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Jamides wananga, a new species from Papua New Guinea and Australia (Lepidoptera: Lycaenidae)

PETER R. WILSON[1], IAN R. JOHNSON[2] & DAVID J. LOHMAN[3*]
[1]*2 Billabong Drive, Bundaberg, Qld. 4670, Australia.* *wilbush@iinet.net.au;* *https://orcid.org/0000-0002-3563-122X*
[2]*260 Grassdale Road, Gumdale, Qld. 4154, Australia.* *ace54johnson@gmail.com;* *https://orcid.org/0000-0002-6762-3603*
[3]*Biology Department, City College of New York, City University of New York, 160 Convent Ave., New York, NY 10031, USA; Ph.D. Program in Biology, Graduate Center, City University of New York, 365 Fifth Ave., New York, NY 10016, USA; Entomology Section, National Museum of Natural History, Manila 1000, Philippines*
[*]*Corresponding author.* *dlohman@ccny.cuny.edu;* *https://orcid.org/0000-0002-0689-2906*

Abstract

Jamides wananga **sp. n**. is described and illustrated from Madang Province of Papua New Guinea and Dauan Island in the Torres Strait (Queensland, Australia). The new species is similar in appearance to several other *Jamides* Hübner species in the *bochus*-group. DNA sequence data and morphology were used to distinguish the nominotypical subspecies found on the New Guinea mainland from *J. w. roxina* **subsp. n.** on Dauan Island. Notes on the habitat and behaviour are also provided.

Key words: DNA barcoding, *bochus*-group, integrative taxonomy, Papilionoidea

Introduction

The genus *Jamides* Hübner occurs from India, Sri Lanka and Taiwan, through Southeast Asia to New Guinea, Australia, the Solomon Islands, Vanuatu, Fiji, and Tonga (Braby 2000, Rawlins *et al.* 2014) and comprises *ca.* 70 described species of which *ca*. 12 belong to the *bochus*-group and the rest in the *celeno*-group (Hirowatari 1992). Larvae of the *bochus*-group feed primarily on Fabaceae, while larvae of *J. alecto* (Felder) and a few other species consume Zingiberaceae (Robinson *et al.* 2010). Larvae are facultatively attended by ants in several subfamilies, and *J. bochus* (Stoll) has been recorded associating with the dolichoderine *Technomyrmex albipes* (Matsuoka 1976, Johnston & Johnston 1980, van der Poorten & van der Poorten 2016). Slight wing pattern differences among species can make identification challenging, and male genitalia in the *bochus*-group often do not differ enough to be useful for identification or species diagnosis.

In September 2008, Legi Sam and F. Kimbeng collected several *Jamides* specimens in the Wanang Conservation Area (-5.25°, 145.27°) in Madang Province near the town of Wanang, approximately 60 km west of Madang, Papua New Guinea (PNG). The area comprises gently undulating lowland rainforest with a mean annual rainfall of 2,000–4,000 mm, and mean monthly air temperature of ~26° C. The forest is diverse and structurally complex with numerous woody vines and a 40–60 m canopy on deep red soils high in iron and aluminum oxides.

On December 2017 and 2020, Peter Wilson and Ian Johnson collected six *Jamides* specimens along a dirt road on the north-western side of Dauan Island, Torres Strait, Queensland. Dauan Island is a small, steep, rocky granitic island at 9.42°, 142.54° with dimensions of 2.7 km from east to west and 2.9 km from north to south, lying just 11 km south of the coast of the island of New Guinea in the northern Torres Strait, which separates Australia from New Guinea. The international border between Australia and the nation of PNG, which occupies the eastern half of the island of New Guinea, passes between Dauan Island and the New Guinea coast. The vegetation is predominately monsoonal vine scrub, and the island receives a mean annual rainfall of approximately 1,750 mm with significant annual and seasonal variation between the wet and dry seasons. The mean air temperature is ~27° C. A small area of cleared sandy beach ridges lined with mangroves occurs on the northern tip.

Preliminary examination of the specimens from Dauan Island indicated that they belonged to the *bochus*-

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group but differed morphologically from known New Guinea and Australian *Jamides* species. The *bochus*-group typically has beige striae (lines) on the underside of the wings and includes these Australasian species (Hirowatari 1992; Parsons 1998): *J. bochus, J. phaseli* (Mathew)*, J. soemias* Druce, *J. cephion* Druce, *J. amarauge* Druce, *J. goodenovii* (Butler), *J. pulcherrima* Butler, *J. candrena* (Herrich-Schaeffer), and *J. carissima* (Butler). Hirowatari (1992) regards *J. purpurata* Grose-Smith 1894 to be a full species and *J. timon* Grose-Smith to be a subspecies of *J. soemias*: *J. soemias timon*. Lamas (2015) follows Parsons (1998), and regards both of these taxa to be the same subspecies of *J. soemias*: *J. soemias purpurata* Grose-Smith. We adopt the usage of Parsons (1998), which is more recent. A distribution map of these species and the new taxa described in this paper are provided in Figure 1. The *celeno*-group has white striae. Chris Müller (pers. comm.) confirmed suspicions that the Dauan specimens differed from known, described *Jamides* species from the PNG and Australia region.

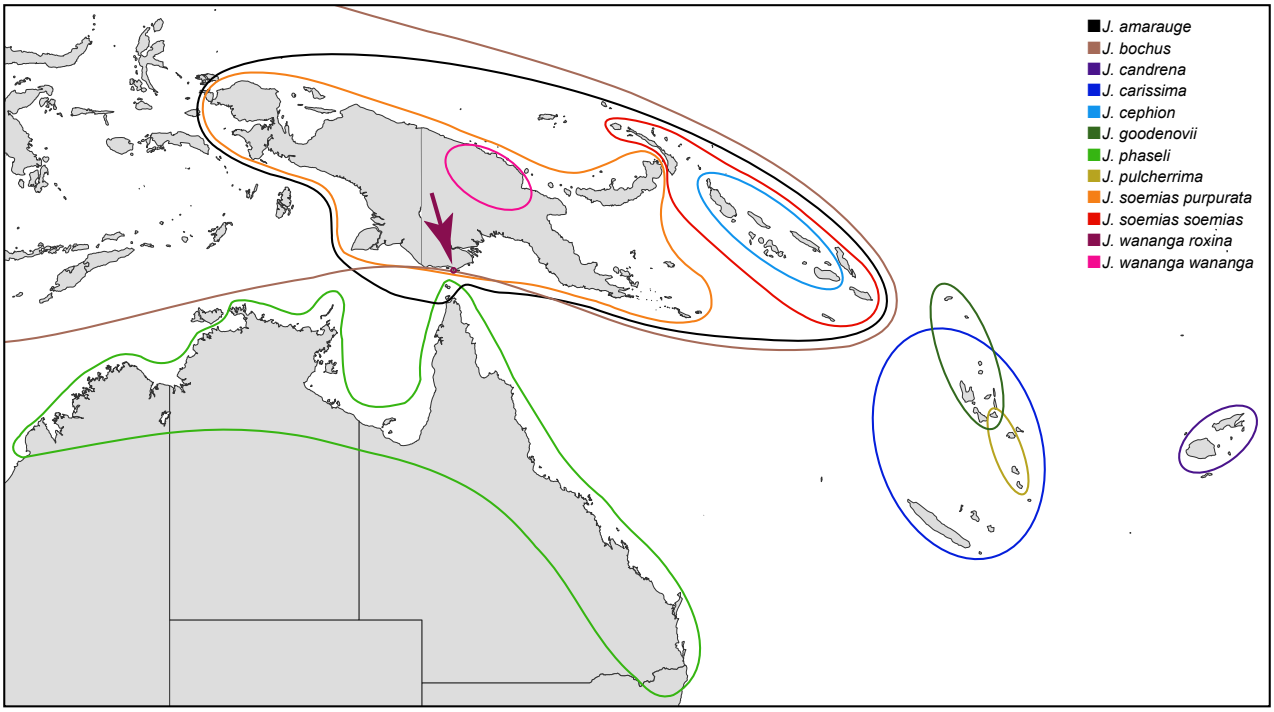

FIGURE 1. Distributions of *Jamides bochus*-group species found in Australasia, including the new taxa described in this paper. Data from Braby, 2000; Holloway & Peters, 1976; Parsons, 1991, 1998; Prasad & Waqa-Sakiti, 2007; Rawlins et al., 2014; Seki, Takanami, & Otsuka, 1991; Tennent, 2002, 2006, 2009.

DNA barcodes from the Dauan Island specimens were queried against the Barcode of Life Datasystem (BOLD) database (boldsystems.org; Ratnasingham 2007) and found to be closely related to other undescribed *Jamides* specimens, including several from Wanang and one from the Solomon Islands. The specimens collected by Sam and Kimbeng were among these close relatives. To assess relatedness among *bochus*-group *Jamides* including these putatively new species, all available DNA barcodes (COI) from putatively new species were aligned with multi-locus sequence data (including COI) from other members of the *bochus*-group. Multi-locus data were subject to phylogenetic analysis, and uncorrected pairwise COI distances were calculated between species pairs. These results were interpreted in light of detailed comparisons of external morphology.

Molecular phylogenetic materials and methods

DNA sequencing. Cytochrome c oxidase I (COI) DNA barcodes of *Jamides* butterflies from Wanang and the Solomon Islands (all deposited at USNM, Washington, D.C.) were sequenced at the Canadian Centre for DNA Barcoding (Ratnasingham & Hebert, 2007). DNA was extracted from legs or other tissues of all other dried butterfly specimens using an OmniPrep Genomic DNA Extraction Kit (gbiosciences.com). The COI barcoding locus was amplified via PCR from the Dauan Island specimens and Sanger sequenced following protocols described in Braby

et al. (2015). From all other specimens, 13 loci (including COI) were captured via anchored hybrid enrichment and sequenced on the Illumina platform by RAPiD Genomics (rapid-genomics.com) as part of ButterflyNet (butterflynet.org) following methods described in Kawahara *et al*. (2018). A preliminary phylogenetic analysis with genetic data from 222 specimens of *ca*. 44 *Jamides* species and 5 outgroup species allowed us to select the closest relatives of the new species described here. Identification based on COI sequences from the new species was also attempted on BOLD to identify close relatives not sampled in the 222-specimen dataset.

Phylogenetic analysis. Each locus was aligned using the MUSCLE algorithm (Edgar 2004) implemented in AliView (Larsson 2014). Multiple loci were concatenated with SequenceMatrix (Vaidya *et al*. 2011). A Bayesian inference analysis (BI) was performed with MrBayes 3.2 (Ronquist *et al*. 2012) on the CIPRES platform (phylo.org; Miller *et al*. 2010). Parameter values for the substitution models were estimated from the data and allowed to vary independently among loci, using the GTR+Γ substitution model for each locus. Four Markov chains, three heated and one cold, were run simultaneously for 10 million generations. Trees were sampled every 1,000 generations, and the first 25% of sampled trees were discarded as burn-in before calculating a consensus tree. A Maximum likelihood (ML) tree was inferred using the IQ-TREE server (Nguyen *et al*. 2015; iqtree.cibiv.univie.ac.at), which inferred substitution models using ModelFinder (Kalyaanamoorthy *et al*. 2017) before running an analysis partitioned by locus (Chernomor *et al*. 2016) with 1000 ultrafast bootstrap replicates (UFboot). Average, uncorrected pairwise distances and their standard error were calculated between each species and subspecies with MEGA X (Kumar *et al*. 2018).

Abbreviations used:

BOLD: Barcode of Life Datasystem; boldsystems.org
USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Molecular phylogenetic results

Our final dataset included COI barcode sequences from 6 *J. wananga* described below; 3 *Jamides* samples of unidentified species from Wanang and Guadalcanal with barcodes similar to *J. wananga*; and 3 *Jamides* from Wanang identified as *J. soemias purpurata* on the basis of barcode similarity. Thirteen loci were included for 1 additional *J. soemias purpurata* and 6 other closely related *Jamides* species including *J. amarauge*, *J. bochus*, *J. candrena* (Herrich-Schäffer) and *J. phaseli* from the *bochus*-group; and *J. alecto* and *J. lugine* (Druce) from the *celeno*-group (Table 1).

We did not have access to sequences from *J. argentina* (von Prittwitz), which a neighbour joining analysis of barcodes on BOLD identified as the closest relative to *J. wananga*. *Jamides argentina* is endemic to the Samoan Islands, and there are 10 unpublished barcodes from this species on BOLD as of 1 September 2019. Lamas (2015) regards *J. argentina* as a synonym of *J. bochus*, and it has also been considered a synonym of *J. candrena* from Fiji (Savela 2019). However, by comparing the phylogeny inferred by BOLD, which includes *J. wananga, J. argentina, J. bochus, J. cephion, J. phaseli*, and other *Jamides* species (but not *J. candrena*), and our phylogenetic analyses, which includes *J. candrena* but not *J. argentina*, it seems that *J. argentina* is a valid species genetically distinct from *J. bochus, J. candrena,* and *J. wananga.*

ModelFinder selected the following substitution models—IDH, MDH, RpS2, and RpS5: K2P+I; CAD, HCL and AACT: HKY+F+I; CAT, DDC, and GADPH: TNe+I; wg: TN+F+I; EF1a: HKY+F; and COI: TIM2+F+I. Although this assortment of different models differs from the highly parameterized GTR+ Γ model used in the Bayesian analysis, it is unlikely that model selection affects the results of phylogenetic analysis (Abadi *et al*. 2019).

Interspecific relationships differed markedly between the BI and ML trees. Figure 2 presents the BI tree. Many relationships among recognized species recovered in the BI tree were not found in the ML tree; these branches have no ML bootstrap support in Figure 2. Posterior probability values above the branches indicate the proportion of trees in the MCMC analysis that have the relationship represented by the branch in the figure. Bootstrap values in the ML analysis indicate the percent of bootstrap replicates with the relationship represented by the branch in the figure. For both measures, higher values indicate greater confidence that the relationship is supported by the data. Colour coding behind the tree demarcates different species within the *bochus* group. Branch support was generally poor, even among recognized species, except for *J. soemias purpurata*, which was monophyletic with strong sup-

TABLE 1. Collection information for specimens included in the molecular phylogenetic portion of this study. Abbreviations: CCNY = City College of New York; MCZ = Museum of Comparative Zoology, Harvard University; MGCL = McGuire Center for Lepidoptera & Biodiversity, University of Florida; MTQ = Museum of Tropical Queensland, Townsville, Queensland, Australia; PNG = Papua New Guinea; USNM = United States National Museum, Washington, DC.

Voucher Code	Voucher Institution	Species	Locality	Collector(s)	Lat/Long; Elevation	Collection Date
TSJ-002	MTQ	*Jamides wananga roxina*	Australia: Queensland, Dauan Island	Ian R. Johnson & Peter R. Wilson	-9.42, 142.53	11-Dec-2017
TSJ-003	MTQ	*Jamides wananga roxina*	Australia: Queensland, Dauan Island	Ian R. Johnson & Peter R. Wilson	-9.42, 142.53	11-Dec-2017
ENT00711064	USNM	*Jamides wananga wananga*	PNG: Madang, Usino Bundi District, Wanang Conservation Area	L. Sam & F. Kimbeng	-5.25, 145.26; 50m	10-Sep-2008
ENT00711071	USNM	*Jamides wananga wananga*	PNG: Madang, Usino Bundi District, Wanang Conservation Area	L. Sam & F. Kimbeng	-5.25, 145.26; 50m	01-Sep-2008
ENT00711079	USNM	*Jamides wananga wananga*	PNG: Madang, Usino Bundi District, Wanang Conservation Area	L. Sam & F. Kimbeng	-5.25, 145.26; 50m	01-Sep-2008
ENT00711089	USNM	*Jamides soemias purpurata*	PNG: Madang, Usino Bundi District, Wanang Conservation Area	L. Sam & F. Kimbeng	-5.25, 145.26; 50m	12-Jul-2008
ENT00711090	USNM	*Jamides* sp.	PNG: Madang, Usino Bundi District, Wanang Conservation Area	L. Sam & F. Kimbeng	-5.25, 145.26; 50m	04-Jun-2008
ENT00711095	USNM	*Jamides* sp.	PNG: Madang, Usino Bundi District, Wanang Conservation Area	L. Sam & F. Kimbeng	-5.25, 145.26; 50m	11-Jun-2008
ENT00711112	USNM	*Jamides soemias purpurata*	PNG: Madang, Usino Bundi District, Wanang Conservation Area	L. Sam & F. Kimbeng	-5.25, 145.26; 50m	08-Sep-2008
ENT00711137	USNM	*Jamides wananga wananga*	PNG: Madang, Usino Bundi District, Wanang Conservation Area	L. Sam & F. Kimbeng	-5.25, 145.26; 50m	15-Jul-2008
ENT00711138	USNM	*Jamides soemias purpurata*	PNG: Madang, Usino Bundi District, Wanang Conservation Area	L. Sam & F. Kimbeng	-5.25, 145.26; 50m	10-Jul-2008
ENT01521394	USNM	*Jamides* sp.	Solomon Islands: Guadalcanal, Honiara	R.H. Carcasson	-9.44, 159.98	31-Mar-1972
LEP59473	MGCL	*Jamides amarauge*	Solomon Islands: Guadalcanal			Aug-98

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TABLE 1. (Continued)

Voucher Code	Voucher Institution	Species	Locality	Collector(s)	Lat/Long; Elevation	Collection Date
YI-16-P075	CCNY	*Jamides bochus bochus*	Thailand: Chiang Mai, Ban Pa Miang, Muaeg Pan District	Yutaka Inayoshi	19.39, 99.66; 1094m	5-Mar-2016
MAC-05-N450	MCZ	*Jamides candrena*	Fiji: Cakaudrove, Taveuni, Matei	Mark A. Cornwall	-16.69, 179.88	21-Jul-2005
LEP-31677	MGCL	*Jamides alecto*	Myanmar: Thephyu Village, Tanintharyi	M. Miko	17.05, 96.07	29-Aug-2015
KD-93-C061	MCZ	*Jamides phaseli*	Australia: Queensland, Mirriam Vale	Kelvyn L. Dunn	-24.33, 151.55	6-May-1993
JT-10-K015	MCZ	*Jamides soemias purpurata*	PNG: Milne Bay, Kiriwina, Trobriand Islands, Losuia	W. John Tennent	-8.54, 151.06	26-May-2010

port (Fig. 2). The new species that we describe below was well differentiated from other *bochus*-group species with strong support but was not monophyletic. Three other morphologically distinct samples were recovered within the clade including the newly described *J. w. wananga* and *J. w. roxina.*

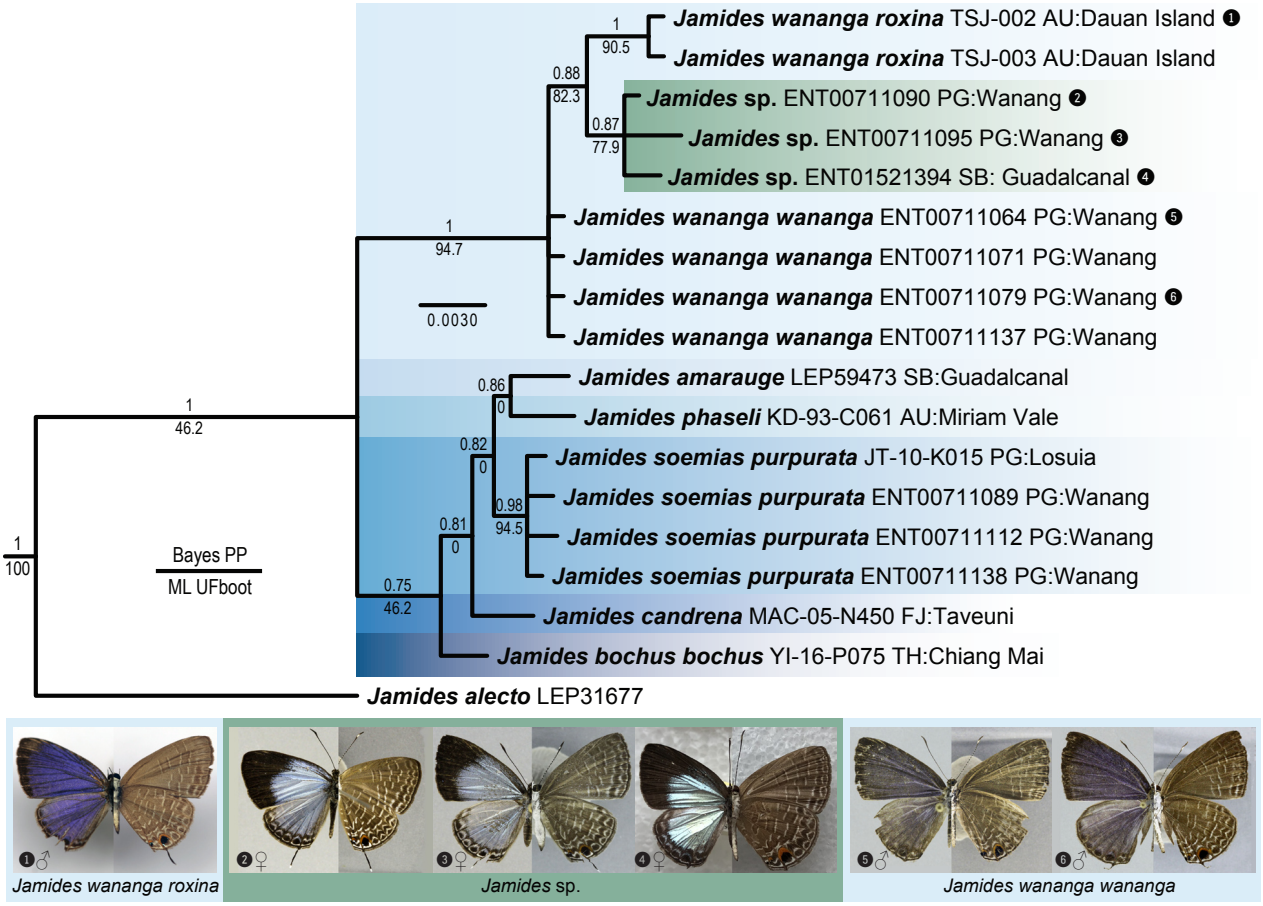

FIGURE 2. Bayesian phylogenetic tree of *Jamides wananga* **sp. n**. and its closest relatives based on COI barcode data and other loci. BI posterior probability and ML bootstrap support is shown for each code. Node labels indicate species, voucher number, and collection locality. Images of select specimens are show below the tree.

Uncorrected pairwise distances between different, related *Jamides* species were unusually low; the *J. amarauge, J. phaseli*, and *J. bochus* specimens that we sequenced shared identical DNA barcodes (Table 2). Across all Lepidoptera, Meier *et al*. (2008) found mean pairwise distances of 6.2 ±2.7% between sister species, and the values that we find closely related *Jamides* species are all below this mean value.

Jamides wananga Wilson, Johnson & Lohman sp. n.

Figure 3.

Material examined. Holotype: male, Papua New Guinea, Wanang Conservation Area, Madang Province, elevation 50 m, -5.25°, 145.267°, 2008-09-01, L. Sam & F. Kimbeng, (in USNM, Washington D. C., Sample ID: **USNM ENT** 00711079). **Paratypes**: 1 male, same data as Holotype (Sample ID: USNM ENT 00711071); 1 male, same data as holotype except 2008-09-10 (Sample ID: USNM ENT 00711064); 1 female, same data as holotype except 2008-07-15 (Sample ID: USNM ENT 00711137).

Description. Male (holotype) (Fig. 3A, B): Forewing length 15mm; antenna black with white bands on the underside; thorax and abdomen upperside black and underside white. Forewing upperside: purplish-blue; black margin narrow ~1mm along termen widening to ~2mm at apex; dorsum straight. Hindwing upperside: purplish blue becoming greyish blue towards the costa; termen margin very narrow (<0.3 mm) black edged with very narrow white on the inner margin particularly towards the tornus; a subtornal submarginal black spot with a series of submarginal black spots along the termen decreasing in size towards the apex at veins Rs and M_1; tornus and costa greyish brown;

tail black with white tip. Forewing underside: uniformly greyish brown; termen margin very narrow (<0.3 mm) black edged with very narrow white on the inner margin between the veins; terminal and subterminal brown bands between each vein narrowly edged with white; a post median band edged with beige, curved and distinctly stepped at each vein; a short medial band at end of cell edged with beige. Hindwing underside: uniformly greyish brown; termen with very narrow black margin (<0.3 mm) edged with very narrow white on the inner margin between the veins; small tornal black spot edged with white adjacent to two subtornal black spots edged with orange; terminal and subterminal brown bands curved between each vein narrowly edged with white; a post median band edged with beige distinctly curved and stepped at each vein, a short medial band at end of cell edged with beige, and a submedial band edged with beige distinctly stepped at each vein.

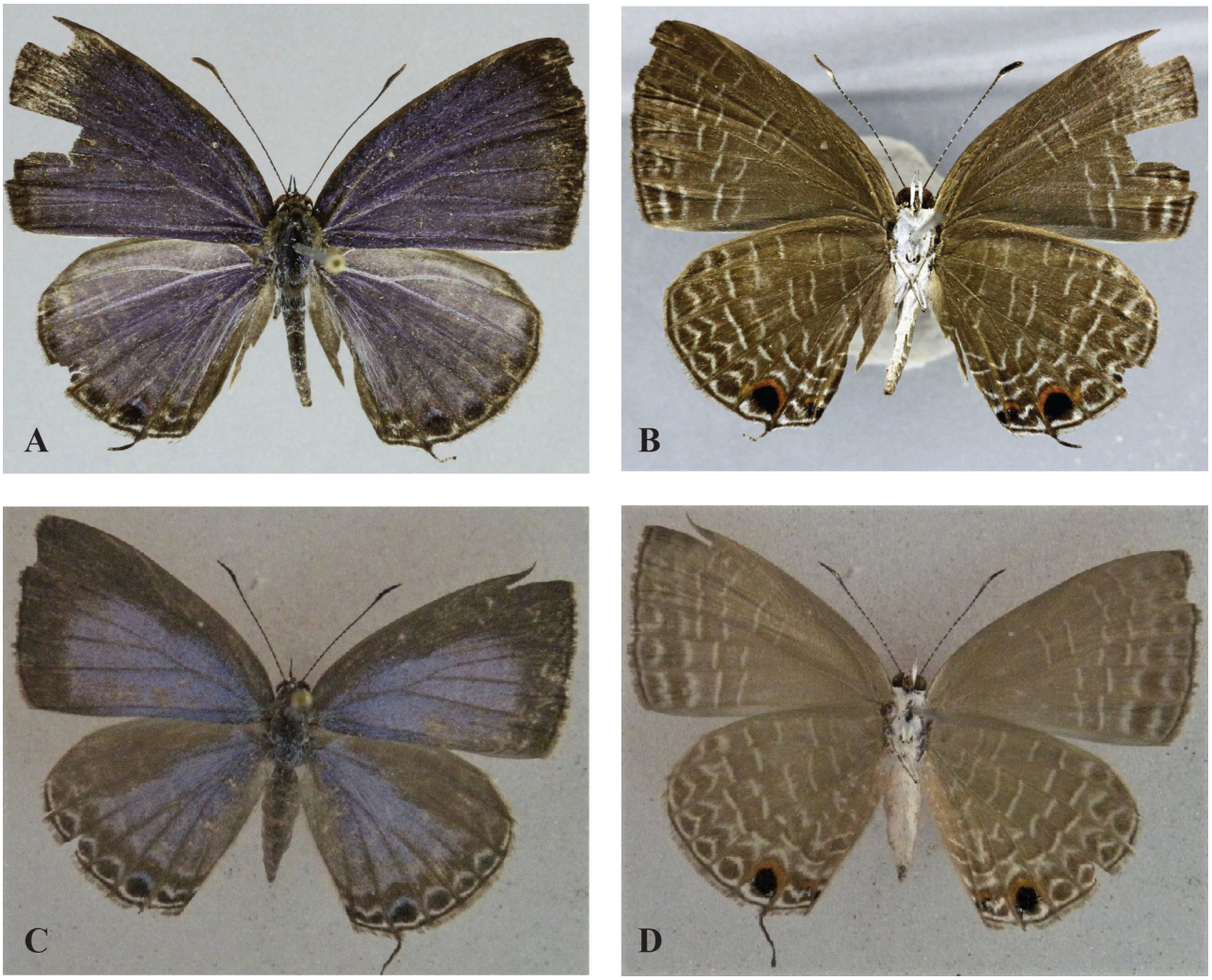

FIGURE 3. *Jamides wananga* **sp. n.** from Wanang, Papua New Guinea: A, holotype male (Sample ID: USNM ENT 00711079) upperside; B, underside; C, paratype female (Sample ID: USNM ENT 00711137) upperside; D, underside.

Male (Paratypes): As above with little variation other than a slight variation in the upperside colour. Forewing length 13–13.5 mm.

Female (Paratype) (Fig. 3C, D): Forewing length 15 mm; thorax upperside brownish black with scattered blue scale and white undeside, abdomen upperside greyish brown and underside brownish white. Forewing upperside: dull purplish blue; margin broadly brown-black increasing in width at apex. Hindwing upperside: dull purplish blue; margin broadly greyish brown , termen margin very narrow (< 0.3 mm) black edged with very narrow white on the inner margin, a subtornal submarginal black spot edged with blue and a series of submarginal greyish brown spots along the termen decreasing in size towards the apex between veins Rs and M_1 and edged with bluish grey on the inner margin. Forewing underside: same as male except ground colour duller greyish brown and post median band less curved between veins M_1 and CuA_1. Hindwing underside: same as male except ground colour duller greyish brown.

Male genitalia. Specimens of the nominate subspecies were not available to the authors, but genitalia of the subspecies *Jamides wananga roxina* are described below. Genitalia of most *bochus*-group *Jamides* are very similar (Hirowatari 1992).

Etymology. Named after the Wanang Conservation Area in Madang Province, PNG where the species was first collected in 2008.

Ecology. The nominotypical subspecies is currently known to occur only in tall rainforest in the Wanang area of PNG. The species was flying with *Jamides soemias purpurata*. The life history is unknown.

Comments. There is no significant variation in size (forewing length 13–15 mm), shape, colour and markings among the limited number of specimens. The distributional extent of the species is unknown.

Jamides wananga roxina Wilson, Johnson & Lohman subsp. n.

Figure 4.

Material examined. Holotype: male: Queensland, Dauan Island, Torres Strait; elevation 5 m, -9.42°, 142.53°, 6–12.xii.2017, I.R. Johnson and P.R. Wilson, (in S. J. Johnson Collection located in the Museum of Tropical Queensland, Townsville, Australia, QM T241069). **Paratypes:** 2 males, same data as Holotype (QM T241068, T250588); 1 male, -9.42°, 142.53°, 12-17 December 2020 (QM T240992); 1 male, 9.42°, 142.53°, 31'47" E, 10 December 2017, P.R. Wilson and I.R. Johnson (in P. R. Wilson collection); 1 male, same location, 16 December 2020, P.R. Wilson and I.R. Johnson (in P. R. Wilson collection).

Description. Male (Holotype) (Fig. 4A, B): Forewing length 13 mm; antenna black with white bands on the underside; thorax and abdomen upperside black and underside white. Forewing upperside: dark blue; black margin narrow ~1mm along termen widening to ~2mm at apex; dorsum straight. Hindwing upperside: dark blue becoming narrowly greyish blue towards the costa; termen margin very narrow (~0.2–0.3 mm) black edged with very narrow white on the inner margin particularly towards the tornus; a subtornal submarginal black spot with a series of submarginal black spots along the termen decreasing in size towards the apex at veins Rs and M_1; tornus and costa brown; tail black with white tip. Forewing underside: uniformly pale brown; termen margin very narrow (~0.2 mm) black edged with very narrow white on the inner margin between the veins; terminal and subterminal brown bands between each vein narrowly edged with white; a post median band edged with beige, curved and distinctly stepped at each vein; a short medial band at end of cell edged with beige. Hindwing underside: uniformly pale brown; termen with very narrow black margin (~0.2 mm) edged with very narrow white on the inner margin between the veins; small tornal black spot edged with white adjacent to two subtornal black spots edged with orange and a few iridescent blue scale; terminal and subterminal brown bands curved between each vein narrowly edged with white; a post median band edged with beige distinctly curved and stepped at each vein, a short medial band at end of cell edged with beige, and a submedial band edged with beige distinctly stepped at each vein.

Male (Paratypes): As above except forewing length 13–15 mm.

Male genitalia. (Fig. 5A, B, C): Tegumen narrow, circular and band like. Vinculum narrow. Brachium curved and cylindrical with a blunt point. Socius on either side of the anus opening large, bulbous and semicircular in dorsal and ventral view, with numerous long hairs. Valva broad and spoon-like with a stout slightly curved dorsal projection above a semi-circular "toothed" indentation extending to a slightly curved very hairy posterior edge.

Etymology. From a Torres Strait Islander song about Roxin (Dauan Island) sung in the traditional Kala Kawa Ya language.

Ecology. Four specimens were collected over two days from 3:30 pm to 5:00 pm on 10–11 December 2017 and two specimens collected at 4 pm on 16 December 2020 on a dirt road through monsoonal vine scrub regrowth with a canopy to a height of approximately 5–6 m. The area had been cleared previously and had remnants of abandoned banana and mango trees. The area is close to sea level and is subject to extended periods of waterlogging over the wet season. The life history is unknown.

Comments. The limited number of available specimens do not vary significantly in size, shape, colour or markings. *Jamides phaseli* and *J. amarauge* have been collected at the same location and are the only other described *Jamides* species previously collected on the island. The specimens flew rapidly and erratically, which made capture extremely difficult. Adults were seen only in the late afternoon and have not been collected elsewhere on the island despite fairly extensive collection over an extended period of time by a number of collectors.

FIGURE 4. *Jamides wananga roxina* **subsp. n.** from Dauan Island, Australia: A, holotype male (Sample ID: QMT241069) upperside; B, underside.

Discussion

Jamides wananga **sp. n.** is morphologically similar to *J. bochus*, *J. phaseli,* and *J. soemias,* which are all found in the PNG and Australian region. The *J. wananga* male upperside is distinguished from *J. bochus* and *J. phaseli* by the purplish-blue colour, the greyish-blue colour towards the costa, the very narrow black margin edged with very narrow white on the inner margin along the hindwing termen, and the prominent row of subterminal black spots on the hindwing. The *J. wananga* male is very similar to *J. soemias* but can be distinguished by the purplish-blue upperside, and the more prominent row of subterminal black spots on the hindwing upperside decreasing in size towards the apex at veins Rs and M_1 and the greyish-blue colour towards the costa. The *J. wananga* female is similar to the female *J. bochus* upperside but is a much duller purplish-blue, and is similar to *J. phaseli* and *J. soemias* but can be distinguished mainly by the upperside blue colour and extent.

The two subspecies are similar, with the main differences being variation in the upperside blue colour and underside ground colour. In comparison with *J. wananga wananga***,** *J. wananga roxina* has: narrower paler greyish-blue on upperside hindwing towards the costa; the post median band on forewing underside less curved between veins M_1 and CuA_1; few iridescent blue scales on the hindwing; underside subtornal black spots, less distance between the medial band at end of cell and the adjacent post median band; and a slightly shorter forewing length.

The male genitalia is typical of the *bochus*-group with the narrow band-like tegumen and narrow vinculum, and the spoon-like valva containing a semi-circular indentation. Comparison of the vulva of species with similar wing patterns in the PNG and Australian region (*J. bochus, J. phaseli, J. soemias*) with *J. wananga roxina* show similar morphology but the semi-circular opening in *J. wananga roxina* is relatively large and distinctly "toothed". The relatively short and cylindrical brachium is distinct to *J. wananga roxina* and not rounded and flattened at the apex typical of the *bochus*-group (Hirowatari 1992). Tennent (2006) acknowledges that the shape of the valva in the *bochus*-group is variable and often does not differ enough to be useful for identification or species diagnosis. However, the variations in other appendages of the genitalia may be useful.

This appears to be among the first studies to analyse sequence data from multiple related *Jamides* species in a phylogenetic context (but see Müller 2016). Much like their morphology, DNA barcodes differ little among the *bochus*-group of *Jamides*. Several closely related species share identical (mitochondrial) DNA barcodes but differ at nuclear loci (Table 2, Fig. 2). This can result from incompete lineage sorting or from introgression following divergence, which can be driven towards fixation within geographic areas by *Wolbachia* infection (Avise *et al.* 1983, Sahoo *et al*. 2018).

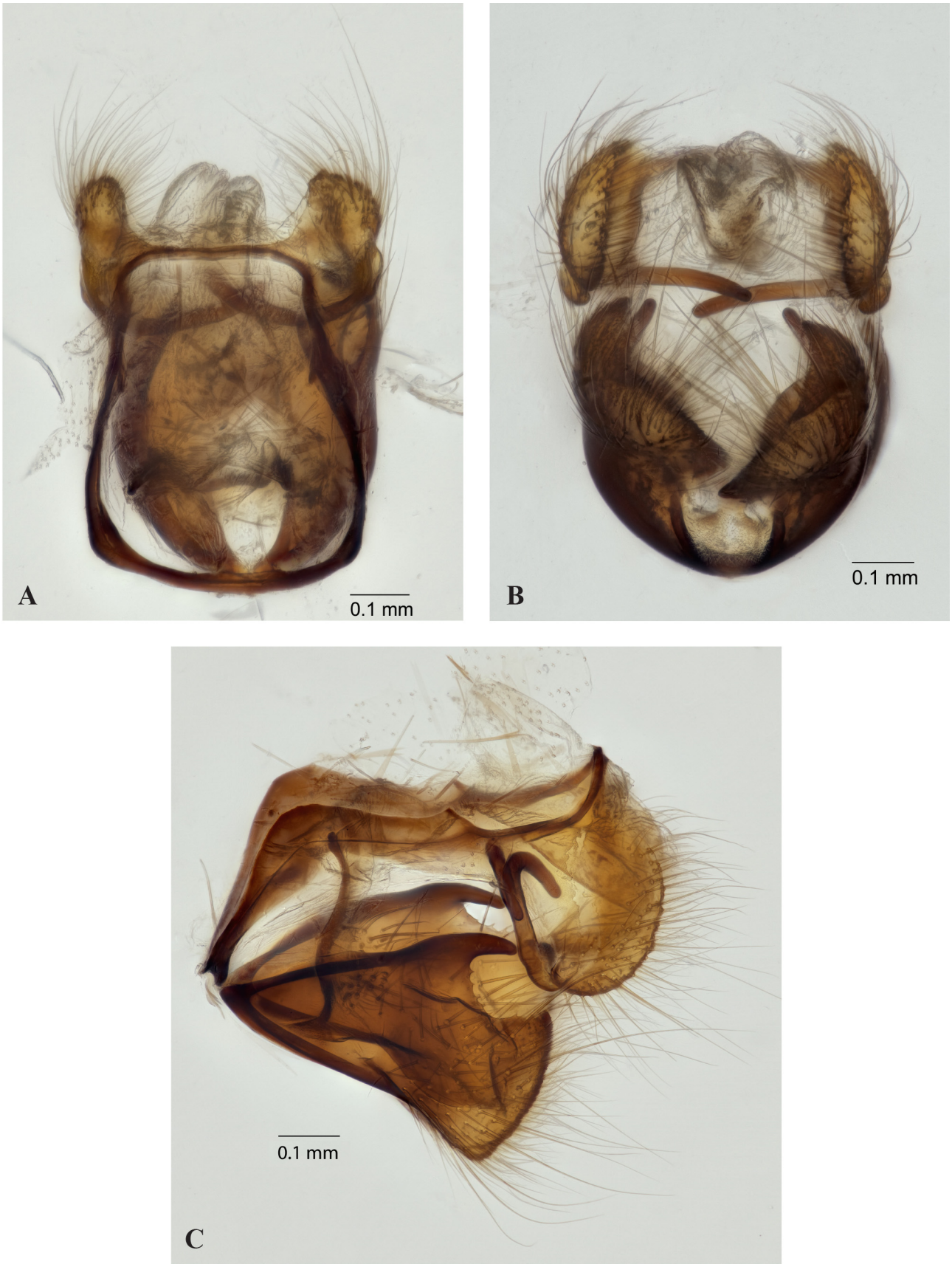

FIGURE 5. Genitalia of *Jamides wananga roxina* **subsp. n.** from Dauan Island, Australia. Paratype (Sample ID: QM T250588): A, dorsal view (QMDIU 03254); B, ventral view (QMDIU 03256); C, lateral external view (QMDIU 03257).

TABLE 2. Mean uncorrected pairwise distances (±SE) of COI DNA barcodes between subspecies of *J. wananga* and eight other *Jamides* species.

	J. alecto	***J. amarauge***	***J. bochus***	***J. candrena***	***J. lugine***	***J. phaseli***	***J. soemias purpurata***	***J. wananga roxina***	***J. w. wananga***
J. amarauge	0.0396 (0.00757)								
J. bochus	0.0396 (0.00757)	0 (0)							
J. candrena	0.0396 (0.00755)	0.00304 (0.00216)	0.00304 (0.00216)						
J. lugine	0.0686 (0.0101)	0.0625 (0.00915)	0.0625 (0.00915)	0.0625 (0.00927)					
J. phaseli	0.0396 (0.00757)	0 (0)	0 (0)	0.00304 (0.00216)	0.0625 (0.00915)				
J. soemias purpurata	0.0389 (0.00794)	0.00692 (0.00393)	0.00692 (0.00393)	0.00308 (0.00247)	0.0656 (0.0106)	0.00692 (0.00393)			
J. wananga roxina	0.0516 (0.00824)	0.0203 (0.00526)	0.0203 (0.00526)	0.0234 (0.00552)	0.0696 (0.00948)	0.0203 (0.00526)	0.0268 (0.00678)		
J. w. wananga	0.0461 (0.00856)	0.0154 (0.00500)	0.0154 (0.00500)	0.0184 (0.00552)	0.0692 (0.01004)	0.0154 (0.00500)	0.0231 (0.00690)	0.00471 (0.00265)	
***Jamides* sp.**	0.0482 (0.00850)	0.0178 (0.00516)	0.0178 (0.00516)	0.0208 (0.00564)	0.0682 (0.00969)	0.0178 (0.00516)	0.0241 (0.00673)	0.00598 (0.00274)	0.00448 (0.00227)

Jamides w. wananga and *J. w. roxina* are paraphyletic with regard to DNA barcodes from three other specimens: two from Wanang (ENT 00711090, 00711095) and one from Guadalcanal, Solomon Islands (ENT 01521394). We regard this trio of specimens as an unidentified species that we do not treat here for lack of information. Their wing patterns are indistinguishable from those of *J. amarauge amarauge*, but their barcodes are phylogenetically distinct from the *J. amarauge* sample that we sequenced (Fig. 2).

The similarity of DNA barcodes between *J. wananga* and this unidentified species is likely due to incomplete lineage sorting or introgression, which may be common among rapidly evolving *Jamides* species. While it is unusual to incorporate molecular phylogenetic analysis into a species delimitation investigation and not accept that species are monophyletic, the morphology of specimens in this group are so strikingly different from *J. wananga* and yet similar to *J. amarauge* that we cannot consider them to be another subspecies of *J. wananga* despite their barcode similarity.

The new *Jamides* from Dauan Island adds to other species newly recorded on the island (Johnson and Wilson 2019).

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APPENDIX 1. GenBank accession numbers of sequences analyzed in this study.

Voucher Code	Species	AACT	CAD	CAT	COI	DDC	EF1a
TSJ-002	*Jamides wananga roxina*	-	-	-	MZ099969	-	-
TSJ-003	*Jamides wananga roxina*	-	-	-	MZ099970	-	-
ENT00711064	*Jamides wananga wananga*	-	-	-	HQ570945	-	-
ENT00711071	*Jamides wananga wananga*	-	-	-	HQ570951	-	-
ENT00711079	*Jamides wananga wananga*	-	-	-	HQ570959	-	-
ENT00711089	*Jamides soemias purpurata*	-	-	-	HQ570968	-	-
ENT00711090	*Jamides* sp.	-	-	-	HQ570969	-	-
ENT00711095	*Jamides* sp.	-	-	-	HQ570973	-	-
ENT00711112	*Jamides soemias purpurata*	-	-	-	HQ570988	-	-
ENT00711137	*Jamides wananga wananga*	-	-	-	HQ571010	-	-
ENT00711138	*Jamides soemias purpurata*	-	-	-	HQ571011	-	-
ENT01521394	*Jamides* sp.	-	-	-	MW927456	-	-
LEP59473	*Jamides amarauge*	MZ100034	MZ099975	MZ099981	MZ099967	MZ099987	MZ099993
YI-16-P075	*Jamides bochus bochus*	MZ100036	MZ099977	MZ099983	MZ099971	MZ099989	MZ099995
MAC-05-N450	*Jamides candrena*	MZ100035	MZ099976	MZ099982	MZ099968	MZ099988	MZ099994
LEP-31677	*Jamides alecto*	MZ100033	MZ099974	MZ099980	MZ099966	MZ099986	MZ099992
KD-93-C061	*Jamides phaseli*	MZ100032	MZ099973	MZ099979	MZ099965	MZ099985	MZ099991
JT-10-K015	*Jamides soemias purpurata*	MZ100031	MZ099972	MZ099978	MZ099964	MZ099984	MZ099990

.....continued on the next page

APPENDIX 1. (Continued)

Voucher Code	Species	GAPDH	HCL	IDH	MDH	RpS2	RpS5	wg
TSJ-002	*Jamides wananga roxina*	-	-	-	-	-	-	-
TSJ-003	*Jamides wananga roxina*	-	-	-	-	-	-	-
ENT00711064	*Jamides wananga wananga*	-	-	-	-	-	-	-
ENT00711071	*Jamides wananga wananga*	-	-	-	-	-	-	-
ENT00711079	*Jamides wananga wananga*	-	-	-	-	-	-	-
ENT00711089	*Jamides soemias purpurata*	-	-	-	-	-	-	-
ENT00711090	*Jamides* sp.	-	-	-	-	-	-	-
ENT00711095	*Jamides* sp.	-	-	-	-	-	-	-
ENT00711112	*Jamides soemias purpurata*	-	-	-	-	-	-	-
ENT00711137	*Jamides wananga wananga*	-	-	-	-	-	-	-
ENT00711138	*Jamides soemias purpurata*	-	-	-	-	-	-	-
ENT01521394	*Jamides* sp.	-	-	-	-	-	-	-
LEP59473	*Jamides amarauge*	-	MZ100004	MZ100010	MZ100016	MZ100022	MZ100028	MZ100040
YI-16-P075	*Jamides bochus bochus*	MZ100000	MZ100006	MZ100012	MZ100018	MZ100024	MZ100030	MZ100042
MAC-05-N450	*Jamides candrena*	MZ099999	MZ100005	MZ100011	MZ100017	MZ100023	MZ100029	MZ100041
LEP-31677	*Jamides alecto*	MZ099998	MZ100003	MZ100009	MZ100015	MZ100021	MZ100027	MZ100039
KD-93-C061	*Jamides phaseli*	MZ099997	MZ100002	MZ100008	MZ100014	MZ100020	MZ100026	MZ100038
JT-10-K015	*Jamides soemias purpurata*	MZ099996	MZ100001	MZ100007	MZ100013	MZ100019	MZ100025	MZ100037