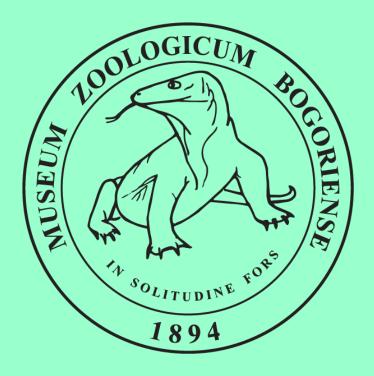
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TREUBIA

A JOURNAL ON ZOOLOGY OF THE INDO-AUSTRALIAN ARCHIPELAGO Vol. 47, no. 1, pp. 1–75, June 2020

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UDC: 595.78(594.73)

David J. Lohman

Syntopic *Elymnias agondas aruana* female forms mimic different *Taenaris* model species (Papilionoidea: Nymphalidae: Satyrinae) on Aru, Indonesia

TREUBIA, June 2020, Vol. 47, No. 1, pp. 1–12.

Wing patterns of female *Elymnias* agondas (Boisduval, 1832) butterflies are highly variable, presumably to mimic different *Taenaris* species throughout New Guinea and surrounding islands. Labels on most E. agondas museum specimens lack precise locality information, complicating efforts to match E. agondas female wing patterns with presumed Taenaris model species. This paucity of data also makes it impossible to determine where different forms occur and whether they are strictly allopatric. During fieldwork on the Aru Archipelago, we found two distinct forms of E. agondas females occurring syntopically. The "light form" resembles T. catops, while the "dark form" seems to mimic T. myops and T. artemis. We discuss the significance of this finding and illustrate species in the Taenaris mimicry ring encountered on Aru.

> (David J. Lohman, Sarino, and Djunijanti Peggie)

Keywords: adaptation, Batesian mimicry, butterfly, mimicry ring, polymorphism

UDC: 598.2:910.4(594.4)

Tri Haryoko

Recent ornithological expeditions to Siberut Island, Mt. Talamau and Rimbo Panti Nature Reserve, Sumatra, Indonesia

TREUBIA, June 2020, Vol. 47, No. 1, pp. 13–38.

Siberut Island, Mt. Talamau, Rimbo Panti Nature Reserve, and intervening locations in West Sumatra Province were visited during two expeditions in 2018-2019 by ornithologists from the Museum Zoologicum Bogoriense-Indonesian Institute of Sciences (LIPI), Louisiana State University Museum of Natural Science, and Andalas University. The main objective of these expeditions was to obtain data and tissue-subsample rich museum specimens for morphological and genetic studies of phylogeny and population genetics of Southeast Asian birds aimed at understanding the causes of avian diversification in the region. We also observed, photographed, and audio-recorded numerous bird species during the expeditions and archived these data. In total, 285 species were identified, and specimen material was collected from 13 species and 26 subspecies not previously represented in tissue resource collections. Here, we provide complete lists of birds location, found at each highlight distributional discoveries, and note cases of potential taxonomic, ecological, and conservation interest.

(Tri Haryoko, Oscar Johnson, Matthew L. Brady, Subir B. Shakya, M. Irham, Yohanna, Rusdiyan P. Ritonga, Dewi M. Prawiradilaga, and Frederick H. Sheldon)

Keywords: birds, distribution, diversity, conservation, West Sumatra

UDC: 598.813.063(59)

Elize Y. X. Ng

Integrative taxonomy reveals cryptic robin lineage in the Greater Sunda Islands

TREUBIA, June 2020, Vol. 47, No. 1, pp. 39–52.

Southeast Asian avifauna is under threat from both habitat loss and illegal poaching, yet the region's rich biodiversity remains understudied. Here, we uncover cryptic species-level diversity in the Sunda Blue Robin (Myiomela diana), a songbird complex endemic to Javan (subspecies diana) and Sumatran (subspecies sumatrana) mountains. Taxonomic inquiry into these populations has previously been hampered by a lack of DNA material and the birds' general scarcity, especially sumatrana which is only known from few localities. We demonstrate fundamental bioacoustic differences in courtship song paired with important distinctions in plumage saturation and tail length that combine to suggest species-level treatment for the two taxa. Treated separately, both taxa are independently threatened by illegal poaching and habitat loss, and demand conservation action. Our study highlights a case of underestimated avifaunal diversity that is in urgent need of revision in the face of imminent threats to species survival.

(Elize Y. X. Ng, Arya Y. Yue, James A. Eaton, Chyi Yin Gwee, Bas van Balen, and Frank E. Rheindt)

Keywords: bioacoustics, bird trade, passerines, songbird crisis, taxonomic neglect

UDC: 595.76:591.46(594.53)

Arif Maulana

A contribution to the taxonomy and ecology of little-known Indonesian *Afissa* ladybird beetles (Coccinellidae, Epilachnini)

TREUBIA, June 2020, Vol. 47, No. 1, pp. 53–62.

We collected the little-known ladybird beetle *Afissa incauta* in the mountainous region of Bandung, West Java. The beetle occurred sympatrically with the very similar species *A. gedeensis*. Here, we provide an update to the current knowledge for these two species. The *A. incauta* we collected have a slightly smaller and duller body compared to the previously known specimens of *Afissa incauta*, with convergent elytral maculation similar to *A. gedeensis*.

> (Arif Maulana, Tri Atmowidi, and Sih Kahono)

Keywords: Afissa gedeensis, Afissa incauta, Coleoptera, Epilachnini, ladybird beetle

UDC: 595.733:574.2(594.57)

Ainun Rubi Faradilla

The life history and microhabitat ecology of a phytotelm-breeding damselfly *Pericnemis stictica* in Jatimulyo forest, Yogyakarta

TREUBIA, June 2020, Vol. 47, No. 1, pp. 63–75.

This study aims to understand the life history and microhabitat ecology of a phytotelmata-breeding species, Pericnemis stictica. Data was collected at 46 breeding sites in the Jatimulyo Forest, Kulonprogo. Several parameters were recorded from each breeding site, i.e. plant species, diameters, depth, water depth, water volume, water pH, and water turbidity. Naiads and imagoes of P. stictica were measured morphometrically. The data taken was analyzed descriptively using Minitab 19. The results showed that 17 naiads of P. stictica were found in 13 bamboo stumps. The bamboo species most commonly used by P. stictica as a breeding site was *Dendrocalamus asper*. Naiads of *P. stictica* were found in the same habitat as larva mosquito from genera Toxorhvnchites, Aedes, Armigeres, and Culex. During the rearing process, it was recorded that P. stictica naiads can eat more than ten mosquito larvae a day. Four males and one female imagoes of P. stictica were found. The imagoes were mostly found in a secondary forest with shady ravine areas. Imago's average total length was 7.19 cm. Naiad's final instar average size was 16.7 mm. Water depth, water temperature, bamboo depth, bamboo volume, and humidity were all positively correlated to P. stictica's phytotelmatabreeding behavior.

(Ainun Rubi Faradilla, Mariza Uthami, Bella Andini, and Hening Triandika Rachman)

Keywords: breeding, Pericnemis, phytotelm, Yogyakarta

DOI: 10.14203/treubia.v47i1.3821

SYNTOPIC *ELYMNIAS AGONDAS ARUANA* FEMALE FORMS MIMIC DIFFERENT *TAENARIS* MODEL SPECIES (PAPILIONOIDEA: NYMPHALIDAE: SATYRINAE) ON ARU, INDONESIA

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ABSTRACT

Wing patterns of female *Elymnias agondas* (Boisduval, 1832) butterflies are highly variable, presumably to mimic different *Taenaris* species throughout New Guinea and surrounding islands. Labels on most *E. agondas* museum specimens lack precise locality information, complicating efforts to match *E. agondas* female wing patterns with presumed *Taenaris* model species. This paucity of data also makes it impossible to determine where different forms occur and whether they are strictly allopatric. During fieldwork on the Aru Archipelago, we found two distinct forms of *E. agondas* females occurring syntopically. The "light form" resembles *T. catops*, while the "dark form" seems to mimic *T. myops* and *T. artemis*. We discuss the significance of this finding and illustrate species in the *Taenaris* mimicry ring encountered on Aru.

Keywords: adaptation, Batesian mimicry, butterfly, mimicry ring, polymorphism

ABSTRAK

Pola sayap kupu-kupu betina *Elymnias agondas* (Boisduval, 1832) bervariasi tinggi, kemungkinan untuk menyerupai spesies *Taenaris* yang berbeda-beda di Nugini dan pulau-pulau sekitarnya. Label pada kebanyakan spesimen museum dari *E. agondas* tidak memiliki informasi lokasi yang tepat, menambah rumit upaya untuk menyandingkan pola sayap betina *E. agondas* dengan terduga jenis model *Taenaris*. Kesenjangan data juga membuat tidak mungkin untuk menentukan di mana terdapat bentuk-bentuk yang berbeda dan apakah mereka sungguh-sungguh *allopatric*. Pada kerja lapangan di Kepulauan Aru, kami menemukan dua bentuk yang berbeda dari betina *E. agondas* yang terdapat secara *syntopic*. Bentuk yang terang menyerupai *T. catops*, dan bentuk yang gelap tampaknya menyerupai *T. myops* dan *T. artemis*. Kami mendiskusikan signifikansi temuan ini dan menunjukkan jenis dalam rantai mimikri *Taenaris* yang dijumpai di Aru.

Kata kunci: adaptasi, mimikri Batesian, kupu-kupu, rantai mimikri, polimorfisme

INTRODUCTION

Natural selection for visual mimicry among species is responsible for marked phenotypic diversity, including morphological divergence and convergence (Mallet & Joron, 1999). In sex-limited mimetic species, only females are Batesian mimics; males do not resemble any distasteful model. In such species, females are frequently polymorphic and mimic different model species in different areas (Kunte, 2009). The African Mocker Swallowtail, *Papilio dardanus* Yeats in Brown, 1776, is a well-studied example of this: males are monomorphic

and not mimetic throughout the species' range, but there are over 30 female forms mimicking a variety of model species in different locales (Thompson & Timmermans, 2014). Sexually dimorphic mimicry or "dual mimicry" in which males and females resemble different models is less common (Vane-Wright, 1971, 1975, 1976). Some populations of the Asian satyrine *Elymnias hypermnestra* (Linnaeus, 1763) exemplify dual mimicry. In some areas including India, Java, Bali, and Seram, the species is dimorphic and each sex mimics a different model: males mimic *Euploea* spp. and females mimic orange *Danaus* spp.—most likely *D. genutia* (Cramer, [1779]) and/or *D. chrysippus* (Linnaeus, 1758). However, in other locales, including Taiwan, Hainan, Borneo, Sumatra, and the Lesser Sundas east of Wallace's Line, males and females are monomorphic and mimic *Euploea* spp. (Wei et al., 2017; Panettieri et al., 2018).

Two or more chemically defended Müllerian mimics sometimes evolve to resemble each other and may be mimicked by one or more palatable Batesian mimic, forming a "mimicry ring" of multiple co-mimetic species that may vary in palatability (Punnett, 1915; Joshi et al., 2017). Phenotypic similarity among co-mimics can be so striking that it is difficult to distinguish species, particularly among Müllerian mimics. Frequently, many or all of the co-mimicking species adopt a different pattern in other locales, creating strong phenotypic matching within communities and marked polymorphism within species (Corbet, 1943; Parsons, 1998). *Heliconius* mimicry rings in South America are probably best known (Jiggins, 2017), but there are many examples in Asia that await further study (Punnett, 1911; Ackery & Vane-Wright, 1984; Parsons, 1998).

Taenaris comprises approximately 25 medium- to large-sized butterfly species, most of which have wings with a white and/or grey background and two conspicuous eyespots on the underside of each hindwing. Wing patterns are variable within each species and between sexes; however, sympatric species often have similar wing patterns (Parsons, 1998), suggesting Müllerian mimicry. Species in the genus Taenaris are often Müllerian mimics of their congeners where they co-occur. They form the basis of mimicry rings on New Guinea and its surrounding islands, where most Taenaris species are distributed (Brooks, 1950; Parsons, 1998). There is strong, indirect evidence that Taenaris species are chemically defended. Larvae of some species feed on cycads (Cycadaceae) and presumably sequester cycasin or related compound(s). Adults of species that do not feed on cycads as larvae imbibe cycad sap as adults (Parsons, 1998), which presumably imparts phytochemical protection. The conspicuous colors and gregarious habits of Taenaris larvae suggest that they are aposematic despite larval diets that may lack defensive compounds. Parsons (1998) postulated that Taenaris and Faunis are sister genera, and molecular phylogenomic data confirms this relationship (Lohman et al., unpublished data; Chazot et al., 2019). Faunis and most other amathusiines are smaller, cryptically colored, and crepuscular. The *Taenaris* lineage is more

conspicuous and diurnal, further suggesting that the taxon is aposematic (Parsons, 1998). The genus is placed in the tribe Amathusiini in the nymphalid subfamily Satyrinae based on molecular phylogenetic evidence (Wahlberg et al., 2009; Chazot et al., 2019), but the tribe has previously been regarded as a family (Amathusiidae; Brooks, 1950; Aoki et al., 1982), a subfamily (Amathusiinae; Ehrlich, 1958; Monastyrskii, 2011), or a tribe within Morphinae (Scott, 1984 (1985); Parsons, 1998).

Vane-Wright (1971) and Parsons (1984, 1998) enumerated butterfly taxa participating in the *Taenaris* mimicry ring. Presumed Müllerian mimics include all *Taenaris* species and the monotypic *Hyantis hodeva* Hewitson, 1862, together with some presumed palatable mimics including female *Elymnias agondas* (Nymphalidae: Satyrinae), some female forms of *Papilio aegeus* Donovan, 1805 (Papilionidae: Papilioninae), female *Hypolimnas deois* Hewitson, 1862 (Nymphalidae: Nymphalinae), and female *Mydosama drusillodes* (Oberthür, 1894) (Nymphalidae: Satyrinae). Some authors also regard *Hypocysta* (Nymphalidae: Satyrinae) of the New Guinea region as diminutive *Taenaris* mimics (Brower, 2009). Average forewing length in *Hypocysta* spp. is around 17-20 mm, but ranges between 44-59 mm in the *Taenaris* spp. encountered on Aru (Parsons, 1998).

Female *E. agondas* are highly polymorphic and mimic different *Taenaris* species throughout the species' range. The species is sexually dimorphic, and male *E. agondas* may resemble darker *Taenaris*, such as *T. onolaus* (Kirsch, 1877) (Parsons, 1998), or they might not be mimetic. Wei et al. (2017) illustrated 21 female *E. agondas* specimens with varying patterns but refrained from revising the taxonomy or indicating the distributions of subspecies on New Guinea because of the extreme variation and lack of detailed locality records. The dearth of precise locality information for most museum specimens (many labels simply state "New Guinea") complicates efforts to study mimicry of *E. agondas*. Existing locality information does not allow the ranges of different forms or subspecies to be determined, thwarts inference of putative model species for these taxa, and prevents determination of whether different female forms of *E. agondas* are strictly allopatric.

During the course of fieldwork on the Aru Archipelago we encountered two different female forms of *Elymnias agondas* that resemble different co-occuring *Taenaris* species. We describe the significance of these syntopic forms and characterize the *Taenaris* mimicry ring on Aru.

MATERIALS AND METHODS

We collected butterflies from 18-23 June 2019 near the west coast of Wokam Island and from 23-25 June 2019 on Ujir Island using aerial nets and pop-up butterfly traps (cone type with 20 cm opening; bugdorm.com) baited with rotting bananas and pineapple sprinkled with

bourbon. Collection information including GPS coordinates was recorded for each specimen. Some specimens were papered in the field and subsequently spread; other specimens had their wings removed and stored in glassine envelopes before placing the bodies in a vial of pure ethanol to preserve DNA.

RESULTS

We recorded over 100 butterfly species from Wokam and Ujir Islands, including several members of the Taenaris mimicry ring: T. artemis myopina Fruhstorfer, 1904, T. catops catops (Westwood, 1851), T. myops myops (C. & R. Felder, 1860), Elymnias agondas aruana Fruhstorfer, 1900, Hypolimnas deois deois (Hewitson, 1858), Papilio aegeus ormenus Guérin-Méneville, [1831] (Fig. 1), Hypocysta osyris osyris (Boisduval, 1832), and Hypocysta haemonia haemonia Hewitson, 1863. While male E. agondas were phenotypically invariant (Fig. 1h), females were variable and could be classified into a "light form" (Fig. 1a) resembling T. catops (Fig. 1c) and a "dark form" (Fig. 1b) resembling T. artemis and T. myops (Fig. 1d, f). Infrasubspecific taxa, including forms, are not recognized by the International Commission on Zoological Nomenclature (ICZN, 2000). Thus, our use of the term "form" is not meant to provide a new taxonomic designation, but rather to introduce descriptive terms to discuss distinctive phenotypes. Dark and light forms of E. agondas females were caught together in the same fruit trap on the same day, demonstrating no spatial or temporal separation between the forms. We collected too few females to determine the relative abundance of different forms, but note that both of these forms seemed to be variable. We sampled individuals that varied slightly from the specimens pictured in Figure 1.

DISCUSSION

The discovery of two different mimetic female forms of *Elymnias agondas* coexisting in the same place at the same time appears to be novel. Apart from developmental abberations, most intraspecific variability is between populations, not within them, because interbreeding within a population homogenizes phenotypic variability. Moreover, individuals within a single population coexist within the same environment and experience the same (or similar) selection pressures, and, thus, the evolution and/or maintenance of different phenotypes within a single panmictic population is unexpected. Extensive studies of inadequately labeled *Elymnias agondas* specimens at several museums did not suggest that any of the various female forms coexisted.

The discovery of these two syntopic forms prompts questions about how this polymorphism evolved, how it is maintained in sympatry, and why it persists. Aru is a land bridge island on the Sahul Shelf ~120 km south of New Guinea, and was intermittently

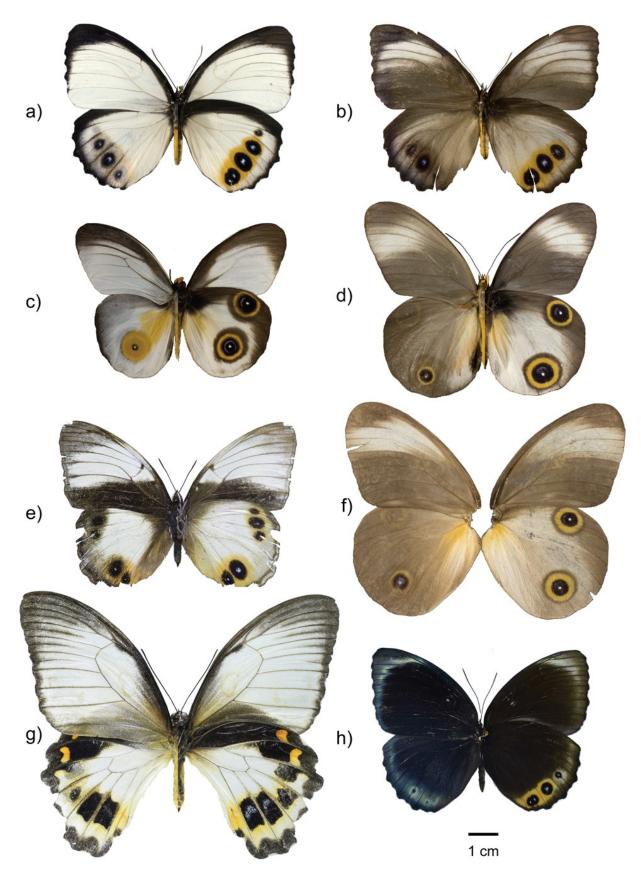


Figure 1. Members of the *Taenaris* mimicry ring on Aru. Each specimen image is a composite showing the upperside (dorsal) on the left and the underside (ventral) on the right. a) *Elymnias agondas aruana* \mathcal{Q} "light form"; b) *Elymnias agondas aruana* \mathcal{Q} "dark form"; c) *Taenaris catops catops* \mathcal{Z} ; d) *Taenaris myops myops* \mathcal{Z} ; e) *Hypolimnas deois deois* \mathcal{Q} ; f) *Taenaris artemis myopina* \mathcal{Q} ; g) *Papilio aegeus ormenus* \mathcal{Q} ; h) *Elymnias agondas aruana* \mathcal{Z} .

connected to New Guinea throughout the Pleistocene (Voris, 2000). These periods of connection and separation could have provided opportunities for the evolution of different forms in allopatry during periods of high sea stand, followed by secondary contact when sea levels were low. Studies on several mimetic butterfly species have found that tightly linked groups of wing patterning loci known as "supergenes" often control development of different forms (Kunte et al., 2014; Timmermans et al., 2014). The co-adapted loci are prevented from being dissociated by recombination because of their linkage and occasionally by chromosomal re-arrangements (Joron et al., 2011). Mimicry supergenes have been demonstrated in distantly related butterflies, and it is therefore plausible to hypothesize that a supergene is responsible for the dimorphism seen in *E. agondas aruana* females. The coexistence of two mimetic forms mimicking similar but distinctly different model species indicates that predators can visually discriminate the two forms and suggests that divergent mimics are more successful than a single phenotype intermediate between the dark and light forms.

One might also ask why two discrete female forms can co-exist without one becoming more advantageous and thus fixed in the population. This is similar to asking why male and female dual mimetic species mimic different models. A dominant hypothesis is that palatable mimics should be less abundant than their models in order for predators to learn to avoid the more common, unpalatable species (but see Ries & Mullen, 2008). When males and females each mimic a different model species, the theoretical maximum abundance of imagos increases because the abundance of each sex is now determined by the commonness of two different models rather than a single species. However, if birds and other predators are not duped by the taxon-specific mimicry of each *E. agondas* form, then the relative abundance of the two forms might be subject to negative frequency-dependent selection. In this scenario, the more common form is at a selective disadvantage because predators encounter and learn to detect it more readily, potentially leading to cycles of alternating commonness and rarity between the forms (Takahashi & Kawata, 2013).

While most *Taenaris* species including all found on Aru have two prominent underside hindwing eyespots, *E. agondas* and *H. deois* females have more eyespots than their model species, and the eyespots are noticeably smaller and in different positions on the wing. Moreover, *Papilio aegeus* female "eyespots" lack concentric rings (Fig. 1g). Although concentric ring patterns are known from the family Papilionidae (in the subfamily Parnasiinae), the developmental mechanisms seem to be different than in Nymphalidae (Shirai et al., 2012). The poor mimicry of the model species' hindwing eyespots is particularly intriguing, as eyespot position and size affect detection by predators in satyrine butterflies (Ho et al., 2016). Vane-Wright (1971) notes that eyespots are atypical of butterfly warning patterns. Some insectivorous birds seem to have innate aversion to eyespots (Blest,

1957a, b), and—at least in *Taenaris*—large eyespots may serve as a second line of defense after their presumed unpalatability. In contrast to the eyespots, the colors and patterns of the two forms of *E. agondas* forewings more accurately resemble their models (Fig. 1). Birds learn color more quickly than shape or pattern (Osorio et al., 1999; Kazemi et al., 2014), which might explain why the mimics' color is more faithful to the model than eyespot number.

Each of the Batesian mimics in the Taenaris mimicry ring on Aru (Fig. 1) could be characterized as an imperfect mimic that can be readily distinguished from its model by human observers. Much has been written on how imperfect mimicry evolves, why it remains effective, and why mimetic perfection is not often achieved (Edmunds, 2000; Ruxton et al., 2004; Wilson et al., 2013; Quicke, 2017). Predators are less likely to attack imperfect mimics when the models are particularly unpalatable and are more likely to learn to avoid imperfect mimics when the models are far more abundant that the mimics (Ruxton et al., 2004). Moreover, the visual acuity of avian and other predators differs from humans (Cuthill & Bennett, 1993; Su et al., 2015). Thus, differences between mimics and models obvious to humans might not be apparent to the butterflies' predators, particularly if they only use a subset of possible visual cues to associate with their learned aversion. Motion blur of the wings in flight may increase resemblance of the model species (Srygley, 1999). The abundance of E. agondas that we observed on Aru and their wide distribution across most of New Guinea and surrounding islands suggests that imperfectly mimicking a toxic model is sufficient for survival of the species in a wide array of environments. While behavioral mimicry (e.g., flight height, wing beat patterns, diel activity, etc.) often accompanies wing pattern mimicry (Srygley, 1999; Elias et al., 2008), we observe that this is rarely the case with *Elymnias* mimics, which tend to fly in short, rapid bursts around their palm (Arecaceae) host plants. This mode of flight might provide potential predators with little opportunity to assess the fidelity of their wing pattern mimicry.

We encountered most of the species from the *Taenaris* mimicry ring previously recorded on Aru: *T. artemis, T. catops, T. myops,* female *Elymnias agondas,* female *Hypolimnas deois,* female *Papilio aegeus,* and the putative mimics *H. osyris* and *H. haemonia. Hyantis hodeva* and female *Mydosama drusillodes* are members of the mimicry ring elsewhere, but are not recorded from Aru. Brooks (1950) recorded an additional *Taenaris* species from the Aru Achipelago based on the extensive collection in The Natural History Museum, London: *T. dimona aruensis* Brooks, 1944. We did not encounter this species, which is a phenotypically variable and could resemble either the dark or light form of female *E. agondas* (Parsons, 1998). We also did not find *Hypocysta calypso aruana* Jordan, 1924, previously recorded from Aru.

Interestingly, none of the four *Taenaris* species recorded from Aru is known to feed on cycads or other host plants that might provide larvae with unpalatable phytochemicals. While there seem to be no larval host plant records for Taenaris from Aru, the species found on the archipelago have been recorded feeding on various monocots in Papua New Guinea and Australia. Taenaris artemis larvae feed on coconut (Cocos nucifera, Arecaceae), and various Pandanus spp. (Pandanaceae) including P. odorus (Parsons, 1984; Merrett, 1996). Taenaris catops has been recorded from Phaius tankervilleae and Spathoglottis sp. (both Orchidaceae), Cordyline fruticosa (Asparagaceae) (recorded as Cordyline terminalis [Liliaceae]) (Parsons, 1984; Merrett, 1996), Musa acuminata, M. balbisiana (Musaceae), Carvota rumphiana and Areca catechu (Arecaceae) (D'Abrera, 1978). Larvae of Taenaris dimona have been recorded feeding on banana leaves (Musa sp., Musaceae) (Parsons, 1998), and Taenaris myops has been recorded feeding on oil palm (Elaeis guineensis), Rhopalostylis baueri (recorded as Ptychosperma robusta), Cocos nucifera (all Arecaceae), Curculigo erecta (Hypoxidaceae), Tapeinochilos sp., Costus sp. (both Costaceae) (Parsons, 1984; Merrett, 1996), Musa acuminata, and M. balbisiana (Musaceae) (Szent-Ivany & Barrett, 1956). We observed coconuts and other palms, bananas, spiral gingers (Costaceae), pandans (Pandanaceae), and cycads on Aru, and the cycad-feeding lycaenid Luthrodes cleotas was common. Taenaris catops has been observed imbibing cycad "juices" (Parsons, 1998), and this habit is presumably how the *Taenaris* species on Aru obtain noxious chemicals to warrant their aposematic coloration. It is also possible that these presumably aposematic butterflies obtain defensive compounds from endophytes infecting their otherwise chemically benign host plants. In Europe, the satyrine Melanargia galathea is defended by loline, a pyrrolizidine alkaloid deried from fungal endophytes infecting its grass (Poaceae) host plant (Rothschild, 2001; Rasooly et al., 2017).

With the possible exception of *P. aegeus*, none of the Batesian mimics feeds on host plants that might impart chemical defense. *Elymnias agondas* larvae feed on palms (Arecaceae) including oil palm (*Elaeis guineensis*), rattan (*Calamus spp.*), and coconut (*Cocos nucifera*). In the wild, immature stages have been found on *Brassiophoenix schumanii, Caryota rumphiana, Calamus caryotoides* and *Ptychosperma* spp. (all Arecaceae). In captivity, banana species *Musa acuminata* and *M. balbisiana* (Musaceae) supported larval development until adulthood (Wood, 1984; Merrett, 1993). *Hypolimnas deois* larvae feed on *Elatostema* sp. (Urticaceae), and *Papilio aegeus* larvae have been recorded eating tender foliage of *Micromelum minutum, Geijera salicifolia, Zanthoxylum megistophyllum*, and *Clymenia polyandra* (all Rutaceae) (Parsons, 1998).

Batesian mimics are frequently variable throughout their range, and this example of distinct co-occuring forms within a single species is not the first example from the genus *Elymnias*. Wei et al. (2017) synonymized *Elymnias kamara* into *E. casiphone* because multiple specimens sampled throughout the range of each "species" demonstrated that they

are a single species, as evidenced by strongly supported polyphyly at every locus in a sixlocus molecular phylogeny. Both of the formerly separate species are sexually dimorphic, suggesting that a supergene underlies mimicry of sexually dimorphic male and female *Euploea mulciber* by males and females of the *casiphone* form (Aoki et al., 1982), and mimicry of male and female *Euploea modesta* (Butler, 1871) by respective sexes of the *kamara* form.

It seems likely that the unpalatable *Taenaris* on Aru and their palatable *Elymnias* mimics all feed on Arecaeae as larvae; a family that presumably lacks defensive compounds. Further study of the natural history and chemical ecology of these taxa, including the possible role of endophytes in their hostplants, will no doubt be interesting.

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