Records of the Australian Museum (2023)
vol. 75, issue no. 2, pp. 65–78
https://doi.org/10.3853/j.2201-4349.75.2023.1826

Records of the Australian Museum
a peer-reviewed open-access journal
published by the Australian Museum, Sydney
communicating knowledge derived from our collections
ISSN 0067-1975 (print), 2201-4349 (online)

A New Subspecies of *Philiris diana* Waterhouse & Lyell, 1914 (Lepidoptera: Lycaenidae) from the Wet Tropics of Northern Australia

Bartholomew S. Hacobian[1], Michael F. Braby[2,3], and Edward A. Petrie[4]

[1] c/o Post Office Millaa Millaa QLD 4886, Australia

[2] Division of Ecology and Evolution,
Research School of Biology, The Australian National University, Acton ACT 2601, Australia

[3] Australian National Insect Collection,
National Research Collections Australia, GPO Box 1700, Canberra ACT 2601, Australia

[4] 26 Hideaway Close, Palm Cove QLD 4879, Australia

Abstract. *Philiris diana* Waterhouse & Lyell, 1914 from the Wet Tropics of northeastern Queensland was previously thought to be monotypic, being most closely related to *Philiris papuanus* Wind & Clench, 1947 from Cape York Peninsula, Australia, and mainland New Guinea. However, a new subspecies was recently discovered on the Atherton Tableland, which we illustrate, diagnose and describe as *Philiris diana fortuna* ssp. nov. It appears to be a narrow-range endemic, restricted to montane forest (750–1,090 m asl) and allopatric or parapatric from the nominotypical subspecies *Philiris diana diana* Waterhouse & Lyell, 1914, which is largely restricted to low to mid-altitude forests in the coastal escarpment in the Cairns-Kuranda district. Despite being separated by a minimum distance of only 20–25 km, the two taxa show substantial phenotypic differences in wing pattern elements, but negligeable differences according to the mitochondrial COI barcode region (mean p-distance = 0.28%). The habitat and biology of the new taxon are summarized, and likely historical processes driving divergence between upland and lowland populations of this species hypothesized.

Introduction

Philiris Röber, 1891 is a large genus of lycaenid butterflies occurring in Australia and mainland New Guinea and its adjacent islands. It is closely related to *Hypochrysops* C. & R. Felder, 1860 in the *Hypochrysops* section of the tribe Luciini (Eliot, 1973), but unlike most related genera in that tribe, the ventral patterns of *Philiris* species are relatively unmarked and they typically exhibit a silvery-white underside ground colour. Parsons (1998) and Braby (2000) noted that the genus, at that time, contained approximately 65 species. Since then, eight more species have been described or recognized, mainly from New Guinea and nearby islands (Müller, 2014; Sands, 2015; Tennent, 2016). Only nine species are currently recognized from Australia (Sands, 2015; Braby, 2016), most of which are restricted to eastern and northeastern Queensland. The majority of species are associated with tropical rainforest or rainforest regrowth (pioneer vegetation).

Parsons (1998), following the classifications of Tite (1963) and Sands (1979, 1981a,b), proposed several informal species groups within the genus according to various morphological

Keywords: Butterfly biodiversity, Lauraceae, *Litsea leefeana*, life history
ZooBank registration: urn:lsid:zoobank.org:pub:632517D3-2D9C-4CEE-AA97-57349E1C8E4E
ORCID: Bartholomew S. Hacobian, 0000-0002-0327-6155; Michael F. Braby, 0000-0002-5438-587X; Edward A. Petrie, 0000-0001-6395-9575
Corresponding author: Michael F. Braby michael.braby@anu.edu.au
Submitted: 19 September 2022 **Accepted**: 16 November 2022 **Published**: 26 April 2023 (in print and online simultaneously)
Publisher: The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)
Citation: Hacobian, Bartholomew S., Michael F. Braby, and Edward A. Petrie. 2023. A new subspecies of *Philiris diana* Waterhouse & Lyell, 1914 (Lepidoptera: Lycaenidae) from the Wet Tropics of northern Australia. *Records of the Australian Museum* 75(2): 65–78.
https://doi.org/10.3853/j.2201-4349.75.2023.1826

characters. One such group, the *diana* species-group, was distinguished in being relatively large in size, without a black spot on the inner margin of the hindwing underside in both sexes, and usually long, asymmetric valvae in the male genitalia. The *diana* species-group consists of seven species, *viz*: *Philiris gloriosa* (Bethune-Baker, 1908); *P. diana* Waterhouse & Lyell, 1914 (Figs 4–6, 8–10); *P. violetta* (Röber, 1926); *P. papuanus* Wind & Clench, 1947; *P. praeclara* Tite, 1963; *P. montigena* Tite, 1963; and *P. siassi* Sands, 1981. Monophyly of the *diana* species-group and phylogenetic relationships of its constituent species have yet to be established, although a preliminary molecular phylogeny indicates that five of these species comprise a monophyletic group, while two species (*P. montigena* and *P. violetta*) are more distantly related (N. E. Pierce *et al*., unpublished data). Only *P. diana* and *P. papuanus kerri* Sands, 2015 occur in Australia, which have allopatric distributions in northern Queensland. *Philiris papuanus kerri* occurs widely on Cape York Peninsula, where it extends from Bamaga (Monteith & Hancock, 1977) south to the Chester River area and the Rocky River (Valentine & Johnson, 1997). In contrast, *P. diana* is restricted to the Wet Tropics, where it is has mainly been recorded from a small number of locations in the Cairns-Kuranda district (Braby, 2000), with the majority of specimens captured from Kuranda early last century by F. P. Dodd. *Philiris diana* has also been recorded further south in montane areas at Paluma (Common & Waterhouse, 1981) and the Bluewater State Forest (Dunn & Dunn, 1991). However, apart from an anomalous specimen from Lake Eacham (Braby, 2000; Sands, 2015), which we discuss later, we know of no intervening records between the Cairns-Kuranda district and the Paluma Range.

In March 2021, a male *Philiris* was captured by one of us (BSH) in montane rainforest at c. 900 m above sea level (asl) near Millaa Millaa on the Atherton Tableland. The specimen resembled *P. diana* in size but there were significant wing pattern differences. Further specimens comprising both sexes were captured during the following wet season. In addition, eggs were obtained from a captive female in early December 2021 and reared to adulthood, and other adults were reared from larvae collected from foliage of the larval foodplant *Litsea leefeana* (F. Muell.) Merrill (Lauraceae) (Petrie & Hacobian, 2022). Close examination and comparison of this material, and of two females from other locations on the Atherton Tableland, have revealed that they are indeed *P. diana* but are sufficiently differentiated to warrant subspecific status. Hence, the purpose of this paper is to describe this new population (*P. diana* ssp. "Atherton Tableland") and to compare it with both nominotypical *P. diana* and *P. papuanus*.

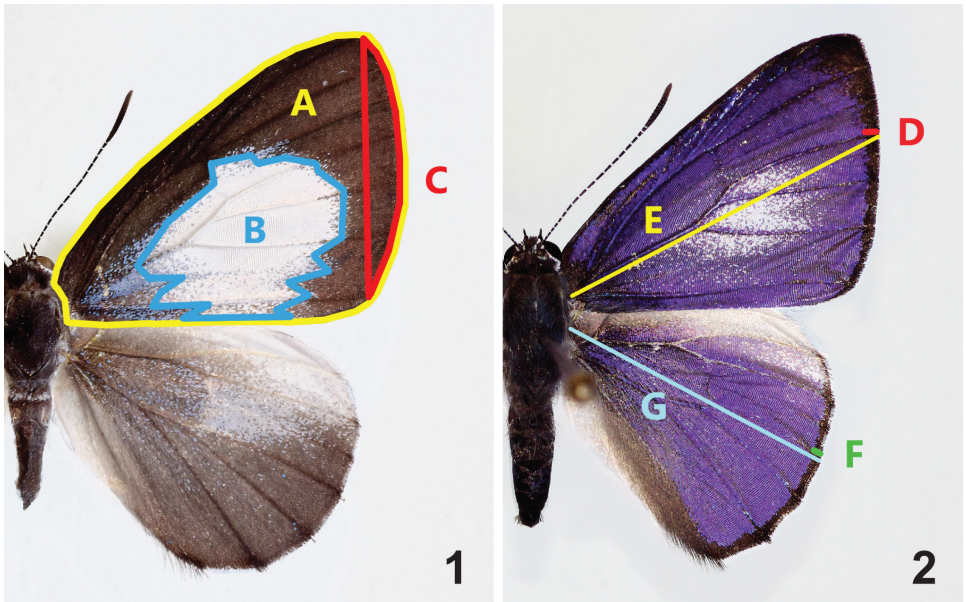
Materials and methods

Character differences between the phenotypes of *P. diana* and *P. diana* ssp. "Atherton Tableland" were assessed by examination of adult specimens in both museum and private collections. Quantitative measurements were made for the following five morphological characters concerning wing shape and colour pattern elements (Figs 1, 2). To account for adult size variation and possible allometric scaling, all measurements were divided by wing area or wing length (as a proxy of body size) to yield dimensionless quantities. Photographic images of individual specimens (with differing scale factors) were used as the basis for all measurements utilizing SketchAndCalc software (Dobbs, 2011). Sample sizes for each sex were as follows: 46 males (24 *P. diana*, 22 *P. diana* ssp. "Atherton Tableland"), and 42 females (26 *P. diana*, 16 *P. diana* ssp. "Atherton Tableland"). Data for each character were analysed using a parametric two-sample t-test.

1 The relative size of the white central patch on the upperside of the forewing of females was calculated for each specimen by measuring the area of the white central patch (character B) and then dividing that measurement by the total forewing area (character A).
2 The degree of curvature of the forewing termen of females was assessed by calculating the "curved area", that is, the area of that portion of the forewing enclosed between the termen and a straight line between the end of veins R_5 and 1A+2A (character C). This area was then divided by character A.
3 The degree of curvature of the forewing termen of males was assessed by calculating the quantity character C/A for each specimen, as described above for the female.
4 The relative width of the black terminal band on the upperside of the forewing of males was calculated by measuring the width of the band at vein M_3 (character D) for each specimen divided by the length of the forewing, measured as the straight-line distance between the wing base and the end of vein M_3 (character E).
5 The relative width of the black terminal band on the upperside of the hindwing of males was calculated similarly to the forewing outlined above, with measurements made on vein M_3 (character F) for each specimen divided by the length of the hindwing, measured as the straight-line distance between the wing base and the end of vein M_3 (character G).

Character differences between the early stages of the two taxa were also assessed by examining and comparing the eggs, larvae and pupae of *P. diana* ssp. "Atherton Tableland" with those of *P. diana* collected from near Cairns and reared by us (Petrie & Hacobian, 2022).

In order to assess the possible influence of ambient temperature on the adult phenotypes of *P. diana*, larvae from eggs laid by a captive female of *P. diana* ssp. "Atherton Tableland" in December 2021 and other larvae collected from the field during January 2022 were divided into two cohorts. One cohort was reared at an altitude of c. 920 m asl under near-ambient conditions of temperature (and humidity) approximating those applicable to wild populations (Table 1). The other cohort was raised near sea-level under a combination of controlled temperature (and humidity) conditions more like those of wild populations of nominotypical *P. diana*. In addition, two cohorts of *P. diana* collected from the field near Cairns in December 2021–February 2022 were reared under the same



Figures 1–2. Right fore- and hindwings of *Philiris diana diana*, showing measurements of quantitative characters for traits 1–5 (see Materials and Methods): (*1*) female; (*2*) male. Letters denote the following characters: A = area of forewing; B = area of forewing white central patch; C = curved area of forewing enclosed between termen and line between end of veins R_5 and 1A+2A; D = width of black terminal band of forewing at vein M_3; E = length of forewing from base to end of vein M_3; F = width of black terminal band of hindwing at vein M_3; G = length of hindwing from base to end of vein M_3.

reciprocal environmental conditions. In both experiments, the larvae were reared on the larval foodplant *Litsea leefeana* (Petrie & Hacobian, 2022).

The male genitalia were compared by dissecting specimens of each taxon as follows: *Philiris diana* ssp. "Atherton Tableland" (1♂ Genitalia No. MFB-121—7 km SSW of Millaa Millaa, QLD, 31 Mar. 2021, B. S. Hacobian, ANIC 31-036203); *P. diana* (1♂ Genitalia No. MFB-139—Kuranda, QLD, Apr. 1907, F. P. Dodd; paralectotype, AMS K.517927); *P. papuanus kerri* (1♂ Genitalia No. MFB-138—West Claudie River, QLD, emg. 30 Aug. 1999, D. P. A. Sands; paratype, ANIC); *P. papuanus papuanus* Wind & Clench, 1947 (1♂ Genitalia No. MFB-137—Musgrave River, Central District, Papua New Guinea, 8 Sep. 1974, D. P. A. Sands, ANIC). These preparations were then compared against the illustrations published in Tite (1963) and Sands (1979).

Dissection of the genitalia was performed using standard techniques: the entire abdomen was removed and placed in 10% KOH and boiled for 20 minutes, and then transferred to 30% ethanol for cleaning, dissection and examination. Completed dissections were fixed in 95% ethanol and then 100% isopropanol. The genitalia were then placed in an alcohol-based gel in an excavated glass block and photographed using a Leica M205A microscope and were stacked using Helicon Focus 5.3 according to the technique of Su. Terminology for genitalia follows Klots (1970) and Eliot (1973).

To test if the midland and upland populations of *P. diana* represented two separate species according to neutral genetic markers, patterns of monophyly and the extent of genetic divergence were analysed for six samples for the "barcode" region of the mitochondrial gene cytochrome c oxidase subunit I (COI), a widely used marker for species level discrimination (Hebert *et al.,* 2003a,b). Three samples of *P. diana diana* collected from near Cairns in 2022 and a single sample of *Philiris diana* ssp. "Atherton Tableland" collected from near Millaa Millaa in March 2021 (ANIC Database No. 31-036203) were sequenced (GenBank accession numbers: *Philiris diana diana*—SUB12522691 MFB-20-C114 OQ214188, SUB12522691 MFB-20-C113 OQ214189, SUB12522691 MFB-20-C112 OQ214190; *Philiris diana fortuna*—SUB12522691 31-036203 OQ214191). In addition, partial sequences (550–658 bp) were downloaded for two samples on BOLD (Ratnasingham & Hebert, 2007): a female *P. diana diana* collected from Paluma in 1969 (accession number: ANICS1826-11), and a female *Philiris diana* ssp. "Atherton Tableland" collected from Lake Eacham in 1998 (accession number: ANICS1824-11). For fresh material, DNA was extracted from one or two legs and then the entire mitochondrial genome was sequenced according to the

Table 1. Environmental conditions under which the immature stages were reared in captivity at two locations in 2022: (*a*) the Cairns district (Palm Cove), and (*b*) Atherton Tableland (Beatrice).

rearing location	altitude (m)	temperature range (°C)	relative humidity (%)	comment
Cairns district	sea-level	26–31	90–99	controlled
Atherton Tableland	920	20–29	50–90	uncontrolled

Table 2. Two sample t-test results for the quantitative analysis of morphological wing characters of *Philiris diana* subspecies (see Figs 1, 2). Values presented are means ± 1 standard deviation. *FW,* forewing; *HW,* hindwing; *UPP*, dorsal or upperside of wing; *n.s*., not significant.

characters	*P. diana fortuna*		*P. diana diana*		t-test		
	$\bar{x}$ ± SD	n	$\bar{x}$ ± SD	n	t	df	P
♀ FW UPP white central patch divided by wing area (character B/A)	0.257 ± 0.0290	16	0.348 ± 0.0286	26	9.78	40	< 0.0001
♀ FW "curved area" divided by wing area (character C/A)	0.109 ± 0.0072	16	0.091 ± 0.0096	26	6.30	40	< 0.0001
♂ FW "curved area" divided by wing area (character C/A)	0.070 ± 0.0054	22	0.066 ± 0.0090	21	1.84	41	n.s.
♂ FW UPP black terminal band width divided by wing length (character D/E)	0.045 ± 0.0075	22	0.040 ± 0.0119	24	2.11	44	n.s.
♂ HW UPP black terminal band width divided by wing length (character F/G)	0.056 ± 0.0074	22	0.037 ± 0.0042	24	10.8	44	< 0.0001

protocols of Zhou *et al.* (2022); only the COI portion was analysed in this study. Sequences were aligned in AliView v1.28 and trimmed to the 658-nucleotide barcode template. A Neighbor Joining (NJ) phylogram was generated using unweighted "p" values with the default neighbour-joining algorithm in PAUP v4.0a (build 168); three other *Philiris* taxa (*P. helena, P. fulgens* and *P. tapini*) downloaded from BOLD were used as outgroups. Pairwise distances were also calculated in PAUP v4.0a using both uncorrected p-distance and those according to the K2P substitution model.

The following abbreviations refer to repositories where material has been examined:

AMS Australian Museum, Sydney
ANIC Australian National Insect Collection, Canberra
BHC B. Hacobian private collection, Millaa Millaa, QLD
CMC C. Müller private collection, Sydney
EPC E. Petrie private collection, Cairns, QLD
NMV Museums Victoria, Melbourne
QM Queensland Museum, Brisbane
RMC R. Mayo private collection, Pomona, QLD
SAMA South Australian Museum, Adelaide

Results

Results for the analysis of five quantitative morphological wing characters are presented in Table 2. Three characters were found to be significant among the two different *P. diana* populations, whereas two traits (male forewing termen curvature and male forewing black terminal band at vein M_3) were found to be not significant.

The reciprocal provenance experiment, with lowland and montane populations of *P. diana* each reared under different laboratory conditions (Table 1), revealed no environmental influence on adult phenotype (Tables 3, 4). Although our samples were small and not amenable to statistical analysis, all adults obtained from immature stages of the montane population *P. diana* ssp. "Atherton Tableland" ($n = 25$) reared in either Palm Cove, Cairns ($n = 4$) or Beatrice, Atherton Tableland ($n = 21$) produced the montane form *P. diana* ssp. "Atherton Tableland" (Table 3). Conversely, all adults obtained from immature stages of the lowland population of *P. diana* ($n = 7$) reared in either Palm Cove, Cairns ($n = 4$) or Beatrice, Atherton Tableland ($n = 3$) produced the typical *P. diana* form (Table 4).

Mt DNA barcodes (COI) revealed negligeable divergence between the two populations, and the pairwise distances estimated using the K2P model were the same as those for uncorrected p-distances. The average pairwise distance within the four *P. diana diana* samples was 0.35%, but for the two samples of *P. diana* ssp. "Atherton Tableland" it was 0%. Although *P. diana* comprised a monophyletic lineage, the two samples of *P. diana* ssp. "Atherton Tableland" were nested within the four samples of *P. diana diana*, indicating lack of reciprocal monophyly between the two taxa (Fig. 3). The average p-distance between *P. diana diana* and *P. diana* ssp. "Atherton Tableland" was 0.28%, with the range varying from 0.15–0.46%. Although the mean level of divergence within *P. diana diana* was greater than between *P. diana diana* and *P. diana* ssp. "Atherton Tableland", these differences were not statistically significant because they were less than 1 bp on average for the COI barcode region (*P. diana diana*: 0.35% * 658 bp = 2.3 bp; *P. diana* ssp. "Atherton Tableland": 0.28% * 658 bp = 1.8 bp).

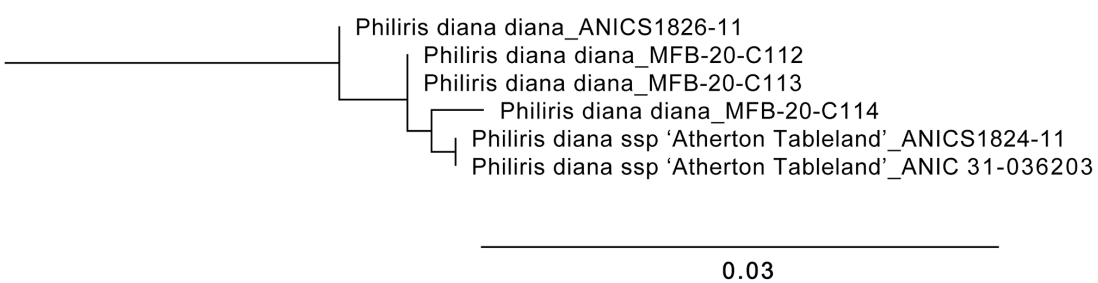


Figure 3. Neighbor Joining phylogenetic tree of *Philiris diana* based on mitochondrial cytochrome c oxidase subunit I (658 bp "barcode" region). Outgroups are not shown. Scale bar represents number of substitutions/site.

Table 3. Adult phenotype of *Philiris diana* based on immature stages collected from the field at Beatrice, Atherton Tableland, QLD and reared in captivity at two locations with different environmental conditions: the Cairns district (Palm Cove), and Atherton Tableland (Beatrice) (see Table 1). A total of 25 immatures was collected and reared to adult (17 males, 8 females), and all conformed to the *fortuna* subspecies phenotype.

immature stage	rearing location			
	Cairns district		Atherton Tableland	
	fortuna	*diana*	*fortuna*	*diana*
egg	—	—	9♂, 4♀	0
larva instar I	—	—	—	—
larva instars II–V	2♂, 1♀	0	5♂, 3♀	0
larva instar VI	1♂	0	—	—
pupa	—	—	—	—
total	3♂, 1♀	0	14♂, 7♀	0

Taxonomy

Lycaenidae

Philiris Röber, 1891

Type species: *Thecla ilias* C. Felder, 1860.

Philiris diana Waterhouse & Lyell, 1914

Philiris diana fortuna ssp. nov.

urn:lsid:zoobank.org:act:0B2CBC15-926A-4949-9D84-29891241A703

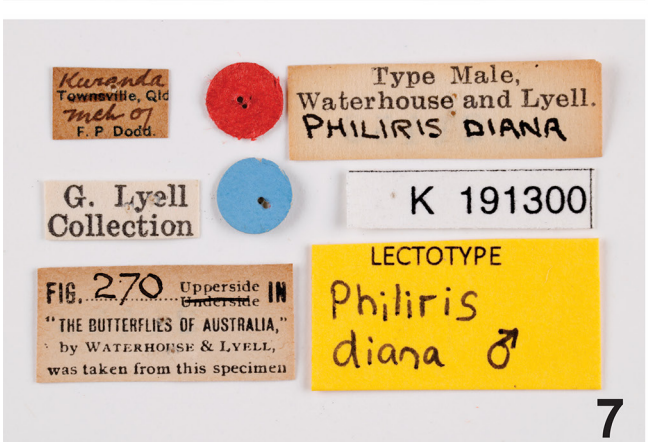
Figs 12–17

Holotype ♂ "7 km SSW of Millaa Millaa, QLD, alt. 920 m asl, emg. 21 Feb 2022, B.S. Hacobian", (ANIC Database no. 31 084524). **Paratypes** 20♂♂, 15♀♀. Queensland: 1♂ "7 km SSW of Millaa Millaa, QLD, alt. 920 m asl, emg. 14 Feb 2022, B.S. Hacobian" (BHC); 1♂ same data but date "emg. 21 Feb 2022" (BHC); 1♂ same data but date "emg. 22 Feb 2022" (BHC); 1♀ same data but date "emg. 26 Feb 2022" (BHC); 1♂ same data but date "emg. 17 Feb 2022" (ANIC); 1♀ same data but date "emg. 26 Feb 2022" (ANIC); 1♂ same data but date "emg. 24 Feb 2022" (AMS); 1♀ same data but date "emg. 26 Feb 2022" (AMS); 1♂ same data but date "emg. 26 Feb 2022" (NMV); 1♂ same data but date "emg. 26 Feb 2022" (QM); 1♂ same data but date "emg. 27 Feb 2022" (CMC); 1♀ same data but date "emg. 5 Mar 2022" (CMC); 1♂ same data but date "emg. 17 Jul 2022" (BHC); 1♂ same data but date "emg. 19 Jul 2022" (BHC); 1♀ same data but date "emg. 20 Jul 2022" (BHC); 1♀ "6.5 km SSW of Millaa Millaa, QLD, alt. 880 m asl, emg. 15 Mar 2022, B.S. Hacobian" (BHC); 1♂ "5.5 km S of Millaa Millaa, QLD, alt. 750 m asl, emg. 26 Feb 2022, B.S. Hacobian" (BHC); 1♂ same data but date "emg. 2 Mar 2022" (BHC); 1♂ same data but date "emg. 7 Mar 2022" (BHC); 2♂, 1♀ same data but date "emg. 8 Mar 2022" (BHC); 1♀ same data but date "emg. 15 Mar 2022" (BHC); 1♂ "Whiting Rd Beatrice QLD, E. Petrie, ", "x-larva, L.leefeana" (EPC); 1♂ same data but date "21.Feb.2022" (EPC); 1♀ same data but date "13. Mar.2022" (EPC); 1♂ "Whiting Rd Beatrice QLD, R. Mayo, 14 March, 2022" (RMC); 1♂ "5.5 km S of Millaa Millaa, QLD, 750 m asl, 12 Mar 2022, B.S. Hacobian" (SAMA); 1♀ same data but date "23 Mar 2022" (QM); 1♂, 1♀ same data but date "24 Mar 2022" (ANIC); 1♀ same data but date "27 Mar 2022" (ANIC); 1♀ same data (NMV); 1♂ "7 km SSW of Millaa Millaa, QLD, 915 m asl, 31 Mar. 2021, B.S. Hacobian", "ANIC Database No. 31-036203", "ANIC DNA Wash number DNA1499", "ANIC Genitalia number MFB-121" (ANIC); 1♀ "7 km SSW of Millaa Millaa, QLD, 920 m asl, 5 Dec. 2021, B.S. Hacobian" (BHC).

Table 4. Adult phenotype of *Philiris diana* based on immature stages collected from the field at Kuranda, QLD and nearby localities and reared in captivity at two locations with different environmental conditions: the Cairns district (Palm Cove), and Atherton Tableland (Beatrice) (see Table 1). A total of seven immatures was collected and reared to adult (3 males, 4 females), and all conformed to the *diana* subspecies phenotype.

immature stage	rearing location			
	Cairns district		Atherton Tableland	
	fortuna	*diana*	*fortuna*	*diana*
egg	—	—	—	—
larva instar I	0	1♂	0	1♀[a]
larva instars II–V	0	2♀	0	1♂
larva instar VI	—	—	0	1♂
pupa	0	1♀	—	—
total	0	1♂, 3♀	0	2♂, 1♀

[a] Larva transferred from Palm Cove to Beatrice after completion of instars I and II.



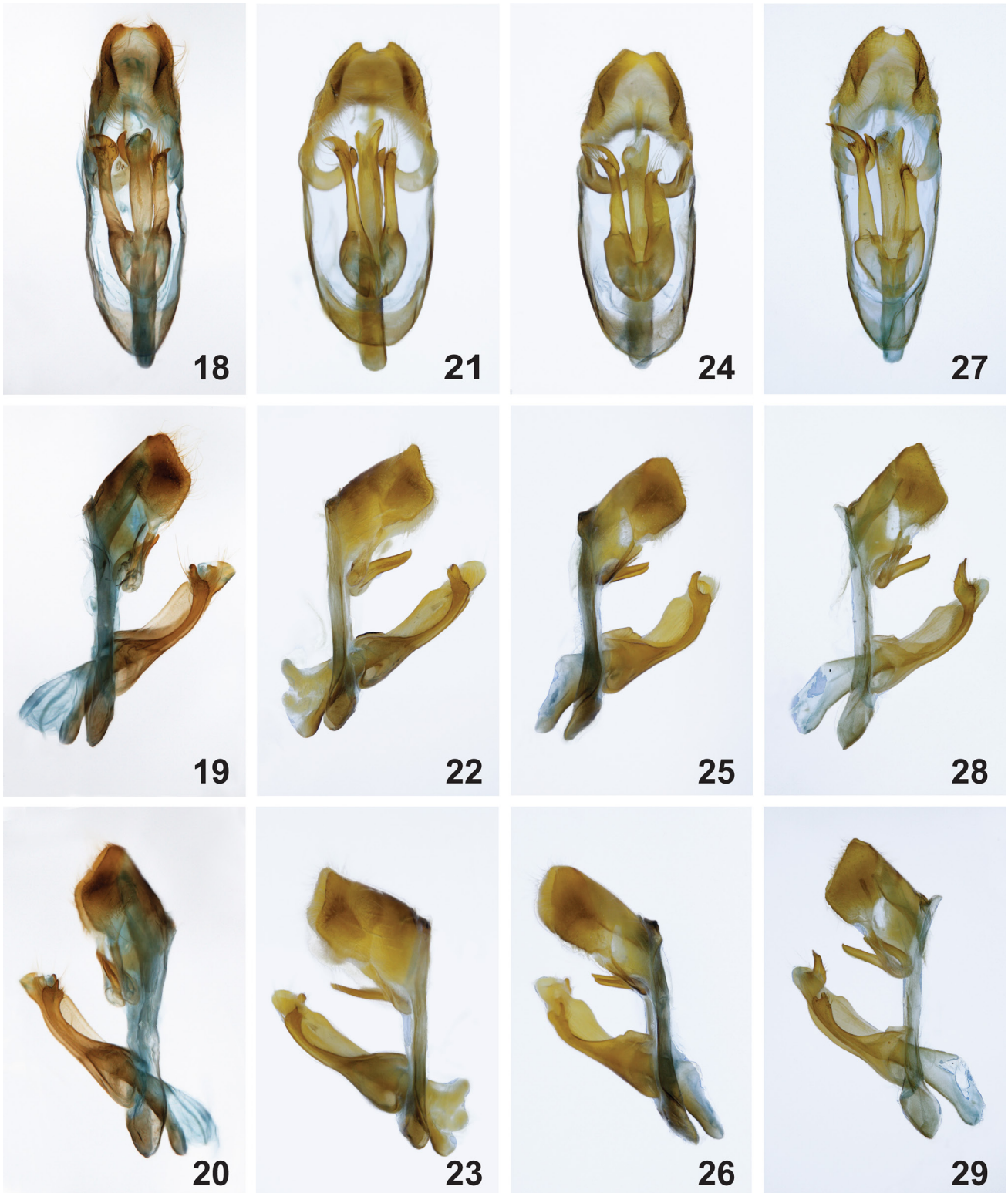
Figures 4–11. Adults of *Philiris diana diana*: (*4, 5, 7*) lectotype male in AMS, showing dorsal and ventral views and label data; (*8, 9, 11*) paralectotype female in AMS, showing dorsal and ventral views and label data; (*6*) male, dorsal view, reared from larva from near Kuranda (BHC); (*10*) female, dorsal view, reared from larva from near Cairns (EPC). Scale bar = 10 mm.

Figures 12–17. Adults of *Philiris diana fortuna* ssp. nov.: (*12, 13*) holotype male, showing dorsal and ventral views (ANIC); (*14*) paratype male, dorsal view showing variation (BHC); (*15, 16*) paratype female, showing dorsal and ventral views (ANIC); (*17*) paratype female, dorsal view showing variation (BHC). Scale bar = 10 mm.

Other material 1♂2♀. Queensland**:** 1♀ "17.17S 145.38E, Lake Eacham NP, Q 760 m GPS, 23 Nov 1998, E.D. Edwards, H. Sutrisno", "ANIC Database No. 31 043392"; "Barcode of Life, DNA voucher specimen, Sample ID: 11ANIC-058824, BOLD Proc. ID: ANICS1824-11" (ANIC); 1♀ "Tinaroo Lake, in rainforest, 25 Apr. 1972, 750 m. N Qu, N & K. Tindale", "SAMA Database No. 31-011382" (SAMA); 1♂ "Millaa Millaa Lookout QLD; E. Petrie; -17.52049° 145.56741°; 17 Nov. 2022" (EPC).

Diagnosis

Adults of *P. diana fortuna* differ from those of *P. diana diana* by the following eight characters concerning wing colour pattern and wing shape: (1) In *P. diana fortuna* males the upperside ground colour varies from deep cobalt-blue to deep purplish-blue, whereas in *P. diana diana* males the ground colour is a paler shade of violet-blue. (2) The costa and apical areas on the upperside of the hindwing in *P. diana fortuna* males are grey, whereas in *P. diana diana* males this area is broadly white. (3) The black terminal band on the upperside of the hindwing is broader in *P. diana fortuna* males, and this difference is statistically significant (Table 2). (4) In *P. diana*



Figures 18–29. Male genitalia of the *Philiris diana* species-group in Australia and Papua New Guinea: (*18–20*) *P. diana fortuna* ssp. nov. showing posterior, left lateral and right lateral views; (*21–23*) *P. diana diana* showing posterior, left lateral and right lateral views; (*24–26*) *P. papuanus kerri* showing posterior, left lateral and right lateral views; (*27–29*) *P. papuanus papuanus* showing posterior, left lateral and right lateral views. Scale bar = 1 mm.

diana males, the upperside of the forewing has a distinct white central patch, which extends below vein CuA_2, whereas in *P. diana fortuna* this white patch is generally absent or occasionally represented by a few scattered grey or greyish-white scales only; this patch, when present, does not extend below vein CuA_2. (5) The shape of the forewing termen is more strongly arched in *P. diana fortuna* females, and this difference is statistically significant (Table 2). (6) The white central patch on the upperside of the forewing in *P. diana fortuna* females (range: 20–35% of wing area) is smaller compared to that of *P. diana diana* females (range: 30–40% of wing area), and this difference is statistically significant (Table 2). (7) On the upperside of the hindwing, the costa and apical areas between veins Rs and M_1 are extensively suffused white and the adjoining central area distal to the discocellular veins between M_1 and M_3 is also white in *P. diana diana* females, whereas in *P. diana fortuna* females these areas are substantially reduced in extent and grey in colour or grey with a few white scales. A consequence of the reduction of the white areas in both fore- and hindwings is that the female of *P. diana fortuna* is a much darker butterfly with more extensive areas of brown-black than the female of *P. diana diana*. (8) The underside ground colour, in reared specimens of both sexes, is silvery-white in *P. diana fortuna*, but white with less silver tone in *P. diana diana*.

The male genitalia of *P. diana fortuna* (Figs 18–20) are similar to those of *P. diana diana* (Figs 21–23), particularly with respect to the shape of the phallus, sociuncus, brachia, and valvae which are asymmetrical in profile. The only difference lies in the width of the long, narrowed middle section of the valvae—in *P. diana fortuna* the middle sections of the right and left valvae are slightly broader than in *P. diana diana*. The genitalia of the two *P. diana* subspecies are similar to those of the two subspecies of *P. papuanus—P. papuanus kerri* and *P. papunus papuanus* (Figs 24–29)—in that they show the same degree of asymmetry among the valvae, but in *P. papuanus* the curved apical spine of the left valva is substantially longer and more robust, and the middle section of the left valva is more strongly arched (in lateral view) than in *P. diana*. The apex of the right valva terminates in a short beak-like projection that is oriented dorsolaterally in both subspecies of *P. diana*, whereas in the two *P. papuanus* subspecies the apex bears a longer but narrower dorsolateral projection that terminates in an outwardly curved spine.

Description

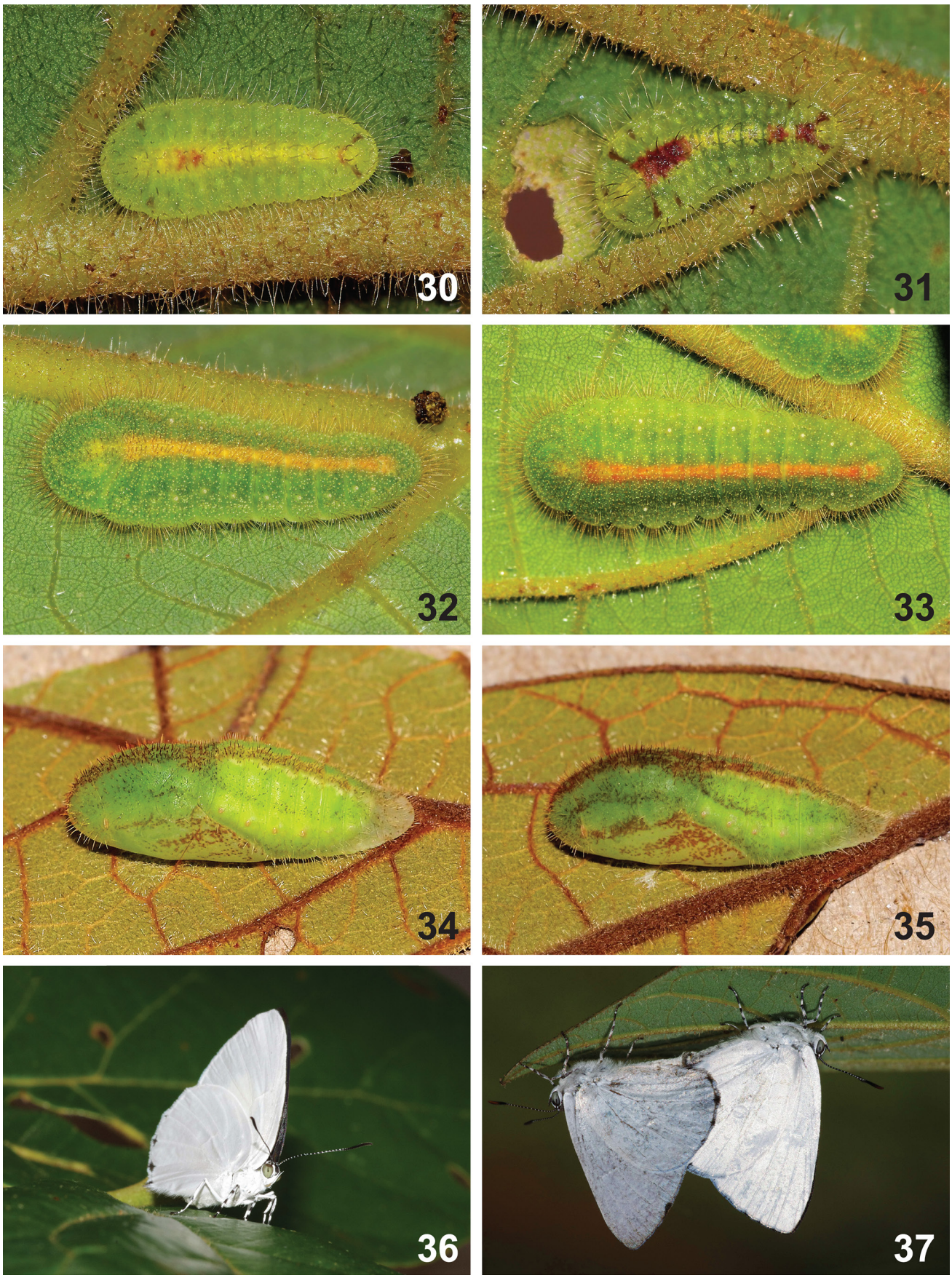
Male. *Head:* eyes brown when alive, black when dead, ringed by white scales; labial palpus dark grey dorsally, white ventrally, clothed in piliform scales, second (middle) segment four times longer than third segment; antennae 8.7–9.3 mm long, flagellum with 32–35 segments (shaft 18–20, club 14–15), shaft black prominently ringed with white, club black variably marked ventrally with orange-brown most extensively in apical half; frons dark brownish-grey; chaetosemata predominantly grey. *Thorax:* dorsal surface dark grey, ventral surface white; legs white, marked with black between segments, tarsi and mid tibiae. *Forewing:* length 15.2–17.8 mm ($\bar{x}$ = 16.7 ± 0.66 mm, n = 19), upperside dark purplish-blue, costa narrowly edged with black, a narrow black terminal band tapered along its length and broadest near apex, end of veins black, an obscure central area between veins M_3 to CuA_2 suffused dull grey, terminal scale fringe black near apex but elsewhere black with white tips; underside uniform silvery-white, costa narrowly edged with black, terminal scale fringe black near apex but elsewhere white; costa and termen slightly convex, apex pointed but with outer costa distinctly rounded, tornus rounded, dorsum straight. *Hindwing:* upperside dark purplish-blue, costal region mid grey, apex dark grey with a few scattered white scales, a narrow black terminal band of constant width between veins M_1 and CuA_2 but broader towards apex and tornus, dorsum broadly grey, terminal scale fringe black near ends of veins M_3, CuA_1, CuA_2 and 1A+2A, elsewhere black with white tips; underside uniform silvery white, black terminal spots at ends of veins M_3, CuA_1, CuA_2 and 1A+2A, a narrow black terminal line joining spots between veins CuA_1 and 1A+2A, terminal scale fringe black adjacent to terminal spots, elsewhere white. *Abdomen:* dorsal surface dark grey, ventral surface white.

Female. *Head:* eyes, labial palpus, antenna and frons similar to male; antennae 8.7–9.1 mm long, flagellum with 34–38 segments (shaft 18–21, club 14–17). *Thorax:* similar to male. *Forewing:* length 16.4–18.7 mm ($\bar{x}$ = 17.6 ± 0.73 mm, n = 13), upperside dark brownish-black, with a prominent white central patch edged with suffusion of iridescent blue scales, blue suffusion more extensive towards base of white patch, sometimes a few white scales below central white patch between vein 1A+2A and dorsum; terminal scale fringe black near apex, elsewhere black with white tips; underside similar to male. *Hindwing:* upperside dark brownish-black, costal and subapical region above vein Rs grey with scattered white scales, sometimes extending to subterminal region below vein Rs, sometimes a few scattered blue scales present in discal cell and subterminal region between veins M_1 and M_3, dorsum grey, terminal scale fringe black near ends of veins M_3, CuA_1, CuA_2 and 1A+2A, elsewhere black with white tips; underside similar to male. *Abdomen:* similar to male.

Variation. Males vary in several traits, including the hue or tone of the dorsal blue colouration, which ranges from dark cobalt-blue to dark purplish-blue; and the extent of the dorsal greyish central suffusion on the forewing, which is usually absent or rarely present as a very obscure patch; in one individual (5% of specimens examined, n = 22) (Fig. 14) it was far more extensive and overlaid with a few greyish-white scales, similar to that of *P. diana diana*. In females, the size of the dorsal white central patch on the forewing shows minor variation, and the white scales may occasionally extend distally into the subterminal area or below vein 1A+2A towards the dorsum; overall, the extent of the white patch varies from 20–35% as a proportion of the wing area. In addition, the extent of the dorsal white scales of the hindwing costa and apex is variable in females, and it may obscure the apex entirely or extend below vein M_1, as does the degree of blue scales between M_1 and M_3, which may be absent.

Remarks

Philiris diana was originally described by Waterhouse & Lyell (1914) based on 17 specimens (10♂, 7♀) from Kuranda, QLD, all collected by F. P. Dodd; however, they did not refer to a type of any sort. Peters (1971) referred to a "holotype" male (registration numbers AMS KL.21453 and K.191300) and an "allotype" female (AMS KL.21455 and K.584428) in the Australian Museum, Sydney. Edwards *et al.* (2001) regarded Peters' incorrect reference to a holotype



Figures 30–37. Life history and habitus of *Philiris diana fortuna* ssp. nov.: (*30, 31*) larva instar III, showing examples of variation in colour pattern, with lightly-marked and heavily-marked forms; (*32, 33*) larva instar VI, showing examples of variation in colour pattern, with yellow-brown striped and red-brown striped forms; (*34, 35*) pupa, showing examples of variation in colour pattern, with lightly marked and heavily marked forms; (*36*) adult female, newly-emerged at rest on foliage of *Litsea leefeana*; (*37*) adult pair in copula, with male on left and female on right.

as a valid lectotype designation. It therefore follows that the subsequent lectotype designations by both Parsons (1998) and Sands (2015) are invalid and thus do not constitute formal nomenclatural acts.

Of the type series in AMS, we have examined and identified the lectotype male (AMS K.191300) and 13 paralectotypes (7♂, 6♀). Waterhouse and Lyell (1914) illustrated two of their syntypes: the lectotype male on pl. 15, figs 270, 271, and a paralectotype female on pl. 13, fig. 183, each in black and white. The lectotype male (Figs 4, 5, 7) and paralectotype female (Figs 8, 9, 11) referred to by Peters (1971) and originally illustrated by Waterhouse and Lyell (1914) are both illustrated here for comparison with *P. diana fortuna*. The lectotype male is slightly unusual compared with the rest of the type series and other material we have examined in ANIC, NMV and SAMA in that it has a much broader black apical band on the forewing. Newly emerged adults of a male (Fig. 6) and a female (Fig. 10) of *P. diana diana* from the Cairns district reared by us are illustrated for comparison; they agree with Waterhouse and Lyell's concept of *diana* considering that the types are 115 years old.

Braby (2000) noted that *P. diana* had been recorded from the Atherton Tableland at Lake Eacham (760 m) based on an anomalous female in the ANIC that was collected at night from a light sheet (E. D. Edwards, pers. comm. 1998). Subsequently, Sands (2015, figs 7, 8) illustrated this specimen and noted that "Females of *P. diana* are very variable in the extent of white areas on the upperside of both wings…" (Sands, 2015, p. 222). However, close examination of this specimen confirms that it is *P. diana fortuna*. Further examination of museum material revealed another female, from Lake Tinaroo (750 m) in SAMA. Thus, the concept of the *P. diana diana* female needs to be reconsidered—females only show slight variation in the extent of the white patches on both wings.

Etymology

The subspecific epithet is derived from the Latin word *fortuna*, which means chance or luck. This name reflects the part played by luck in the discovery of this subspecies. The first specimen collected by us was a crippled male that could not fly which was found walking on the ground of a vehicle track through rainforest; the second specimen was a female captured whilst laying eggs on foliage of a rainforest tree, thereby enabling documentation of the early stages and confirmation of the larval foodplant.

Distribution and habitat

Philiris diana fortuna is currently known only from the Atherton Tableland in the Wet Tropics of northeastern Queensland. It has been recorded from Lake Tinaroo, Lake Eacham, Beatrice near Millaa Millaa and Millaa Millaa lookout at altitudes between 750–1,090 m asl. All sites occur in upland and montane tropical rainforest where the larval foodplant *Litsea leefeana* occurs as a medium-size tree reaching the rainforest canopy or along edges of smaller patches of rainforest regrowth. Within the known extent of occurrence, the foodplant is a relatively common component of regenerating rainforest following disturbance. All known occurrence records of *Philiris diana fortuna* are from vegetation communities growing on basalt soils.

Biology

The larval foodplant and morphology and colour pattern of the immature stages of *P. diana fortuna* (Figs 30–35) are fundamentally the same as those of *P. diana diana*. The only observable differences concern the ground colour of instar III, which is always green in *P. diana fortuna* but sometimes yellow in *P. diana diana*, and in the colour of the reddish dorsal blotches in the early instars, which are deep red-brown in *P. diana fortuna* but often pinkish in *P. diana diana*. The larvae of *P. diana fortuna* undergo six instars, like *P. diana diana* (Petrie & Hacobian, 2022) and *Philiris ziska titeus* D'Abrera, 1971 (Samson & Johnson, 2009). The pupae are usually more heavily striped in *P. diana diana*, although the degree of pale brown lateral bands or stripes on the wing case and abdomen is variable in *P. diana fortuna* and our samples of the former taxon are limited. In *P. diana fortuna*, the extent of red-brown blotching on segments T1-A2 is variable in larval instars II–IV, and the colour of the dorsal longitudinal band varies from yellow-brown to reddish-brown in instars V and VI.

Males have been observed perching on sunlit leaves during the early and late afternoon, between 1230–1400 h and again c. 1700 h AEST, in late March in the canopy of trees of the larval foodplant *Litsea leefeana* and other adjacent tree species at heights of 10–25 m above the ground. An adult female was observed, and subsequently captured, perched and basking on a leaf in the lower canopy of the foodplant growing in a small patch of regenerating rainforest approximately 5 m above ground level during the early afternoon (c. 1300 h). Another female was observed at a similar time (1320 h) being pursued by two or three males around sunlit foliage of *Flindersia brayleyana* F.Muell. growing adjacent to the foodplant. The female was subsequently found in copulation with one of the males (Figs 14, 37) settled on foliage c. 10 m above ground level close to the original pursuit. The pair was captured and remained in copulation for 35 mins until they finally separated at c. 1400 h.

Females (Fig. 36) have been observed ovipositing on dried skeletonized patches on the abaxial surface of mature leaves of the foodplant, as low as 1 m above ground level. Hatched eggs and larvae have been found in similar situations. Eggs were never found on soft new growth or juvenile leaves. Larvae were never observed to be attended by ants. However, pupae were noted to stridulate when exposed to strong light. A pupal exuvium was found on the abaxial surface of a partly eaten leaf, but no live pupae were located in the field. In captivity, all but one larva reared (n = 28) pupated on the abaxial surface of the leaf of the foodplant; the single exception pupated on the adaxial surface just above the junction with the petiole.

In terms of phenology and duration of the immature stages, the following developmental times were recorded in captivity during the wet season in December-March: egg 7–10 days; larva 51–82 days (instar I 6–7 days, instar II 6–8 days, instar III 7–9 days, instar IV 8–12 days, instar V 9–15 days, instar VI 15–31 days); pupa 10–14 days. Total developmental time from egg to adult varied from 2–3 months. Adults were collected from the field in November, December, March, and April. Some adults reared from eggs (laid by a captive female in early December) emerged in late February, and three adults reared under laboratory conditions

from larvae collected in April emerged in mid-July. One larva, collected from the field in early June, was reared under unheated conditions and pupated in late October. Thus, the broad flight period, as currently known, extends from November to April, with at least two generations completed annually.

Discussion

In their original description of *P. diana papuanus*, Wind & Clench (1947, p. 6) admitted that "there is more than a possibility that *papuanus* may be a species in its own right." Sixty-eight years later, Sands (2015) treated *P. papuanus* as a distinct species with two subspecies: *P. papuanus papuanus* Wind & Clench, 1947 from mainland New Guinea, and *P. papuanus kerri* Sands, 2015 from northern Australia. In our study, fundamental differences in the male genitalia observed between *P. diana* and *P. papuanus*, particularly the shape of the asymmetric valvae, confirm the two species hypothesis recently proposed by Sands (2015) for this set of taxa based mainly on adult phenotype. Tite (1963, p. 235) stated that "The male genitalia [*papuanus*] are basically the same as those of the nominate race [*diana*]", although his illustrations (figs 83–84, p. 238) clearly show differences in the morphology of apical spine of the left valva. Sands (2015) also drew attention to this character difference between *P. diana* and *P. papuanus*. Within *P. papuanus*, negligible differences were observed in the genitalia between *P. papuanus papuanus* and *P. papuanus kerri*, supporting the subspecific classification proposed by Sands (2015). *Philiris diana* and *P. papuanus* are also differentiated according to larval foodplant specialization and morphology of the immature stages (Wood, 1984; Parsons, 1998; Petrie & Hacobian, 2022). The larval foodplant of *P. diana* is *Litsea leefeana* (Petrie & Hacobian, 2022; this study), whereas for *P. papuanus* it is *L. breviumbellata* C. K. Allen in Australia (Valentine & Johnson, 1997) and *L. guppyi* F.Muell. ex Forman in Papua New Guinea (Parsons, 1998). Wood's (1984) reference to *L. leefeana* as the foodplant for both *P. papuanus* and *P. fulgens kurandae* Waterhouse, 1903 from Iron Range is erroneous and is actually *L. breviumbellata* (G. A. Wood, pers. comm. 2022). The known distribution of *L. leefeana* does not extend to Cape York Peninsula, its northern-most limit being Cooktown (AVH, 2022).

Within *P. diana*, there are considerable differences in the wing colour pattern elements and one morphological character (total of 8 characters) between the low to mid-altitude and the upland-montane populations; however, the male genitalia, larval foodplant and life history, including morphology of the immature stages, of *P. diana fortuna* are fundamentally the same as those of *P. diana diana*. The habitat preferences of adults of the two taxa also appear to be very similar based on our limited observations. Despite substantial differences in adult phenotype, lack of differentiation in other traits (morphology, ecology), as well as lack of reciprocal monophyly and negligible (< 0.3%) pairwise divergence in mitochondrial COI sequences between the two taxa, suggests subspecific classification is the most appropriate taxonomic rank for the montane population of *P. diana* according to the criteria of Braby *et al.* (2012). Limited rearing of the immature stages of each subspecies under different environmental conditions produced identical phenotypes for each respective subspecies (Tables 3, 4). Although further experimentation is needed to confirm this pattern, the results do suggest the distinct phenotype of each subspecies is under genetic control rather than environmental influences.

The Wet Tropics biome of northeastern Queensland, stretching from Cooktown to Townsville, is noted for its high level of species richness and endemism, including invertebrates (Yeates *et al.* 2002; Yeates & Monteith, 2008). The region is also exceptionally rich for butterflies (Kitching, 1981; Kitching & Dunn, 1999), with around 225 species or 57% of the butterfly fauna recorded from the Australian mainland (Braby, 2000). Braby & Müller (2014) also noted that the region was an important area of endemism for rainforest butterflies, with five species and 14 subspecies found nowhere else. At that time, *P. diana* was considered to be a polytypic species that included *P. papuanus* from mainland New Guinea and Cape York Peninsula. Following the taxonomic revision of Sands (2015), *P. diana* must now be considered a narrow-range endemic and thus one of a set of six butterfly species endemic to the Wet Tropics.

The discovery of *P. diana fortuna* further highlights the importance of the Wet Tropics as a biodiversity hotspot. This taxon appears to be restricted to the Atherton Tableland where it occurs in upland and montane forest between 750–1,090 m a.s.l. The Atherton Tableland has been identified as a key upland biogeographic unit (the Atherton Uplands subregion) noted for its high level of regional endemism (Nix, 1991; Williams *et al.*, 1996; Yeates *et al.*, 2002). By contrast, *P. diana diana* is mainly restricted to low to mid-altitudes in the coastal escarpment in the Cairns-Kuranda district between 50–500 m with an outlying record from the Paluma Range at c. 910 m in the Spec Uplands subregion (based on a female in ANIC labelled "4 miles W of Paluma, Q, 3000 ft, 15 Apr. 1969, I. F. B. Common & M. S. Upton"). We have not been able to trace the female specimen recorded from the Bluewater Range (Halifax Uplands) mentioned by Dunn & Dunn (1991). The northern-most occurrence of *P. diana fortuna* is Lake Tinaroo, whereas the southern-most occurrence of *P. diana diana* in the Cairns district is near Lake Morris 20–25 km NE of Lake Tinaroo. Thus, the two subspecies of *P. diana* appear to be allopatric, or possibly parapatric, separated by a minimum distance of only 20–25 km. Presumably, the ancestor of *P. diana fortuna* became isolated during past glacial cycles of the Pleistocene and its range contracted to montane rainforest refugia in the Atherton subregion (Nix, 1991) after which it differentiated allopatrically from *P. diana diana.* However, unlike a few other insects (Yeates & Monteith, 2002), its range has not expanded into adjacent upland subregions. Further sampling within the zone of allopatry is required to determine if the two taxa are indeed spatially separated. A study of the phylogeography of *P. diana* may help determine the extent of historical and contemporary gene flow between the two subspecies and elucidate the timing and process of differentiation.

Acknowledgements. We are grateful to Derek Smith and Natalie Tees (AMS), Simon Hinkley (NMV), Susan Wright (QM) and Ethan Beaver (SAMA) for provision of photographs and/or access to material in their care, and to Andreas Zwick for coordinating the mt DNA sequencing and analysis of our samples. Naomi Pierce (Museum of Comparative Zoology, Harvard University) and her colleagues kindly provided her unpublished data on the molecular phylogeny of *Philiris*. We thank Chris Müller and Rod Eastwood for critically reviewing the manuscript. Russell Mayo assisted with collection of larvae in the field, Juergen and Stella Freund assisted with photography of some of the paratypes and provided the image for Figure 14, and Patrick McDonnell provided photographs of the egg and first instar larvae of *P. diana fortuna* to facilitate detailed comparison with those of *P. diana diana*. Chris Müller provided much encouragement throughout the project and many helpful suggestions regarding tropical climate rearing techniques for early stages as well as comments relating to the biology of other species of *Philiris* occurring in Papua New Guinea.

References

AVH. 2022. *The Australasian Virtual Herbarium.* Council of Heads of Australasian Herbaria. [Accessed 27 July 2022.] https://avh.chah.org.au

Braby, M. F. 2000. *Butterflies of Australia. Their Identification, Biology, and Distribution*. Melbourne: CSIRO Publishing. xxvii+976 pp. https://doi.org/10.1071/9780643100770

Braby, M. F. 2016. *The Complete Field Guide to Butterflies of Australia. Second Edition*. Clayton South, Melbourne: CSIRO Publishing. xxi+384 pp. https://doi.org/10.1071/9781486301010

Braby, M. F., R. G. Eastwood, and N. Murray. 2012. The subspecies concept in butterflies: has its application in taxonomy and conservation biology outlived its usefulness? *Biological Journal of the Linnean Society* 106: 699–716. https://doi.org/10.1111/j.1095-8312.2012.01909.x

Braby, M. F., and C. J. Müller. 2014. Taxonomy of the genus *Udara* (Lepidoptera: Lycaenidae) in New Caledonia and the Wet Tropics of Australia, with a review of butterfly endemism in these regions. *Austral Entomology* 53: 89–98. https://doi.org/10.1111/aen.12051

Common, I. F. B., and D. F. Waterhouse. 1981. *Butterflies of Australia. Revised Edition*. Sydney: Angus and Robertson. xiv+682 pp.

Dobbs, E. M. 2011. *SketchAndCalc*. [Accessed May 2022.] https://www.sketchandcalc.com

Dunn, K. L., and L. E. Dunn. 1991. *Review of Australian Butterflies: Distribution, Life History and Taxonomy. Parts 1–4*. Published by authors: Melbourne. 660 pp.

Edwards, E. D., J. Newland, and L. Regan. 2001. *Lepidoptera: Hesperioidea, Papilionoidea. Zoological Catalogue of Australia. Vol. 31.6*. Collingwood, Melbourne: CSIRO Publishing. x+615 pp.

Eliot, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bulletin of the British Museum (Natural History) Entomology* 28: 371–505. https://doi.org/10.5962/bhl.part.11171

Hebert, P. D. N., A. Cywinska, S. L. Ball, and J. R. deWaard. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society B* 270: 313–321. https://doi.org/10.1098/rspb.2002.2218

Hebert, P. D. N., S. Ratnasingham, and J. R. deWaard. 2003. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society B (Supplement)* 270: S96–S99. https://doi.org/10.1098/rsbl.2003.0025

Kitching, R. L. 1981. The geography of the Australian Papilionoidea. In *Ecological Biogeography of Australia,* ed. A. Keast, pp. 978–1005. The Hague: Dr W. Junk bv Publishers. https://doi.org/10.1007/978-94-009-8629-9_34

Kitching, R. L., and K. L. Dunn. 1999. The biogeography of Australian butterflies. In *Biology of Australian Butterflies. Monographs of Australian Lepidoptera. Volume 6,* ed. R. L. Kitching, R. E. Jones, E. Scheermeyer, and N. E. Pierce, pp. 53–74. Collingwood, Melbourne: CSIRO Publishing. https://doi.org/10.1071/9780643105140

Klots, A. B. 1970. Lepidoptera. In *Taxonomist's Glossary of Genitalia in Insects. Second Edition,* ed. S. L. Tuxen, pp. 115–130. Copenhagen; Munksgaard.

Monteith, G. B., and D. L. Hancock. 1977. Range extensions and notable records for butterflies of Cape York Peninsula, Australia. *Australian Entomological Magazine* 4: 21–38.

Müller, C. J. 2014. Six new species of *Philiris* Röber, 1891 (Lepidoptera, Lycaenidae) from Papua New Guinea. *ZooKeys* 395: 33–55. https://doi.org/10.3897/zookeys.395.7110

Nix, H. A. 1991. Biogeography: pattern and process. In: *Rainforest Animals: Atlas of Vertebrates Endemic to Australia's Wet Tropics,* ed. H. A. Nix and M. A. Switzer, pp. 11–40. Canberra: Australian National Parks and Wildlife.

Parsons, M. J. 1998. *The Butterflies of Papua New Guinea. Their Systematics and Biology*. London: Academic Press. xvi+736 pp.

Peters, J. V. 1971. *A catalogue of the type specimens of the Hesperioidea and Papilionoidea (Lepidoptera) in the Australian Museum*. N.S.W.: Australian Entomological Press. 36 pp.

Petrie, E. A., and B. S. Hacobian. 2022. Notes on the life history of the Large Moonbeam *Philiris diana* Waterhouse and Lyell, 1914 (Lepidoptera: Lycaenidae), including confirmation of its native larval foodplant. *Australian Entomologist* 49:137–143

Ratnasingham, S., and P. D. N. Hebert. 2007. BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes* 7: 355–364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Samson, P. R., and S. J. Johnson. 2009. The life history and adult morphology of *Philiris ziska titeus* D'Abrera (Lepidoptera: Lycaenidae). *Australian Entomologist* 36: 113–118.

Sands, D. P. A. 1979. New species of *Philiris* Röber (Lepidoptera: Lycaenidae) from Papua New Guinea. *Australian Journal of Entomology* 18: 127–133. https://doi.org/10.1111/j.1440-6055.1979.tb00824.x

Sands, D. P. A. 1981a. New species of *Philiris* Röber (Lepidoptera: Lycaenidae) from mainland New Guinea. *Journal of the Australian Entomological Society* 20: 89–96. https://doi.org/10.1111/j.1440-6055.1981.tb01006.x

Sands, D. P. A. 1981b. *The Ecology, Biogeography and Systematics of the Tribe Luciini*. Unpublished PhD Thesis. Brisbane: University of Queensland.

Sands, D. P. A. 2015. Review of Australian *Philiris* Röber (Lepidoptera: Lycaenidae), with notes on variation and description of two new subspecies from Cape York Peninsula. *Australian Entomologist* 42: 219–252.

Su, Y. N. 2016. A simple and quick method of displaying liquid-preserved morphological structures for microphotography. *Zootaxa* 4208: 592–593. https://doi.org/10.11646/zootaxa.4208.6.6

Tennent, W. J. 2016. Resolution of Parsons' "*Philiris* species a" from Papua New Guinea (Lepidoptera, Lycaenidae). *Nachrichten des Entomologischen Vereins Apollo* 37: 141–144.

Tite, G. E. 1963. A revision of the genus *Candalides* and allied genera (Lepidoptera: Lycaenidae). *Bulletin of the British Museum (Natural History), Entomology* 14: 197–259. https://doi.org/10.5962/bhl.part.8782

Valentine, P. S., and S. J. Johnson. 1997. Ecological observations and notes on the life history of *Philiris diana papuana* Wind & Clench (Lepidoptera: Lycaenidae). *Australian Entomologist* 24: 35–36.

Waterhouse, G. A., and G. Lyell. 1914. *The Butterflies of Australia. A Monograph of the Australian Rhopalocera*. Sydney: Angus and Robertson. vi+239 pp.

Williams, S. E., R. G. Pearson, and P. J. Walsh. 1996. Distributions and biodiversity of the terrestrial vertebrates of Australia's Wet Tropics: a review of current knowledge. *Pacific Conservation Biology* 2: 327–362.
https://doi.org/10.1071/PC960327

Wind, R. G., and H. K. Clench. 1947. New Indo-Australian Lycaenidae (Lepidoptera). *Bulletin of the Brooklyn Entomological Society* 42: 1–16.

Wood, G. A. 1984. The early stages of *Philiris fulgens kurandae* Waterhouse and *Philiris diana papuana* Wind and Clench. *Australian Entomological Magazine.* 10: 11–12.

Yeates, D. K., P. Bouchard, and G. B. Monteith. 2002. Patterns and levels of endemism in the Australian Wet Tropics rainforest: evidence from flightless insects. *Invertebrate Systematics* 16: 605–619.
https://doi.org/10.1071/IT01032

Yeates, D. K., and G. B. Monteith. 2008. The invertebrate fauna of the Wet Tropics: diversity, endemism and relationships. In *Living in a Dynamic Tropical Forest Landscape,* ed. N. E. Stork and S. M. Turton, pp. 178–191. Oxford, UK: Blackwell Publishing.
https://doi.org/10.1002/9781444300321.ch13

Zhou, Y.-L., J. A. Nicholls, Z.-H. Liu, D. Hartley, A. Szito, A. Ślipiński, and A. Zwick. 2022. Molecular phylogeny of Dermestidae (Coleoptera) reveals the polyphyletic nature of *Trogoderma* Latreille and the taxonomic placement of the khapra beetle *Trogoderma granarium* Everts. *Insect Systematics and Diversity* 6(6): 1–24.
https://doi.org/10.1093/isd/ixac026

Bartholomew S. Hacobian https://zoobank.org/urn:lsid:zoobank.org:author:8161CF47-76AC-4A51-8272-8BC8668E2739
Michael F. Braby https://zoobank.org/urn:lsid:zoobank.org:author:4D3A7605-EBD0-40F6-A5F2-7F67F59E3D60
Edward A. Petrie https://zoobank.org/urn:lsid:zoobank.org:author:CB5CAC21-FA74-4048-A83B-FAC541788DBF