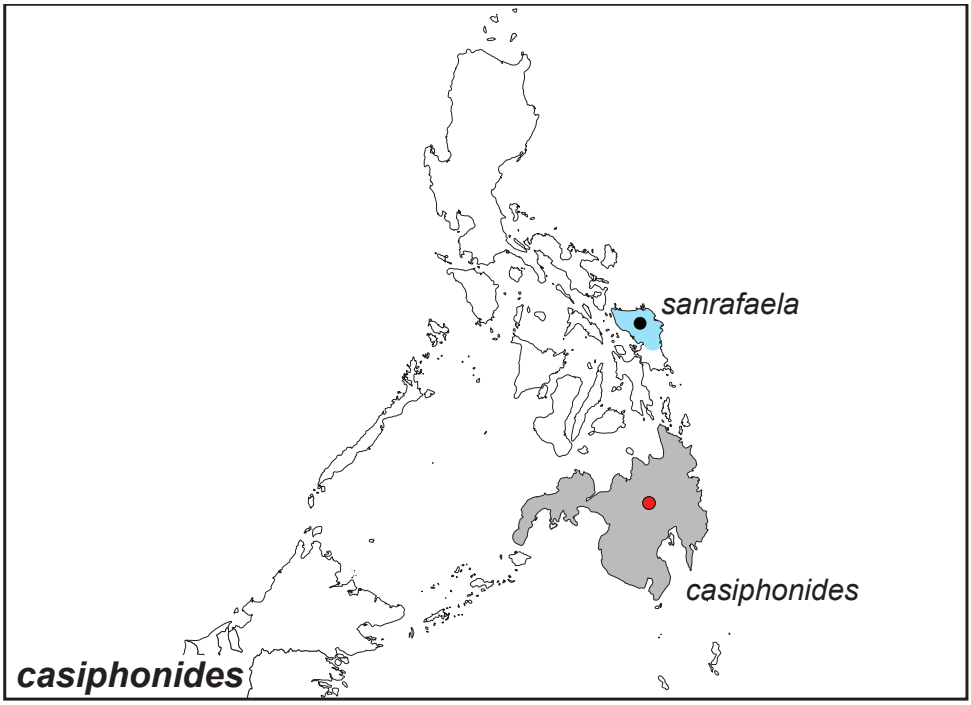

Figure 56. Distribution map of *Elymnias casiphonides*.

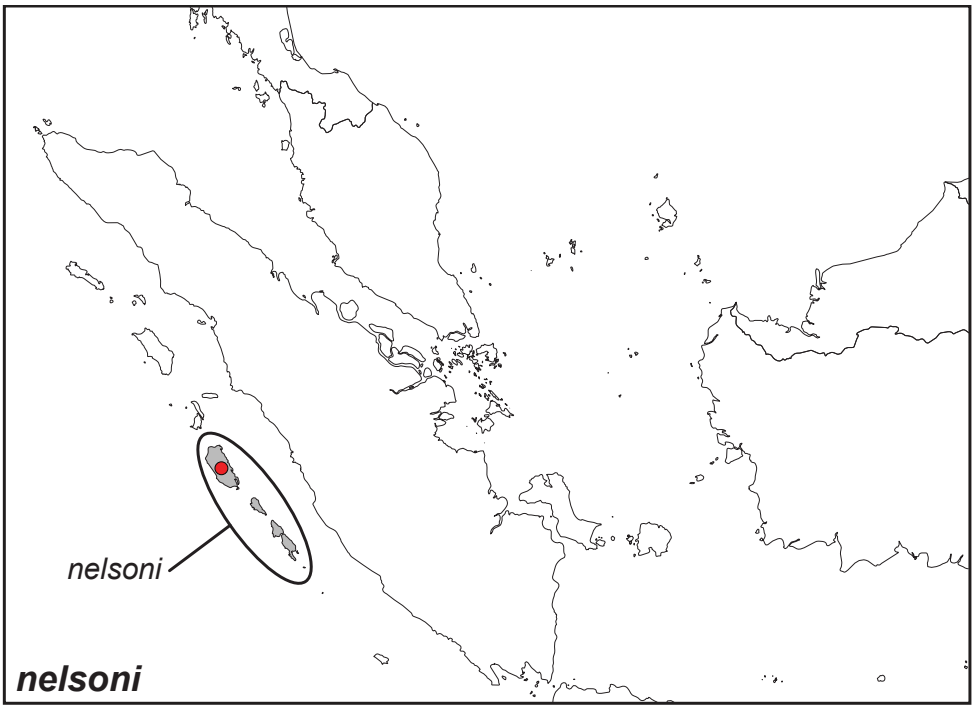

Figure 57. Distribution map of *Elymnias nelsoni*.

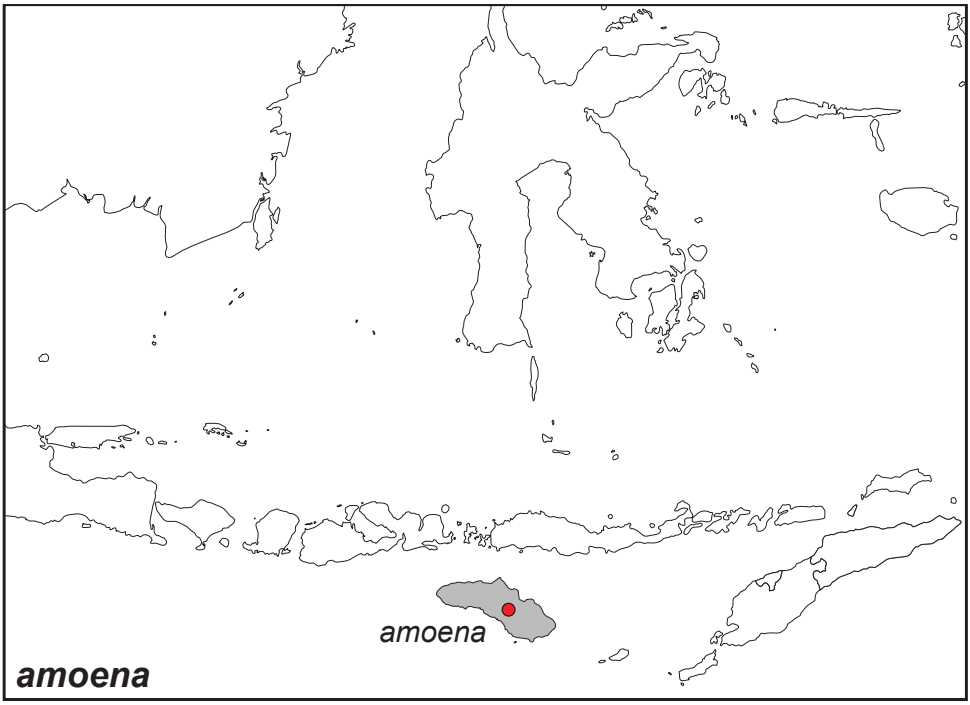

Figure 58. Distribution map of *Elymnias amoena*.

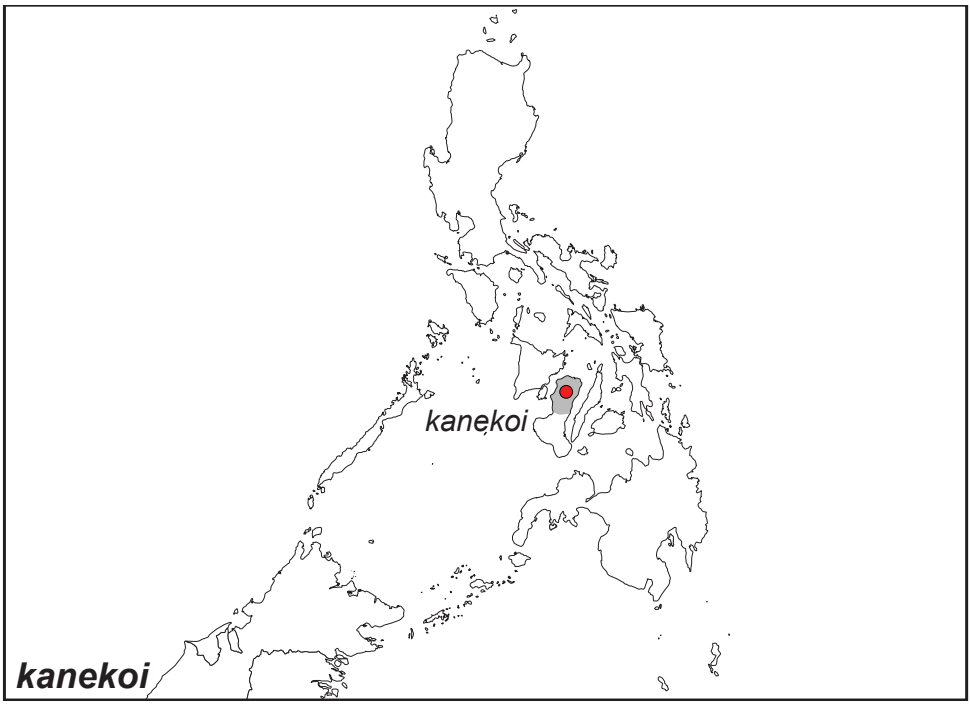

Figure 59. Distribution map of *Elymnias kanekoi*.

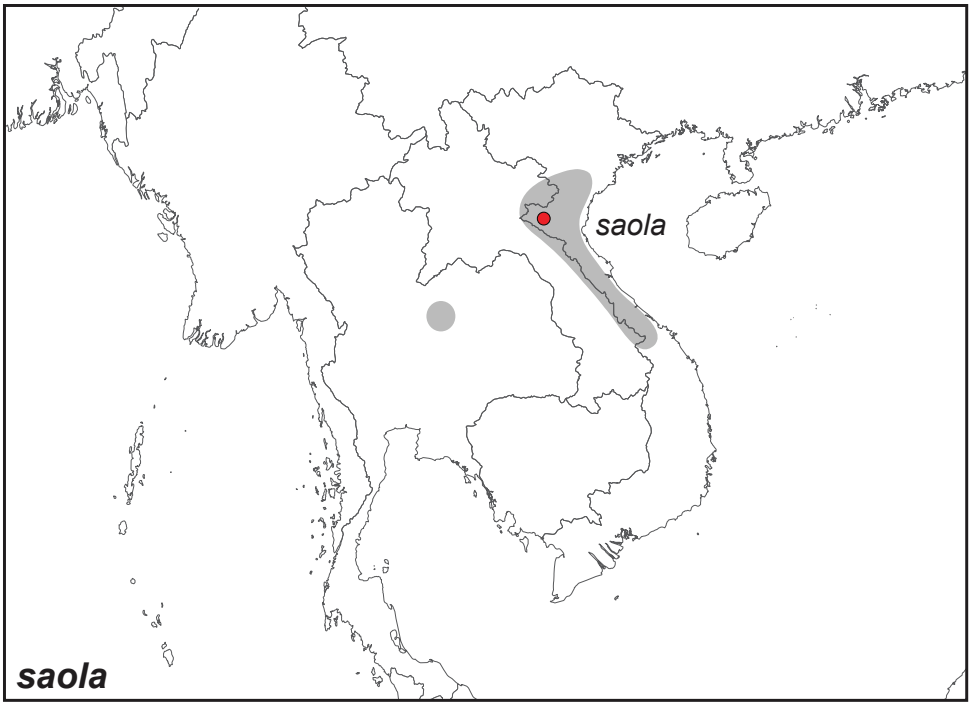

Figure 60. Distribution map of *Elymnias saola*.

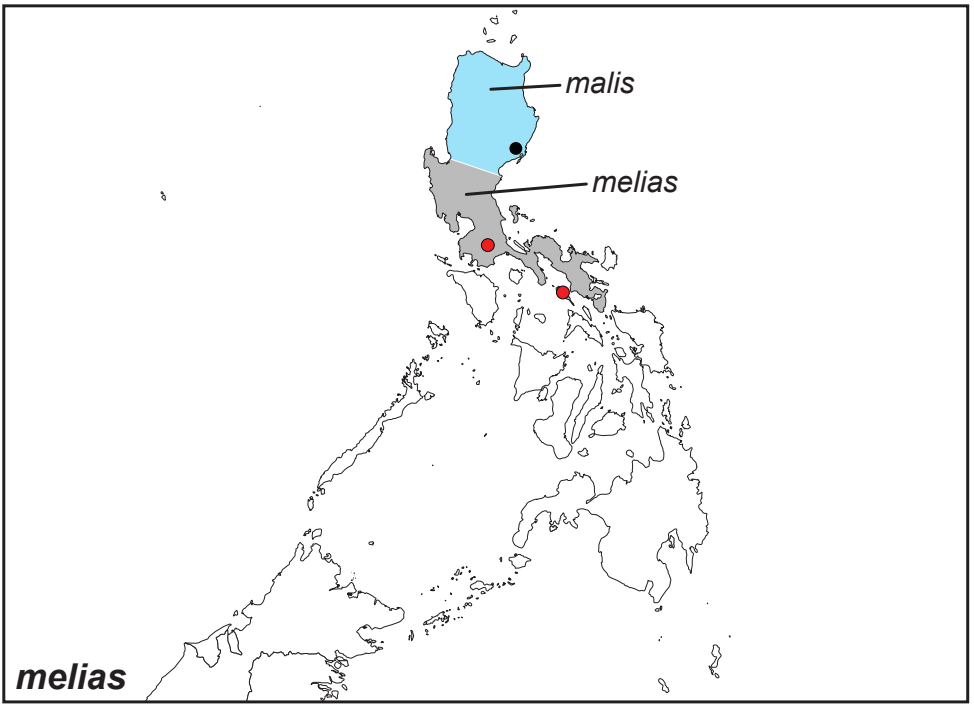

Figure 61. Distribution map of *Elymnias melias*.

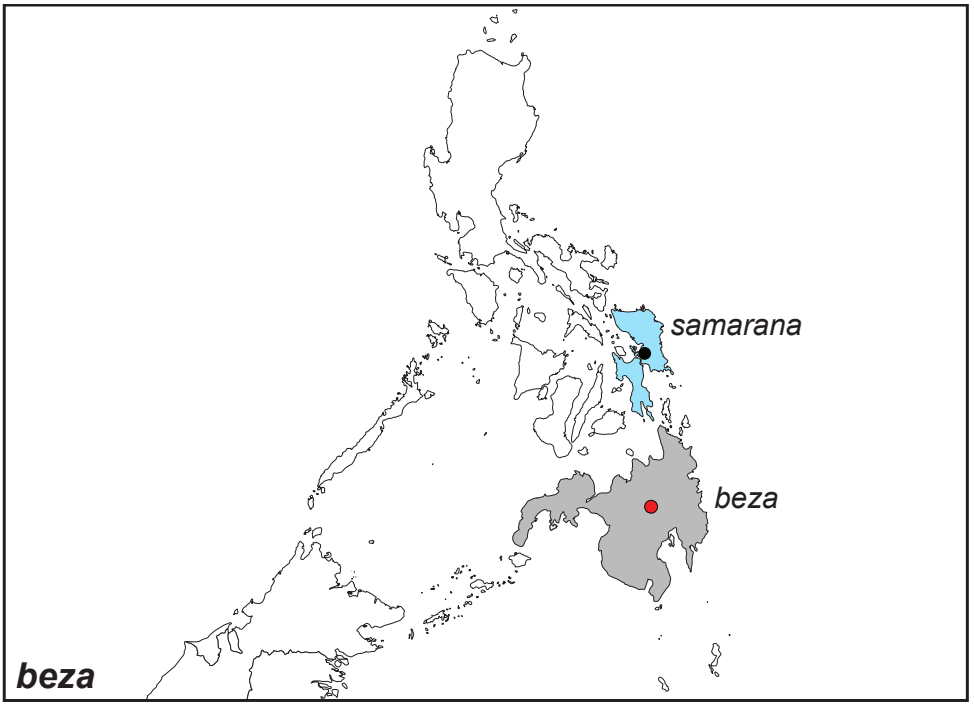

Figure 62. Distribution map of *Elymnias beza*.

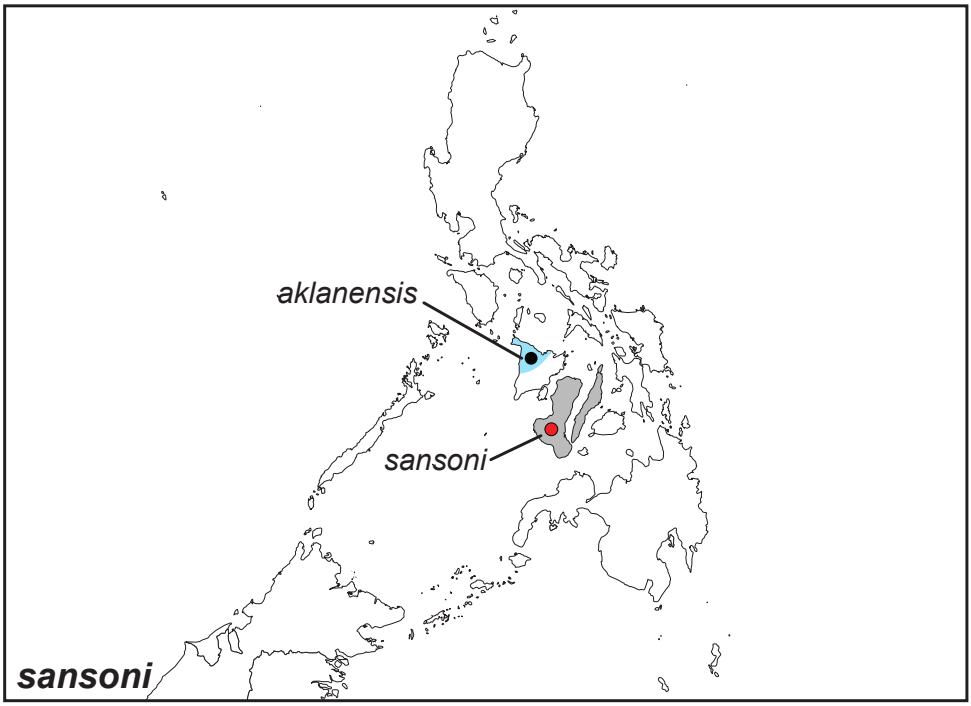

Figure 63. Distribution map of *Elymnias sansoni*.

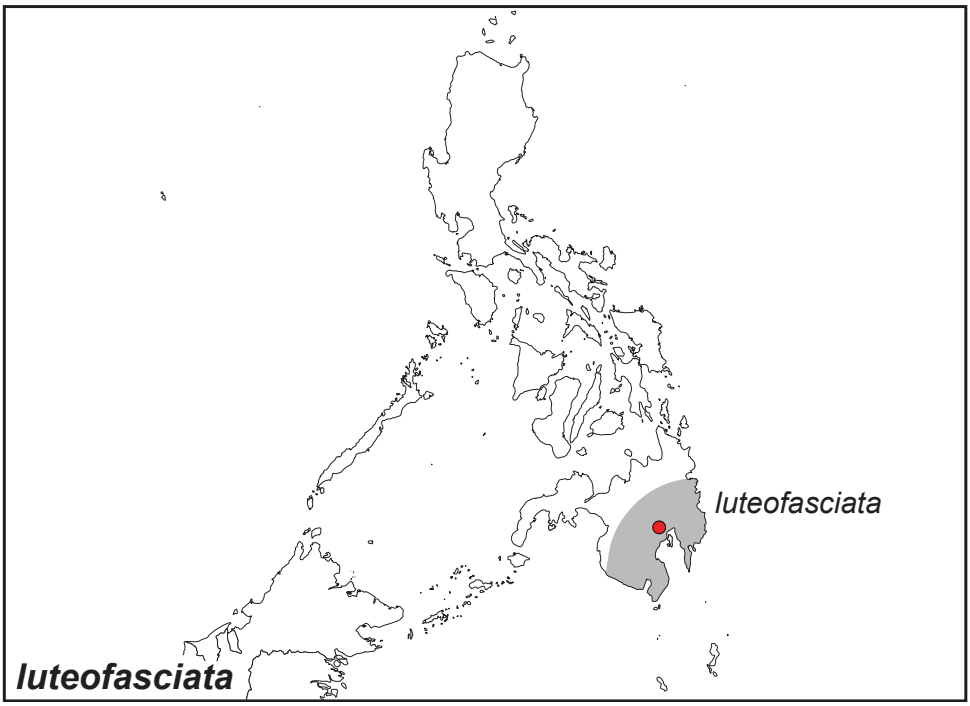

Figure 64. Distribution map of *Elymnias luteofasciata*.

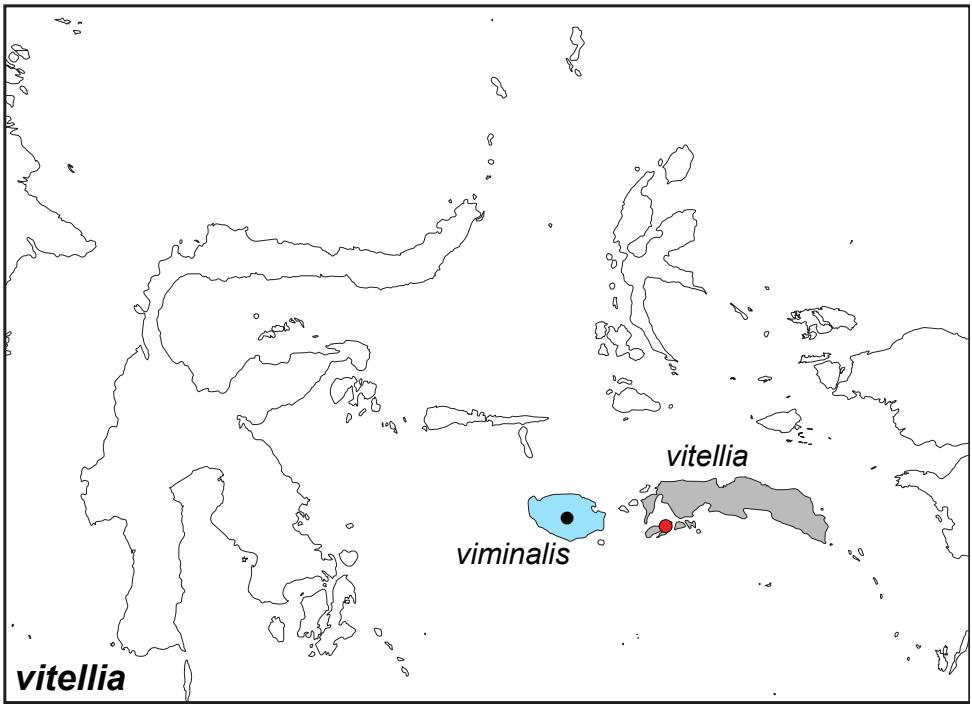

Figure 65. Distribution map of *Elymnias vitellia*.

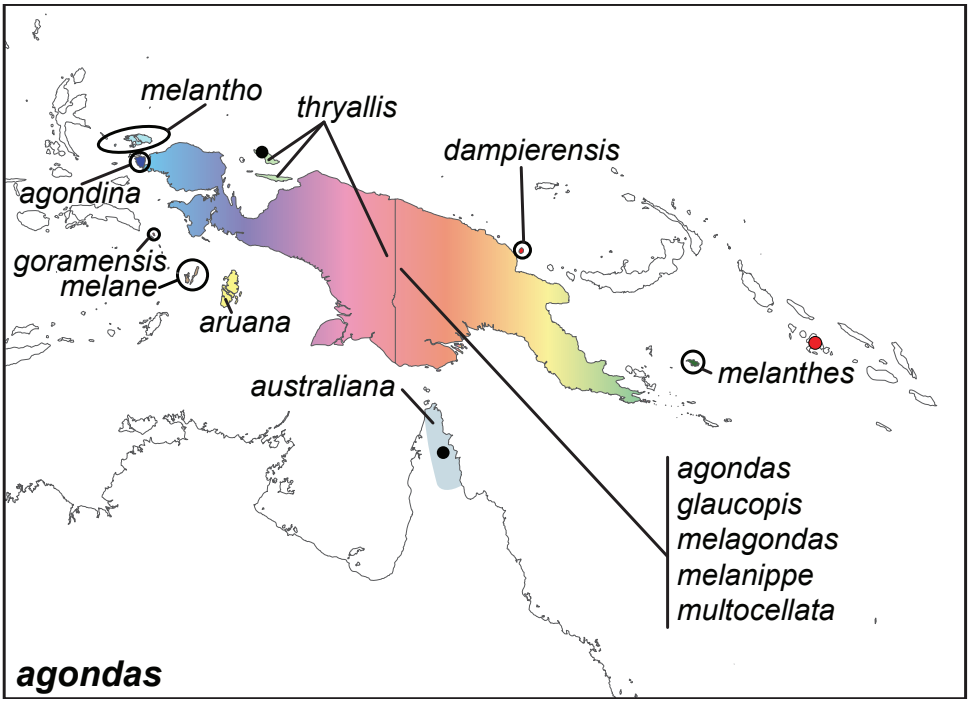

Figure 66. Distribution map of *Elymnias agondas*.

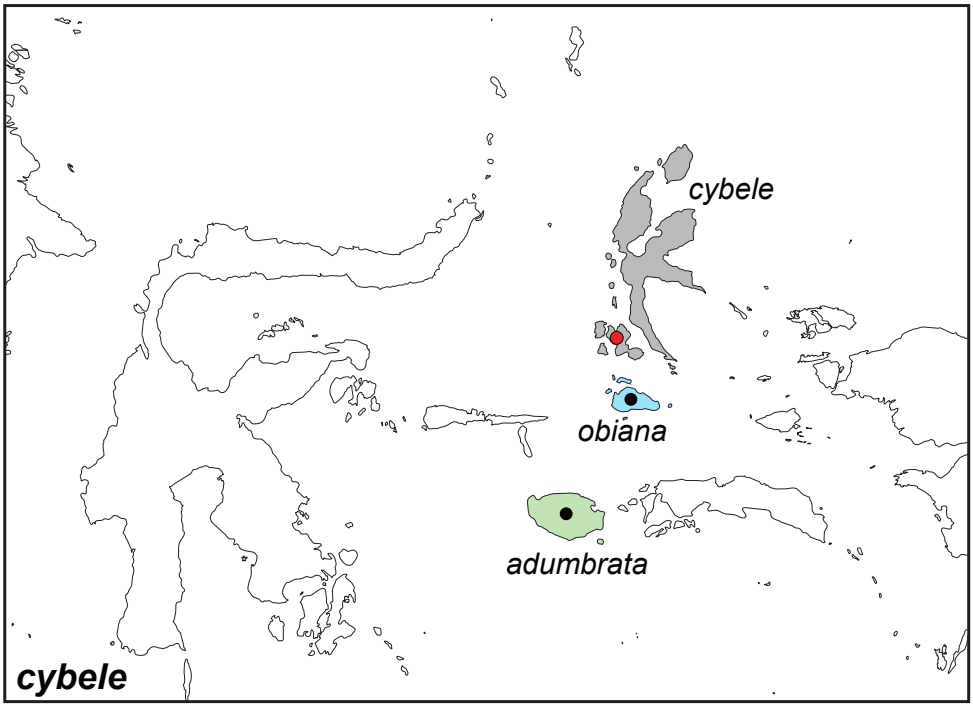

Figure 67. Distribution map of *Elymnias cybele*.

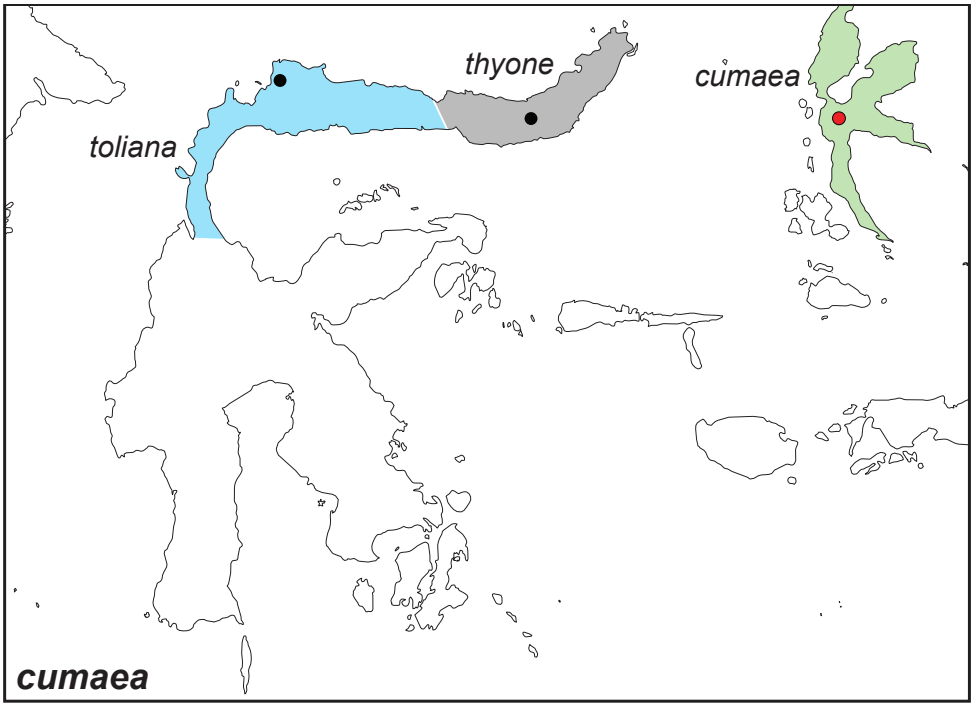

Figure 68. Distribution map of *Elymnias cumaea*.

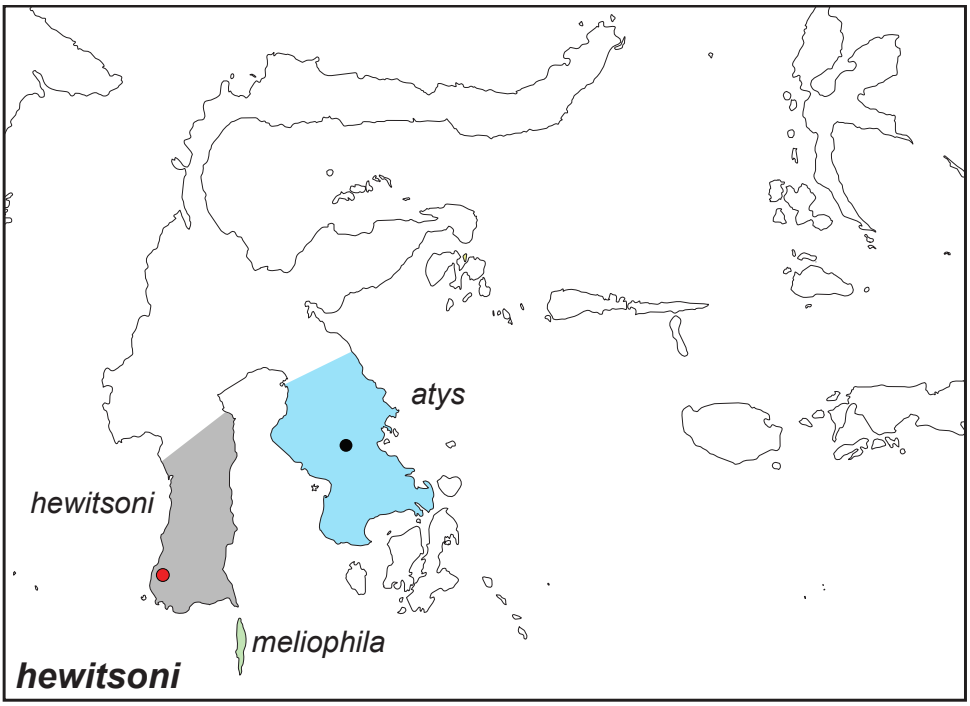

Figure 69. Distribution map of *Elymnias hewitsoni*.

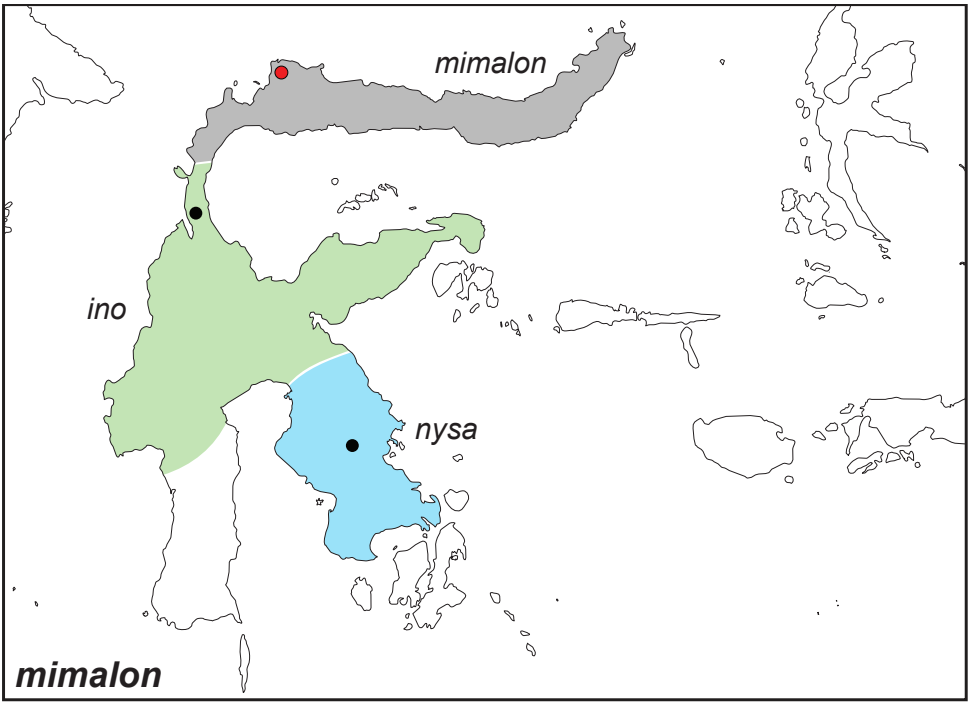

Figure 70. Distribution map of *Elymnias mimalon*.

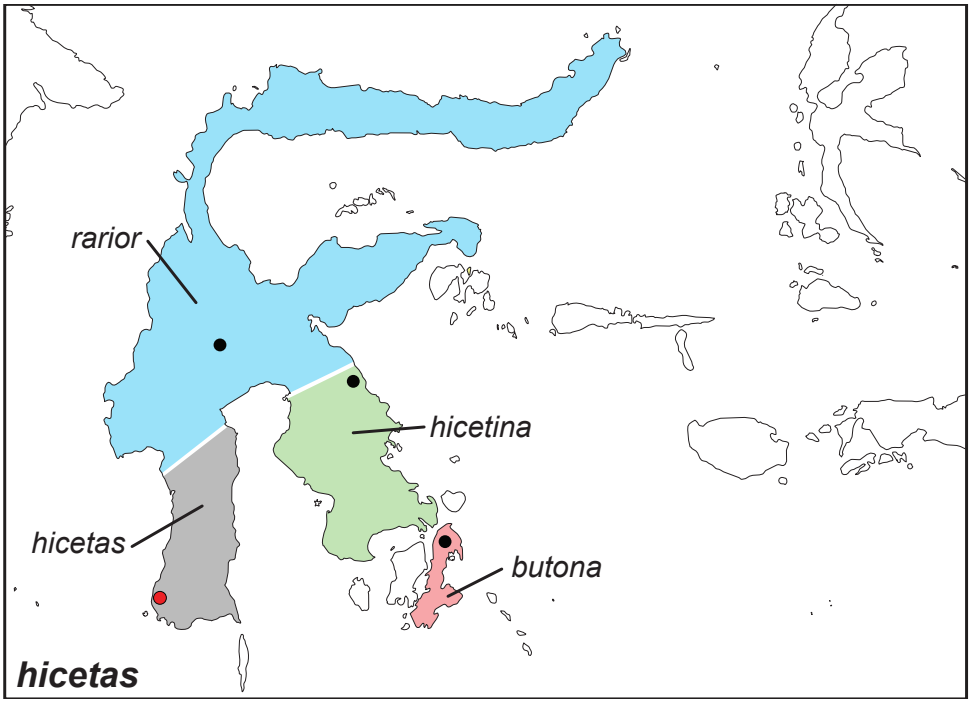

Figure 71. Distribution map of *Elymnias hicetas*.

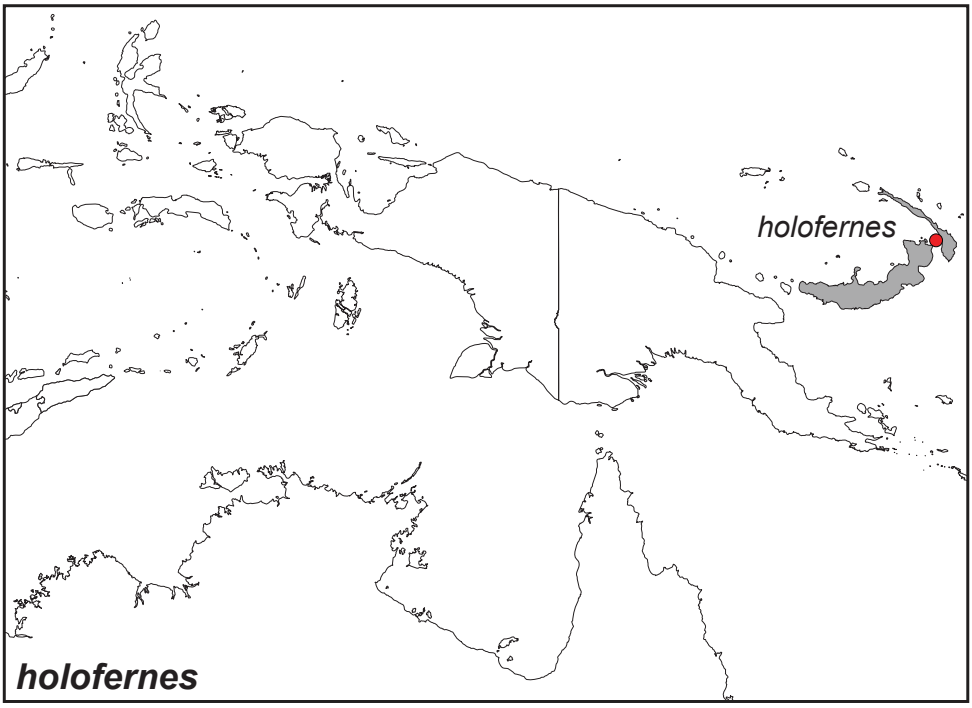

Figure 72. Distribution map of *Elymnias holofernes*.

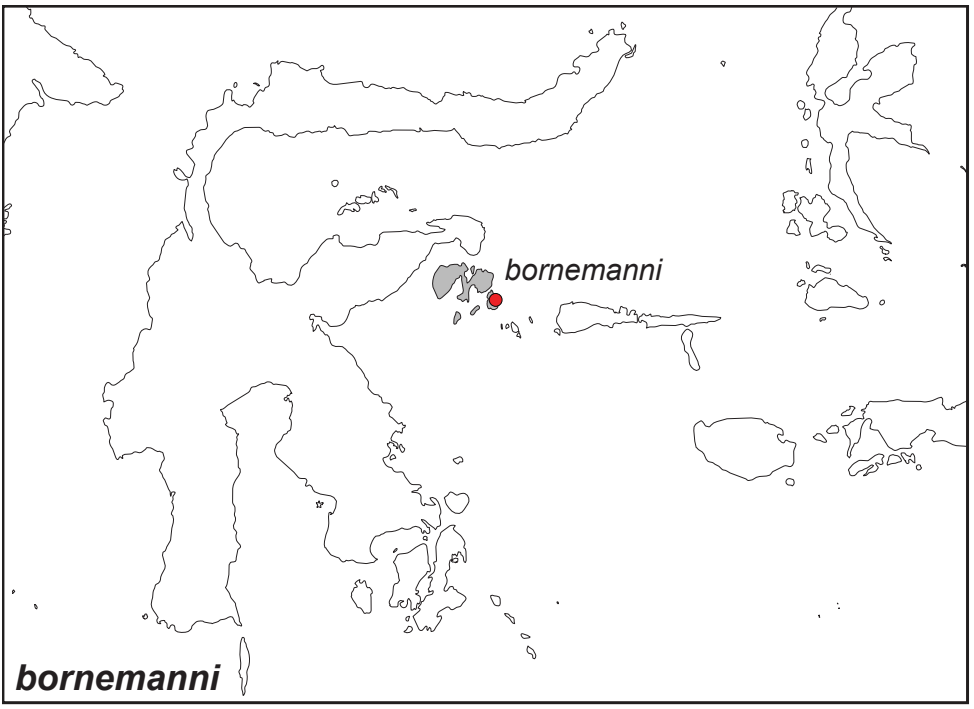

Figure 73. Distribution map of *Elymnias bornemanni*.

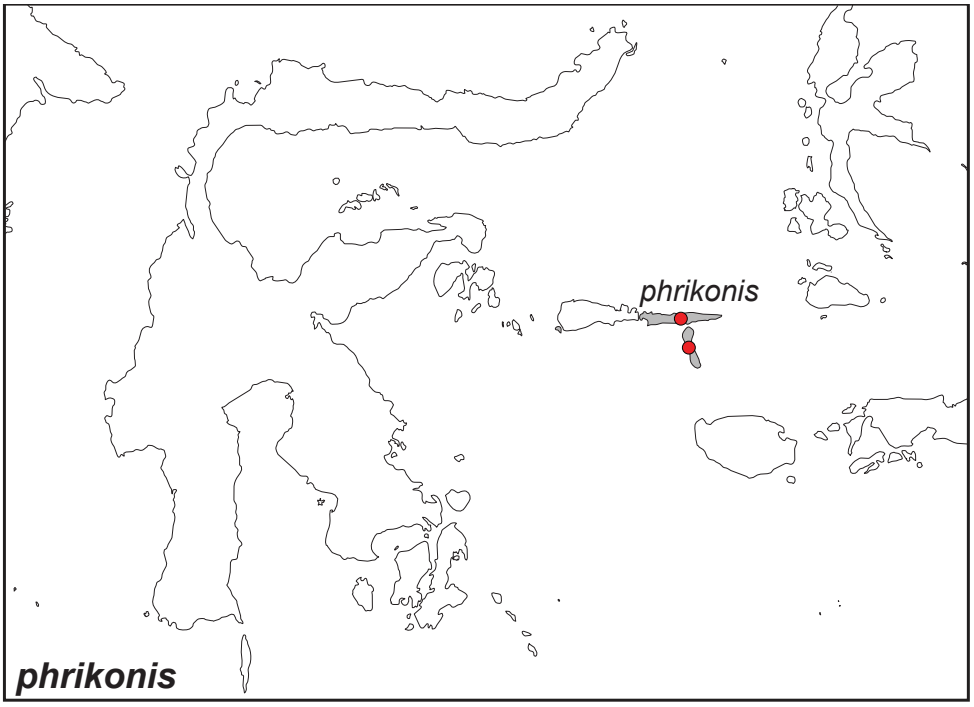

Figure 74. Distribution map of *Elymnias phrikonis*.

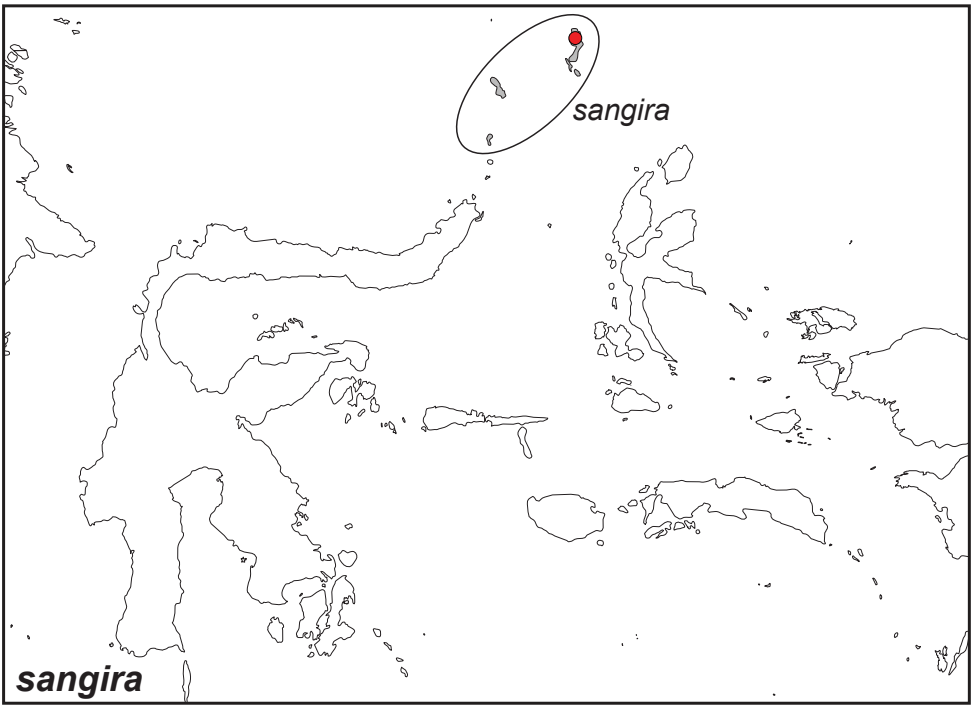

Figure 75. Distribution map of *Elymnias sangira*.

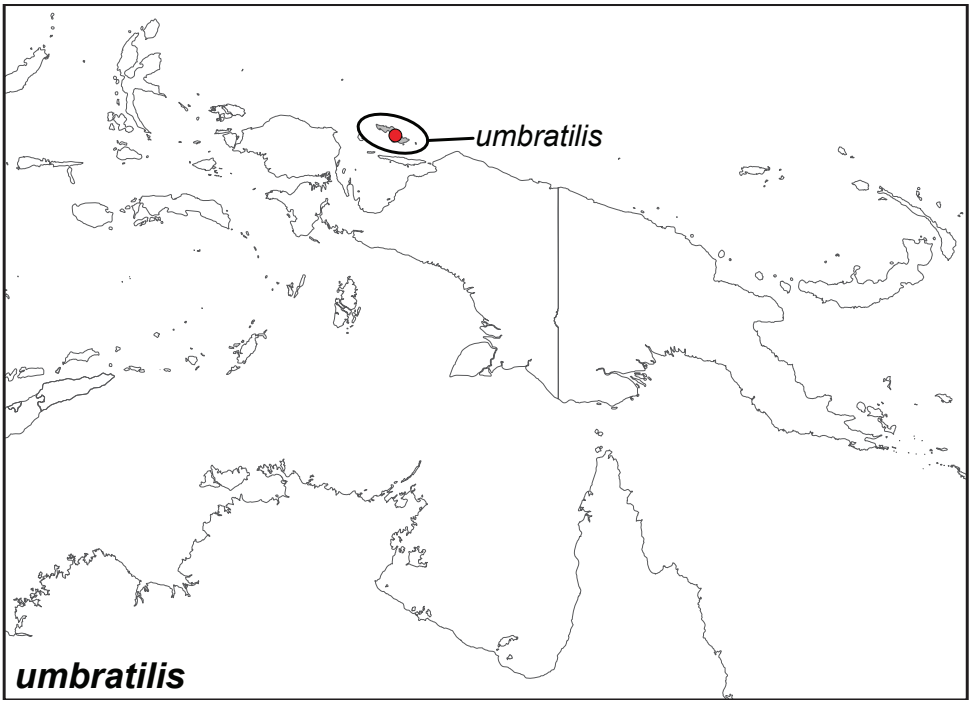

Figure 76. Distribution map of *Elymnias umbratilis*.

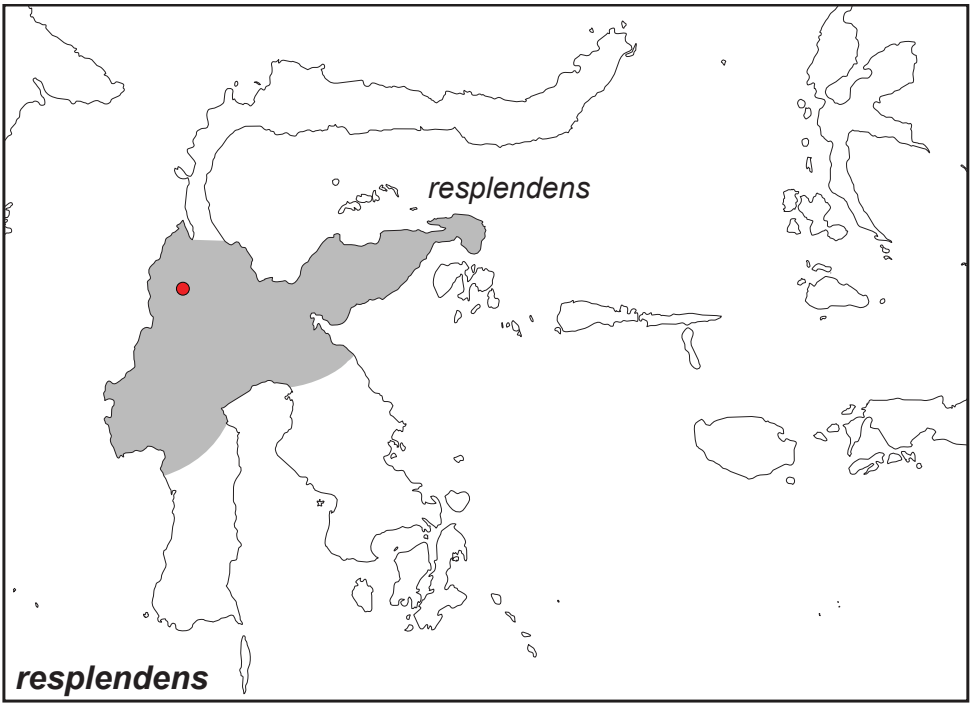

Figure 77. Distribution map of *Elymnias resplendens*.

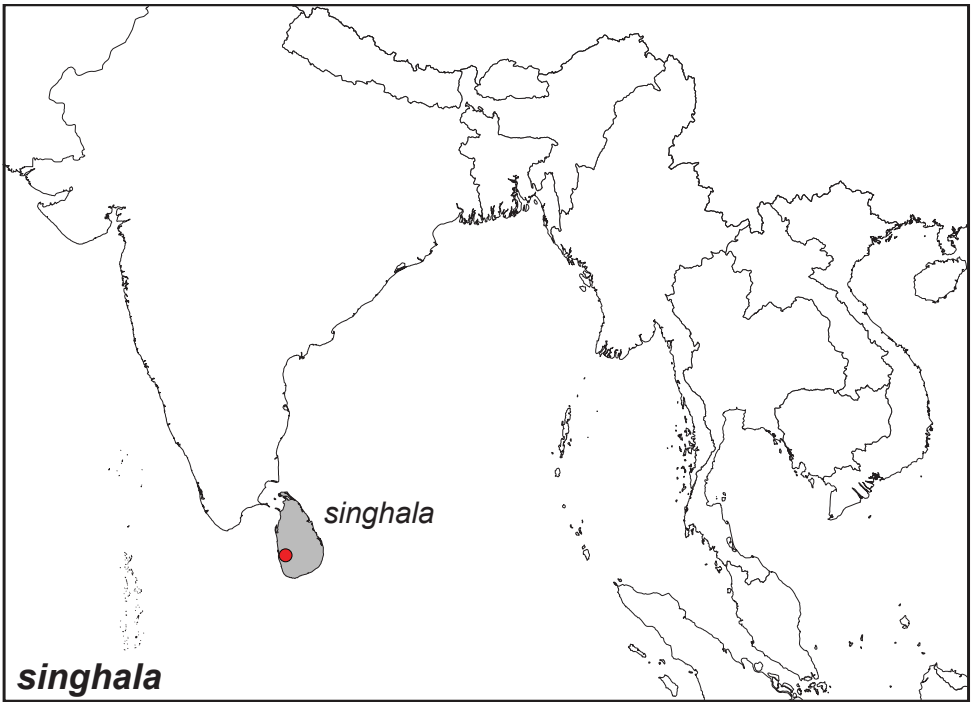

Figure 78. Distribution map of *Elymnias singhala*.

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