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Trogonoptera brookiana mollumar d'Abrera, Doggett & Parker, 1976 (Lepidoptera: Papilionidae), a subspecies or a synonym?

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Abstract. The birdwing butterfly *Trogonoptera brookiana* (Wallace, 1855) is a well-known conservation icon, yet questions remain about the infraspecific status of regional populations. The eastern Peninsular Malaysian population has been described as the subspecies *mollumar* d'Abrera, Doggett & Parker, 1976, but its status as a subspecies distinguishable from the taxon *trogon* (Vollenhoven, 1860) in Sumatra has been disputed. Wing characters and measurements of specimens from the two regions were therefore examined quantitatively using discriminant function and correspondence analyses. Eastern Peninsular specimens differ on average from Sumatran specimens in having more extensive green, especially in the female. This is reflected in many of the measurements and characters analysed. Females from the Peninsula also have a characteristically blacker upperside ground colour in which the outer areas of both wings barely contrast with the black veins and forewing cell. The extent of these differences enables a reliable differentiation of the females of both regions. The magnitude and consistency of differences are comparable to that between other subspecies of undisputed status. Behavioural differences also exist. The name *mollumar* therefore merits subspecific status. In addition, we consider the male forms *walshi* Haugum & Low, 1982 and *walshoides* Haugum & Low, 1982 to be chemically discoloured specimens of *trogon* rather than biological forms.

Keywords. *Trogonoptera brookiana trogon*, Peninsular Malaysia, Sumatra, taxonomy, morphometrics.

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Introduction

Trogonoptera brookiana (Wallace, 1855) is a large birdwing butterfly that ranges from Sumatra through the Riau Archipelago and Peninsular Malaysia to Borneo. A related species, *T. trojana* (Staudinger, 1889), which is sometimes considered a subspecies of *T. brookiana*, occurs further east on the island of Palawan. *Trogonoptera brookiana* exhibits morphological variation across its range, usually in the female sex, and as a result several subspecies have been described. The males of some of these subspecies puddle, sometimes in large monospecific aggregations along forest streams and rivers (Tsukada & Nishiyama 1982; Panchen 1980), making them very conspicuous and easy to observe. The birdwing is therefore very iconic, featuring on stamps, artwork and promotional material for tourism. It is also the subject of ecotourism in some forest areas (Phon *et al.* 2011).

The birdwing is also a species of conservation importance that is listed under CITES Appendix II (CITES 2017). It faces ongoing loss and degradation of its forest habitat (Phon *et al.* 2011) and is sought after by commercial dealers (Kirton 1991; Phon & Kirton 2009). Peninsular Malaysia is unusual in having two subspecies that occur in different habitats. The better-known subspecies, *T. b. albescens* (Rothschild, 1895), occurs on the central west of the Titiwangsa Mountain Range in the Peninsula, and a lesser-known subspecies named *T. b. mollumar* d’Abrera, Doggett & Parker, 1976 occurs on the north-central and southern plains of the east (Tsukada & Nishiyama 1982; Corbet & Pendlebury 1992; Kirton 2014; Fig. 1) where forest is under great pressure from land conversion to agriculture. The iconic character of this birdwing, however, gives it the potential to be a flagship species for conservation of the habitats in which it occurs.

Despite being a well-known and iconic species of conservation importance, there remain questions about the taxonomy of the birdwing’s geographically separate populations, particularly the subspecific status of the eastern Peninsular Malaysian population. This population, which occurs from eastern Johor to southernmost Pahang and more rarely from central to southern Terengganu, does not appear to interbreed with the subspecies *albescens* on the western side of the central mountain range (Fig. 1). It was originally regarded by Corbet & Pendlebury (1956) as subspecies *trogon* (Vollenhoven, 1860), the subspecies described from Sumatra (Fig. 1), but was later described as a new subspecies, *mollumar* d’Abrera, Doggett & Parker, 1976. However, Haugum & Low (1982) disputed the reliability of the characters used and the subspecific status of *mollumar*, treating it only as a locality form of *trogon* without formally synonymising it. Subsequently, Eliot in Corbet & Pendlebury (1992), synonymised *mollumar* with *trogon*, probably based on Haugum and Low’s views. Despite this, Matsuka (2001) and Ohya (in Matsuka 2001) retained usage of *mollumar* as a subspecies. In response to Haugum & Low (1982), d’Abrera (2003) argued against synonymy and formally reinstated *mollumar* as a subspecific taxon.

d’Abrera *et al.* (1976) used seven characters on the wings of males and three on the wings of females to differentiate between *mollumar* and *trogon*, in addition to differences in the male genitalia. These characters are as follows:

- 1) a more extensive green discal area on the hindwing upperside in male *mollumar*, extending more than halfway from the base of the hindwing to the dorsum;
- 2) a noticeably convex distal margin of the green disc on the hindwing upperside in male *mollumar*, which is either straight or concave in male *trogon*;
- 3) green suffused scaling just above vein 7 on the hindwing upperside in male *mollumar*, which is usually absent or weakly developed in male *trogon*;
- 4) a more bowed hindwing vein 8 close to the costa in male *mollumar*;
- 5) a less bowed hindwing vein 7 along its length in male *mollumar*;
- 6) a hindwing apex that is more sharply angled away from the costa in male *mollumar*;

- 7) the absence of a scallop or incurved margin at the end of the hindwing costa between veins 7 and 8 in male *mollumar*, which is present in male *trogon*;
- 8) a more extensive green discal area on the hindwing upperside in female *mollumar*, covering more than half of the area of the hindwing;
- 9) a better developed whitish sub-apical area on the forewing upperside in female *mollumar*;
- 10) better developed white sub-marginal spots on the hindwing upperside in female *mollumar*.

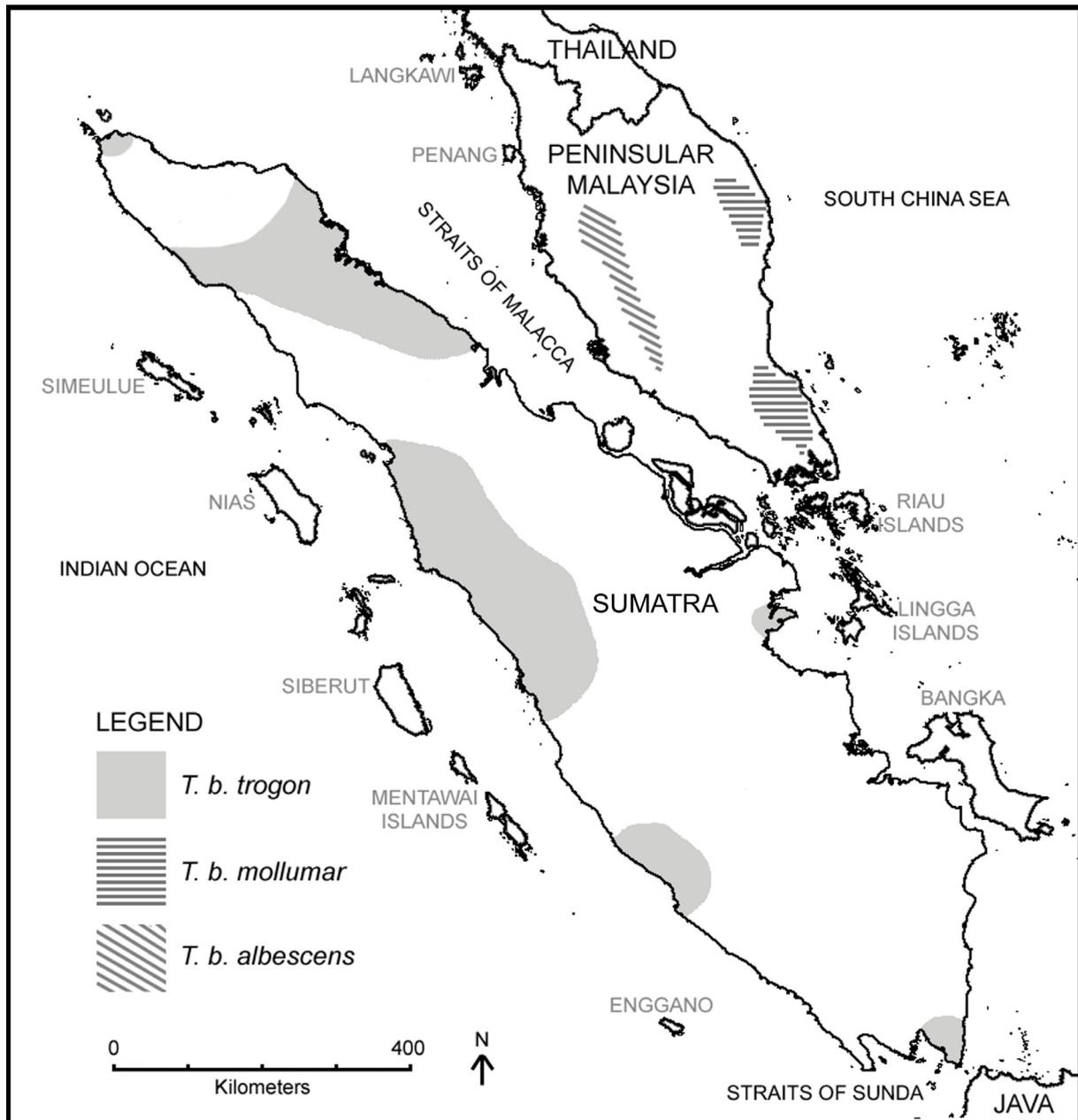


Fig. 1. Distribution map of *Trogonoptera brookiana* (Wallace, 1855) subspecies *albescens* (Rothschild, 1895), *mollumar* d'Abrera, Doggett & Parker, 1976 and *trogon* (Vollenhoven, 1860). Ranges are based on localities given in specimen labels and the literature, where georeferencing was possible.

Haugum & Low (1982) disagreed with almost all the differences described by d’Abrera *et al.* (1976). They concluded that the males do not differ and that the females are almost indistinguishable, but likely to have a darker ground colour and an extended green discal area on the hindwing. They stated that the characters described for *mollumar* could also be found in some specimens of *trogon*, and that d’Abrera *et al.* (1976) may have examined too few specimens of *trogon* to make a valid comparison. Haugum and Low’s sample size is difficult to determine accurately because the number of specimens that was stated as examined in the text differs somewhat from the number listed in their section on material examined. Assuming the latter is more reliable, they examined 212 Sumatran males, only 10 Sumatran females, and very few specimens of either sex from Peninsular Malaysia (3 males and 4 females). The number of specimens examined by d’Abrera *et al.* (1976) was not stated.

Previous attempts to diagnose character differences between the subspecies *trogon* and the nominal taxon *mollumar* have been limited by inadequate examples of females of *trogon* and both sexes of *mollumar* (d’Abrera *et al.* 1976; Haugum & Low 1982). In addition, the characters used are sometimes difficult to apply objectively because they are based on wing or vein shape and the extent and size of wing markings, which require subjective judgement. In this study, we examine wing characters quantitatively using measurements, ratios and scores for males and females from Sumatra and the Peninsula. The sample represents the largest number of females from Sumatra and of both sexes from the Peninsula examined thus far. We analyse to what extent the populations differ from each other in the male and female, and whether there are characters that consistently or almost always differentiate them. Based on the analysis, we discuss whether the nominal taxon *mollumar* merits subspecific status.

Recognising and defining subspecies is important because it provides names to distinct populations that have their own morphological and genetic characteristics. These names provide greater awareness of the need for conservation of such populations.

Material and methods

We examined specimens and photographs of 188 males and 17 females from Sumatra, and 22 males and 18 females from Johor, southeastern Pahang and Terengganu in Peninsular Malaysia. Specimens examined were from the following collections:

Chong-Arshad	=	The joint private collection of Chow-Yang Chong and Sabri John Arshad
FRIM	=	Entomological Reference Collection of the Forest Research Institute Malaysia, Kepong, Malaysia
Kirton	=	The joint private collection of Eric, Colin and Laurence Kirton
MCZ	=	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MZB	=	Museum Zoologicum Bogoriense, Cibinong, Indonesia
MZUM	=	Museum of Zoology in the University of Malaya, Kuala Lumpur, Malaysia
NHMUK	=	Natural History Museum (formerly British Museum of Natural History, BMNH), London, UK
RMNH	=	Naturalis Biodiversity Center, Leiden, the Netherlands (comprising collections from the Rijksmuseum van Natuurlijke Historie and the Zoological Museum Amsterdam or ZMA)
ZRC	=	Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore

Specimens from MCZ, MZB, ZRC, Chong-Arshad and Kirton were examined only in photographs. Several unlabelled specimens, a few damaged specimens and a small bred female were excluded. A few other bred individuals of normal size were included. A specimen in RMNH (ZMA) that is almost

certainly from Borneo (subsp. *brookiana*) but labelled as being from Sumatra (Sumatra, Oost Kust, coll. v. d. Bergh, 1905) was also excluded.

Wing pattern morphology was chosen for analysis for practical as well as technical reasons. Differences in the genitalia disputed by Haugum & Low (1982) and d'Abrera (2003) are irrelevant when small numbers of specimens are dissected, because subspecies do not differ greatly in structural characteristics, and the slight differences that might occur are likely to be obscured by individual variation. Sampling enough tissue for a molecular analysis of *T. brookiana* presents legal difficulties, since it is a protected species in both Indonesia and Malaysia, and poses technical challenges because sampling would ideally need to be done non-destructively. Furthermore, in many insect groups percentage differences between DNA sequences do not necessarily predict even species boundaries (Cognato 2006). Studies on Asian Papilioninae (Tsao & Yeh 2008) show that COI sequence divergences between subspecies are generally very slight, and yet the divergence among subspecies of several species was greater than the average divergence between all species.

A selection of wing characters mentioned by d'Abrera *et al.* (1976) was quantified, that is nos 1–3 and 8 listed above. These characters demonstrate the relative size and extent of the green disc on the hindwing in both sexes (Figs 2A, C, 3A) and its shape in the male (Fig. 3A–E). Other characters mentioned by d'Abrera *et al.* (1976), that is characters nos 4–7, 9–10 (see above), were omitted because we could not observe sufficient consistency in these characters to be useful. Forewing length of the male and the ground colour of the female (Fig. 2A, C) – characters mentioned by Haugum & Low (1982) – were also investigated. Haugum & Low (1982) stated that the forewing length of males of *mollumar* fell within the norm of *trogon*, but the non-overlapping ranges they reported contradicted this statement and instead showed the former as being larger. We included two other characters of our own that demonstrate the distal extent of green scaling on the forewing of the female (Fig. 2A–B, D–H). In addition, we quantified characters suggested by C.Y. Chong at a later stage of our study, which demonstrate the extent and location of the green arrow-shaped markings in relation to the dark ground colour of the forewing (Figs 2A, C, 3A). Complete measurement data was available for 13 females and 16 males of each taxon, the sample size of taxa deliberately equalised within sexes to eliminate any bias in the multivariate analysis of numeric data. The specimens were a random subsample without bias to any wing character. Analysis of categorical data was based on a larger data set.

The characters used are defined in Table 1 and are illustrated in Figures 2 and 3. Measurements and scores were generally based on the side right of the specimens and made with a ruler, for physical specimens, or with image analysis software, for specimens photographed against a ruler. The left side was used when damage to the wings on the right side precluded its use. The different methods of measurement are not expected to introduce significant inaccuracies or biases, as the birdwings were large, making differences between individuals relatively large in comparison to the very small differences that may result from the different methods. Ground colour was judged in contrast with the basal half of the forewing cell, which was always virtually black. In this way, a bias due to scale pigment fade as a result of differing specimen ages and differing levels of light exposure was avoided. Fade occurs uniformly across the whole specimen, and the contrast in ground colour could still be seen in relation to each specimen's forewing cell base.

Ratios calculated from the measurement data were analysed by discriminant function analysis to determine the relative strength of the different characters in separating the Sumatran and Peninsular Malaysian populations of each sex. Forewing length was analysed separately using a Mann-Whitney test, since its inclusion in discriminant function analysis resulted in a deviation from multivariate normality and homogeneity of the variance-covariance matrices even after data transformation.

Table 1 (continued on next page). Character descriptions. Numerators, denominators and scores for categorical data (numerals in parentheses) are illustrated in Figs 1–2.

No.	Character abbreviation	Sex	Character	Calculation or categorisation
1.	FwL	♂ ♀	Forewing length (cm) measured on the underside from the base of the forewing costa to the distalmost margin of the apex.	ab
2.	UpHwSp5GrRatio	♂ ♀	On the hindwing upperside, a ratio formed by the distance to which the green scaling in space 5 reaches at its distal end (d) on a straight line between the base of the cell (c) and the end of vein 6 (e), divided by the entire length of the straight line.	cd / ce
3.	UpHwSp4GrRatio	♂ ♀	On the hindwing upperside, a ratio formed by the distance to which the green scaling in space 4 reaches at its distal end (g) on a straight line between the base of vein 5 (f) and the end of vein 5 (h), divided by the entire length of the straight line.	fg / fh
4.	UpHwSp2GrRatio	♂ ♀	On the hindwing upperside, a ratio formed by the distance to which the green scaling in space 2 reaches at its distal end (i) on a straight line between the base of the cell (c) and the end of vein 3 (j), divided by the entire length of the straight line.	ci / cj
5.	UpFwV2GrRatio	♂ ♀	On the upperside forewing, on a straight line intersecting the forewing costa (k), the inner (l) and outer (m) edges of the green marking along vein 2, and the termen (n), a ratio formed by the length of the green scaling (lm) divided by the distance between its inner edge and the termen (ln).	lm / ln
6.	UpFwV2BIRatio	♂ ♀	On the same straight line defined above for UpFwV2GrRatio, a ratio formed by the width of the black area between the costa and the inner edge of the green marking (kl) divided by the width of the wing from costa to termen (kn).	kl / kn
7.	UpFwV4GrRatio	♂ ♀	A ratio similar to UpFwV2GrRatio on the forewing upperside but along vein 4.	pq / pr

Table 1 (continued). Character descriptions. Numerators, denominators and scores for categorical data (numerals in parentheses) are illustrated in Figs 1–2.

No.	Character abbreviation	Sex	Character	Calculation or categorisation
8.	UpFwV4BlRatio	♂ ♀	A ratio similar to UpFwV2BlRatio on the forewing upperside but along vein 4.	op / or
9.	GColour	♀	On the upperside of both wings, the ground colour of the dark distal areas, in comparison to the black basal half of the forewing cell.	(1) Brown, or (2) black (as black or nearly as black as the cell)
10.	UpFwV7Gr	♀	On the forewing upperside, the density of postdiscal green scales just below vein 7.	(1) None, (2) sparse, or (3) dense
11.	UnFwSp4Gr	♀	On the forewing underside, the density and extent of discal green scales in space 4.	(1) None, (2) sparse, or forming a (3) broken patch or (4) dense patch
12.	UpHwGrDisc	♂	On the hindwing upperside, the shape of the distal margin of the green disc.	(0) Indented, (1) straight, (2) convex
13.	UpHwSp7Gr	♂	On the hindwing upperside, the density of discal green scales in space 7 just above vein 7.	(0) None, (2) sparse, or (3) dense

Characters in nos 2, 3, 4, 12 and 13 are quantified from d'Abrera *et al.* 1976. Characters in nos 1 and 9 are quantified from Haugum & Low 1982. Characters in nos 5, 6, 7 and 8 are suggested by C.Y. Chong. The present authors suggested characters in nos 10 and 11.

Simple correspondence analysis was used for the categorical characters of each sex, to explore their association with each other and with the Sumatran and Peninsular Malaysian populations. For characters that formed stronger species associations in the correspondence analysis, chi-square tests were used to determine whether they were significant, with the significance level taken as the normal α value of 0.05 divided by the number of tests (Bonferroni correction). Discriminant function analysis was conducted using SPSS® 20.0.0. All other analyses were conducted using Minitab® 18.1.

Results

Analyses of characters

Females

There is no significant difference in median forewing length of females (Mann-Whitney $W = 188.0$, $P = 0.537$), which measure 8.00 cm (range 7.40–8.80 cm) and 7.85 cm (7.30–8.70 cm) respectively in Peninsular and Sumatran females that we examined. A summary of the ratio data for female birdwings from Sumatra and Peninsular Malaysia is shown in Table 2. Peninsular females have on average more extensive green scaling relative to black ground colour on both the forewing and hindwing, compared to

Sumatran females (Figs 2A, C, 4A–B). The ranges of the ratios of green on the forewing do not overlap between populations, but they overlap on the hindwing, as do the ratios of black.

Using discriminant function analysis with cross-validation, the resulting canonical discriminant function has an eigenvalue of 4.205 and a high canonical correlation of 0.899 and is significant (Wilk's Lambda = 0.192, $\chi^2 = 33.819$, $df = 7$, $P < 0.001$). The standardised canonical discriminant function was used to examine the relative strength of each character (Table 3). Cross-validation results in 88.5% of the specimens being classified correctly to their original geographic regions by the classification functions for the Peninsular and Sumatran specimens (Table 3). The group centroid from the unstandardised coefficients (Table 3) is positive and negative 1.970 for Peninsular and Sumatran females, respectively. Tests of equality of group means in the discriminant function analysis reveal four out of seven characters that differ significantly between populations (Table 2). Of these, the extent of green in space 4 of the

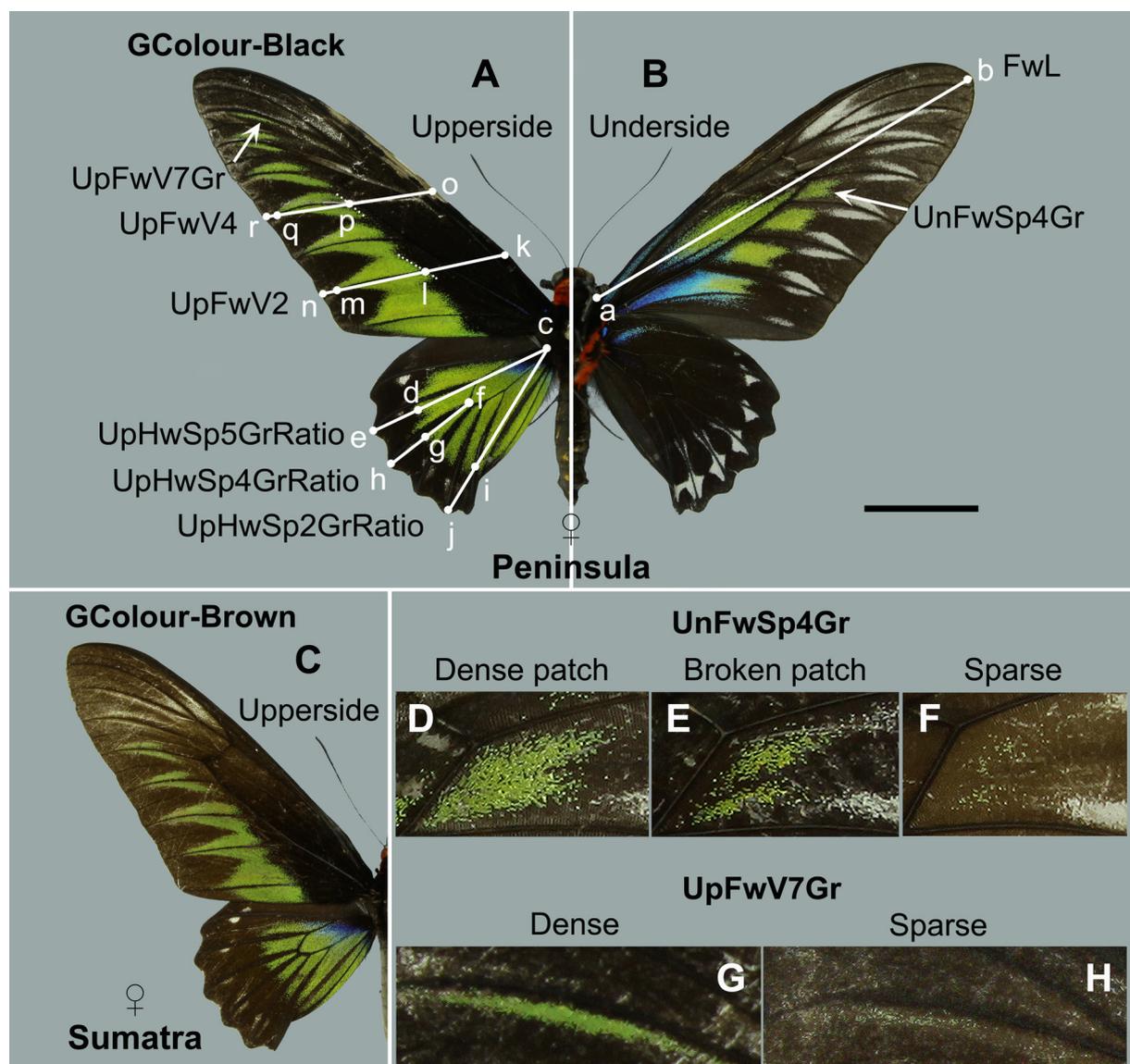


Fig. 2. Illustrations of measurements used for both sexes, and categorical characters used for females. Scale bar: A–C = 2.00 cm. See Table 1 for descriptions.

hindwing upperside (UpHwSp4GrRatio) and along vein 2 of the forewing upperside (UpFwV2GrRatio) have the greatest coefficients in the standardised canonical discriminant function and thus the greatest discriminatory impact between the two populations (Table 3). The extent of green and black along vein 4 of the forewing upperside (UpFwV4GrRatio and UpFwV4BIRatio, respectively) has a lower discriminatory impact in the standardised canonical discriminant function (Table 3) but is significantly different between populations (Table 2).

Table 4 summarises the data for the categorical characters of females, and Figure 5 shows a two-dimensional plot of the first two components of simple correspondence analysis. Sumatran and Peninsular specimens are distributed on opposite ends of the two-dimensional plot, primarily because of the first component. Sumatran specimens are strongly associated with a brown ground colour (GColour_Brown; Figs 2C, 4B), less green scaling in space 4 of the forewing underside (UnFwSp4Gr_None or Sparse; Fig. 2F), and less green scaling just below vein 7 on the forewing upperside (UpFwV7Gr_None or Sparse; Figs 2C, H, 4B). Peninsular specimens are strongly associated with a black ground colour (GColour_Black; Figs 2A, 4A), a dense and complete or broken patch of green scales in space 4 of the forewing underside (UnFwSp4Gr_BrokenPatch or DensePatch; Fig. 2B, D–E), and dense green scaling just below vein 7 on the forewing upperside (UpFwV7Gr_Dense; Figs 2A, G, 4A). There is more scatter in the characters on the Sumatran end of the biplot (Fig. 5). Except for one Sumatran female, the difference in ground colour is sufficiently distinct in the two populations (Table 4). Among females from Sumatra, 94% are categorised as brown (Figs 2C, 4B), while all Peninsular Malaysian females are categorised as black (Figs 2A, 4A). Differences between the ground colour, the green scaling below vein 7 on the forewing upperside and in space 4 on the forewing underside are significant (Chi square test, Table 4). Dense green scaling below vein 7 occurs in 89% of the Peninsular females compared to 29% of the Sumatran females. All Peninsular females examined have a dense or broken patch of green scales in

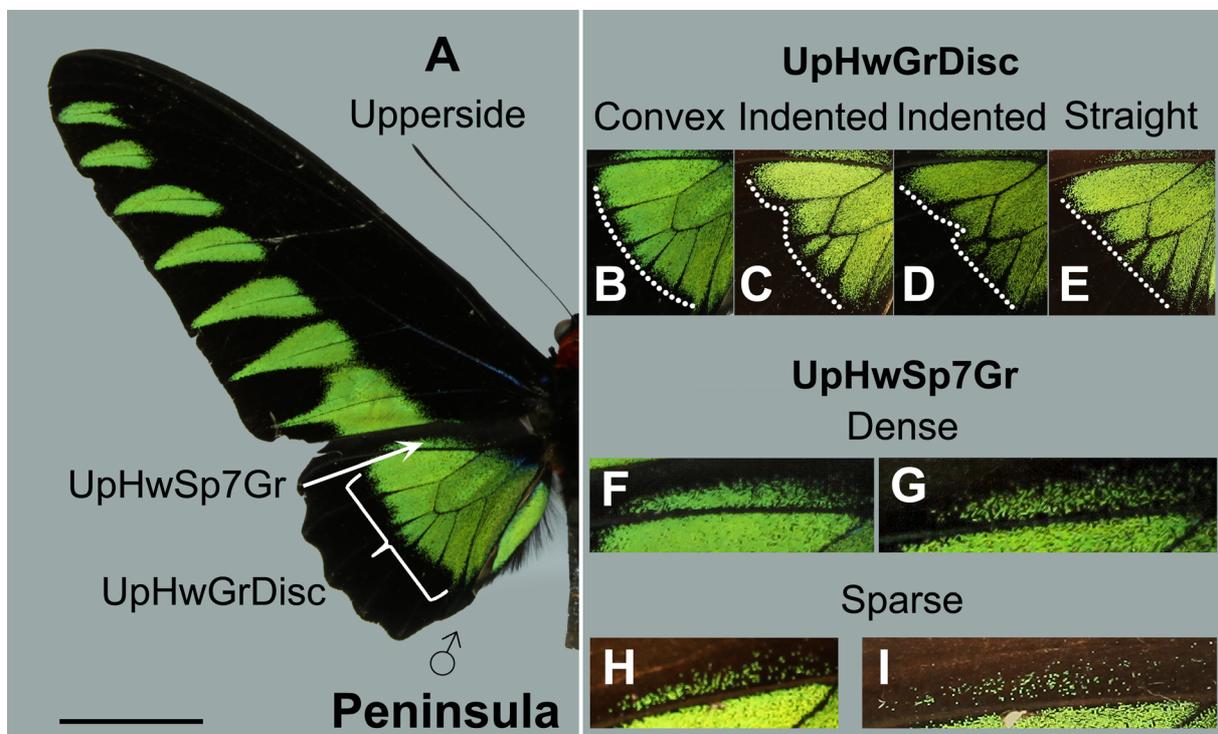


Fig. 3. Illustrations of categorical characters in males. Scale bar = 2.00 cm. See Table 1 for descriptions.

Table 2. Ratio characters for Sumatran and Peninsular Malaysian females (mean \pm standard error, and range).

Character abbreviation	Sumatra	Peninsular Malaysia	F _{1,24}	P
UpHwSp4GrRatio *	0.43 \pm 0.02 (0.35–0.55)	0.52 \pm 0.01 (0.45–0.62)	18.565	< 0.001
UpHwSp2GrRatio	0.71 \pm 0.01 (0.64–0.81)	0.71 \pm 0.02 (0.59–0.78)	0.027	0.870
UpHwSp5GrRatio	0.67 \pm 0.01 (0.56–0.75)	0.71 \pm 0.01 (0.58–0.78)	3.913	0.060
UpFwV2GrRatio *	0.84 \pm 0.01 (0.80–0.87)	0.90 \pm 0.00 (0.88–0.92)	47.225	< 0.001
UpFwV2BIRatio	0.44 \pm 0.01 (0.41–0.48)	0.42 \pm 0.01 (0.36–0.45)	5.354	0.030
UpFwV4GrRatio *	0.80 \pm 0.01 (0.69–0.85)	0.89 \pm 0.00 (0.86–0.91)	39.077	< 0.001
UpFwV4BIRatio *	0.52 \pm 0.01 (0.45–0.56)	0.48 \pm 0.01 (0.44–0.51)	12.864	0.001

N = 13 each from Sumatra and Peninsular Malaysia. * Significantly different between regions at $\alpha = 0.007$ (Bonferroni correction).

Table 3. Coefficients and constants for each ratio character in the cross-validated canonical discriminant and classification functions of female birdwings from Sumatra and Peninsular Malaysia.

Characters	Canonical discriminant function		Classification function	
	Standardised	Unstandardised	Peninsular	Sumatran
Constant		-34.681	-1923.349	-1786.687
UpHwSp4GrRatio	0.757	13.282	121.231	68.893
UpFwV2GrRatio	0.670	29.477	1824.531	1708.376
UpHwSp2GrRatio	-0.376	-6.457	165.830	191.273
UpFwV4GrRatio	0.319	9.201	719.110	682.854
UpFwV2BIRatio	0.231	9.404	593.061	556.004
UpFwV4BIRatio	-0.212	-7.507	1336.465	1366.045
UpHwSp5GrRatio	0.050	-1.008	697.522	701.493

Table 4. Numbers and percentages (in parentheses) of females from Sumatra and Peninsular Malaysia with each categorical character.

Region	Characters (abbreviated) and categories								
	GColour ‡		UpFwV7Gr #			UnFwSp4Gr *			
	Brown	Black	None	Sparse	Dense	None	Sparse	Broken patch	One dense patch
Sumatra	16 (94.12)	1 (5.88)	4 (23.53)	8 (47.06)	5 (29.41)	3 (17.65)	12 (70.59)	2 (11.76)	0 (0.00)
Peninsular Malaysia	0 (0.00)	18 (100.00)	0 (0.00)	2 (11.11)	16 (88.89)	0 (0.00)	0 (0.00)	15 (83.33)	3 (16.67)

N = 17 (Sumatra) and 18 (Peninsular Malaysia). $\alpha = 0.017$ after Bonferroni correction. ‡Chi Square = 31.207, df = 1, $p < 0.001$. #Chi Square = 13.344, df = 2, $p = 0.001$. *Chi Square = 27.935, df = 3, $p < 0.001$.

space 4 of the forewing underside (Fig. 2B, D–E), whereas only 12% of Sumatran females have broken patches (Fig. 2E), 71% have sparse scaling (Fig. 2F) and 18% have none.

Males

Peninsular and Sumatran males examined have significantly different median forewing lengths of 8.05 cm (range 6.80–8.40 cm) and 7.38 cm (range 6.45–7.80 cm), respectively (Mann-Whitney $W = 354.50$, $P < 0.001$). Table 5 summarises the ratio data for male birdwings from the Peninsula and Sumatra. On average, Peninsular males have more green scaling on both the forewing and hindwing (Figs 3A, 4C), although overlapping ranges occur in all characters.

The cross-validated discriminant function is significant (Wilk's Lambda = 0.266, $\chi^2 = 35.112$, df = 7, $P < 0.001$) with an eigenvalue of 2.762 and canonical correlation value of 0.857. The group centroid for Peninsular and Sumatran males is positive and negative 1.609, respectively, in the unstandardised canonical discriminant function (Table 6). In the cross-validation, 87.5% of specimens are classified to their correct region by the classification functions for the Peninsular and Sumatran specimens (Table 6). The relative extent of black along vein 4 of the forewing upperside (UpFwV4BlRatio) has the most impact in discriminating between populations, as seen in its high coefficient in the standardised canonical discriminant function (Table 6), but it does not differ significantly between geographical regions in the tests of equality of the group means (Table 5). It is followed in importance by the extent of green in spaces 4 (UpHwSp4GrRatio) and 5 (UpHwSp5GrRatio) of the hindwing upperside (Table 6), both of which are significant in the tests of equality of the group means (Table 5). The extent of green along vein 2 of the forewing upperside (UpFwV2GrRatio) is also significant (Table 5) although fifth in importance in the standardised canonical discriminant function (Table 6).

Data for the categorical characters is summarised in Table 7, and Figure 6 shows the first two components of the correspondence analysis. Peninsular Malaysian and Sumatran males are more scattered in the graph compared to females, but males from the Peninsula are still located on the right and males from Sumatra on the left (Fig. 6). Sumatran males are most associated with a straight green disc on the hindwing upperside (UpHwGrDisc_Straight; Figs 3E, 4D) and little or no green scales in space 7 of the hindwing upperside (UpHwSp7Gr_None and _Sparse; Figs 3H–I, 4D). Peninsular males are most

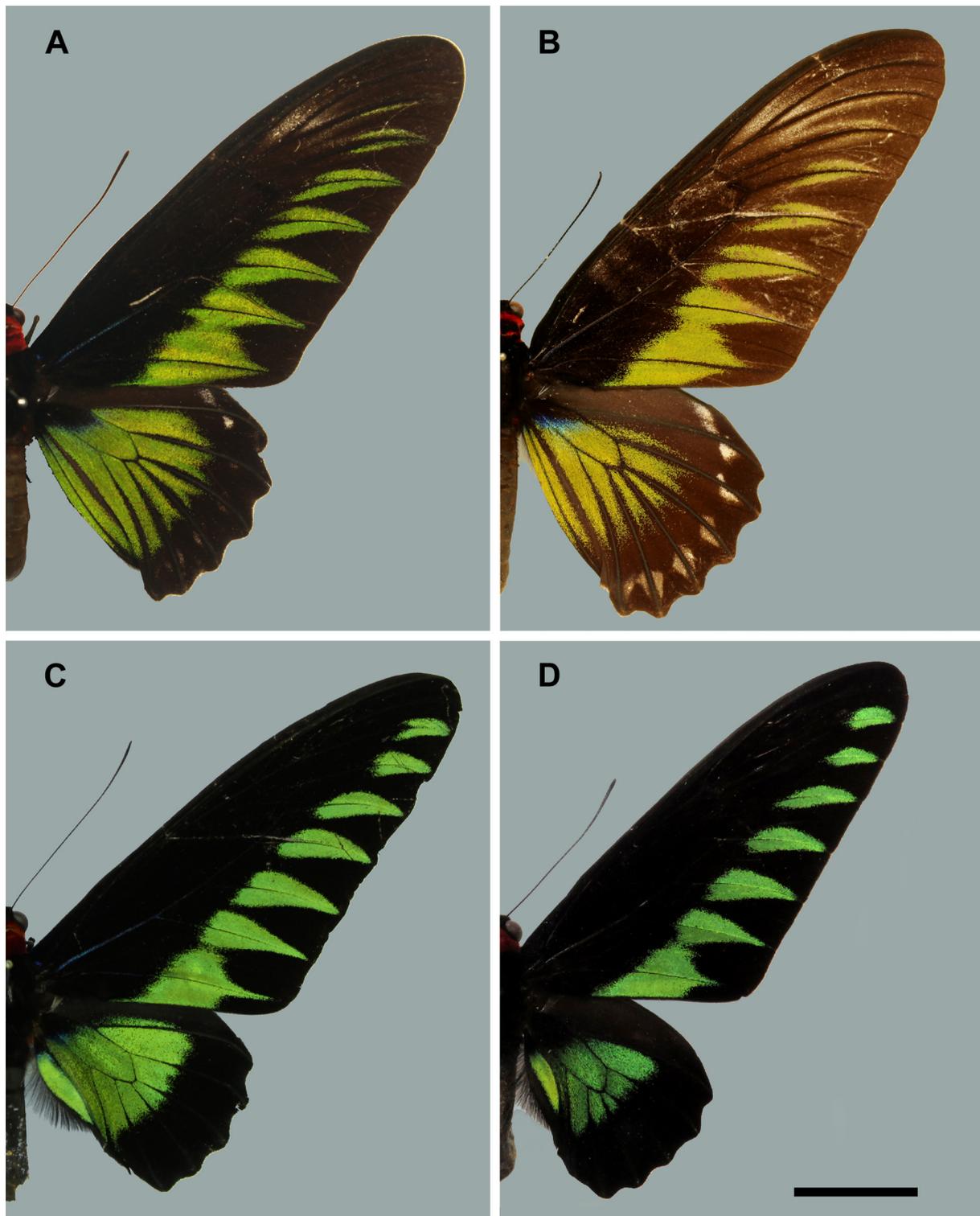


Fig. 4. Females (top) and males (bottom) of *Trogonoptera brookiana mollumar* d’Abrera, Doggett & Parker, 1976 (A and C) and *T. b. trogon* (Vollenhoven, 1860) (B and D). Scale bar = 2.00 cm.

associated with a convex and indented green hindwing disc (UpHwGrDisc_Convex and _Indented; Figs 3B–D, 4C) and with dense green scales in space 7 of the hindwing upperside (UpHwSp7Gr_Dense; Figs 3A, 3F–G, 4C), but they share these characters to some extent with Sumatran males. Differences between the populations are significant for both characters (Chi Square test, Table 7).

Synthesis of character analyses

The discriminant function analysis shows a significant difference between populations in both sexes when all characters are considered. Individual variables that differ significantly between populations in the univariate comparisons of the present study (Tables 2, 5) are not always variables that make an important contribution towards discrimination of the populations when all variables are considered in the multivariate dimension (Tables 3, 6). In the females examined, these variables are the extent of green and black measured on vein 4 (UpFwV4GrRatio and UpFwV4BIRatio, respectively; Fig. 2A), which are fourth and sixth in importance, respectively, in the seven-variable discriminant function (Table 3). In males, the extent of green on veins 2 and 4 (UpFwV2GrRatio and UpFwV4GrRatio, respectively; Figs 2A, 3A), though significant in univariate tests, are the fifth and sixth terms, respectively, in the function (Table 6).

Conversely, some variables in the present study that hardly differ in a univariate comparison (Tables 2, 5) between populations make an important contribution towards discrimination in the multivariate dimension (Tables 3, 6). Such variables are the ratio of green in space 2 of the hindwing upperside (UpHwSp2GrRatio; Fig. 2A) in the female, which is the third term in the function (Table 3), and the extent of black measured on vein 4 of the forewing upperside (UpFwV4BIRatio) in the male (Figs 2A, 3A), which is the first term in the function (Table 6). These outcomes show that while some characters

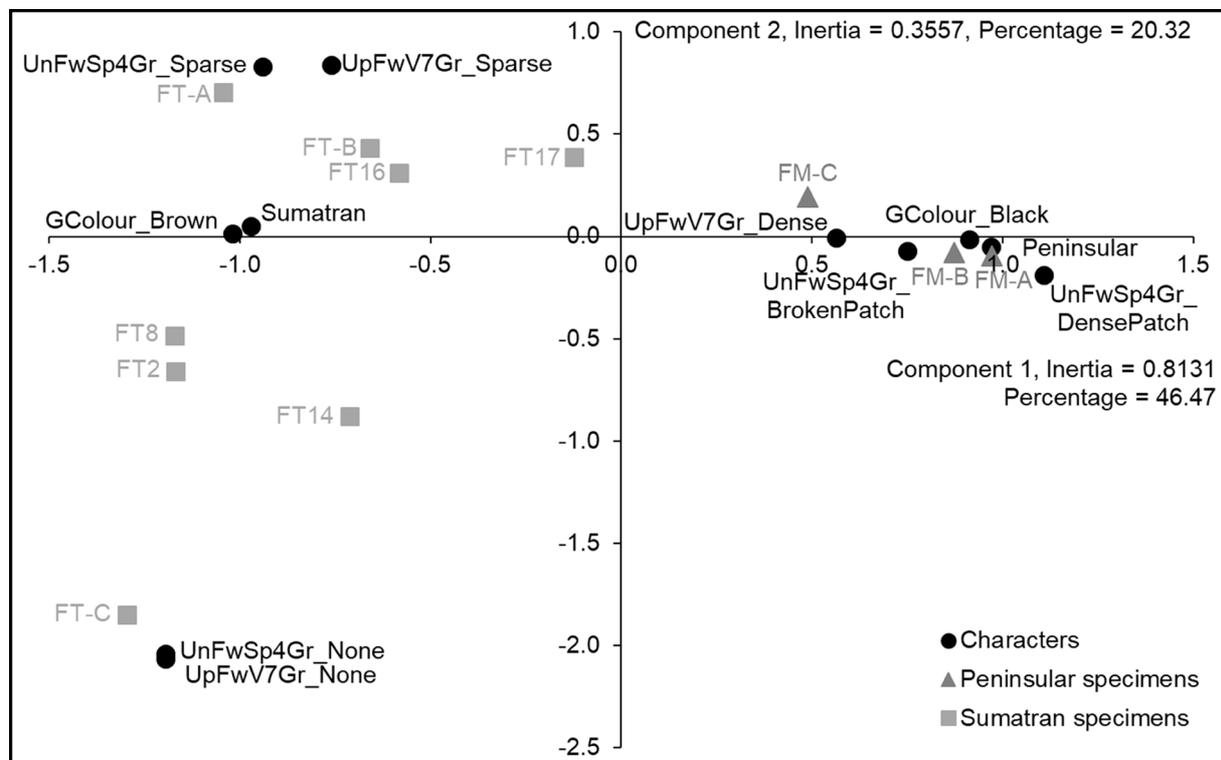


Fig. 5. Two-dimensional plot of correspondence analysis components 1 and 2 for females. Specimens with identical coordinates are grouped together (e.g., FT-A = female, Sumatra, group A; FM-A = female, Peninsular Malaysia, group A).

Table 5. Ratio characters for Sumatran and Peninsular Malaysian males (mean \pm standard error, and range).

Character abbreviation	Sumatra	Peninsular Malaysia	F_{1,30}	P
UpHwSp4GrRatio *	0.21 \pm 0.02 (0.12–0.36)	0.32 \pm 0.01 (0.22–0.44)	25.809	< 0.001
UpHwSp2GrRatio	0.63 \pm 0.01 (0.60–0.68)	0.67 \pm 0.01 (0.61–0.78)	8.000	0.008
UpHwSp5GrRatio *	0.62 \pm 0.01 (0.56–0.70)	0.66 \pm 0.01 (0.59–0.70)	12.214	0.001
UpFwV2GrRatio *	0.90 \pm 0.01 (0.85–0.93)	0.93 \pm 0.00 (0.91–0.95)	19.957	< 0.001
UpFwV2BIRatio	0.51 \pm 0.00 (0.48–0.54)	0.51 \pm 0.00 (0.48–0.55)	0.385	0.540
UpFwV4GrRatio *	0.90 \pm 0.01 (0.86–0.95)	0.93 \pm 0.00 (0.89–0.96)	15.569	< 0.001
UpFwV4BIRatio	0.55 \pm 0.01 (0.51–0.60)	0.55 \pm 0.00 (0.52–0.60)	0.167	0.686

N = 16 each from Sumatra and Peninsular Malaysia. * Significantly different between regions at $\alpha = 0.007$ (Bonferroni correction).

are useful when examined as the sole character of differentiation between the two populations, they do not hold as true when a multi-character approach is used in separating the populations. And while some variables are useful in a multi-character approach, they can be much less useful when used on their own.

Variables that are both significant in the univariate tests and make important contributions in the discriminant function can be considered more reliable characters to use either on their own or in conjunction with other characters. These are the extent of green in space 4 of the hindwing upperside (UpHwSp4GrRatio) and along vein 2 of the forewing upperside (UpFwV2GrRatio) in the female (Fig. 2A), which are the first and second terms respectively in the function (Table 3), and the extent of green in spaces 4 (UpHwSp4GrRatio) and 5 (UpHwSp5GrRatio) of the hindwing upperside in the male (Figs 2A, 3A), which are the second and third terms respectively in the function (Table 6).

Among the categorical characters used in the female, the ground colour (GColour) of the distal area of the upperside of both wings is the most distinguishing character (Figs 2A, C, 4A–B, 5; Table 4), being almost always paler and browner than the forewing cell in Sumatran specimens (Figs 2C, 4B, 5; Table 4). The only exception seen is a specimen that is otherwise typical of the Sumatran population in all other respects. The green scaling in space 4 of the forewing underside (UnFwSp4Gr) usually is also a reliable character, generally forming a broken or complete patch in Peninsular specimens (Figs 2B, D–E, 5; Table 4), or being absent or reduced to sparse scales in Sumatran specimens (Figs 2F, 5; Table 4). The green scaling below vein 7 on the forewing upperside (UpFwV7Gr), which is generally reduced in Sumatran females, is useful though a much less reliable character because of variation in the Sumatran population (Figs 2C, H, 4B, 5; Table 4). The greater variation in Sumatran specimens results in a greater scatter in the characters on the Sumatran end of the biplot in the correspondence analysis (Fig. 5). Categorical characters used in the male are less useful in differentiating the Sumatran and Peninsular

Table 6. Coefficients and constants for each ratio character in the cross-validated canonical discriminant and classification functions of male birdwings from Sumatra and Peninsular Malaysia.

Characters	Canonical discriminant function		Classification function	
	Standardised	Unstandardised	Peninsular	Sumatran
Constant		-14.537	-2071.954	-2025.168
UpFwV4BIRatio	-1.013	-46.773	283.549	434.082
UpHwSp4GrRatio	0.975	16.012	-760.562	-812.094
UpHwSp5GrRatio	0.628	17.990	476.427	418.529
UpHwSp2GrRatio	-0.456	-13.034	789.090	831.039
UpFwV2GrRatio	0.361	17.893	1329.498	1271.911
UpFwV4GrRatio	0.322	15.978	1772.206	1720.781
UpFwV2BIRatio	0.084	4.208	993.803	980.259

Table 7. Numbers and percentages (in parentheses) of males with each categorical character from Sumatra and Peninsular Malaysia.

Region	Characters (abbreviated) and categories					
	UpHwGrDisc [#]				UpHwSp7Gr [*]	
	Convex	Indented	Straight	None	Sparse	Dense
Sumatra	47 (25.00)	35 (18.62)	106 (56.38)	27 (14.36)	94 (50.00)	67 (35.64)
Peninsular Malaysia	13 (59.09)	7 (31.82)	2 (9.09)	0 (0.00)	5 (22.73)	17 (77.27)

N = 188 (Sumatra) and 22 males (Peninsular Malaysia). $\alpha = 0.025$ (Bonferroni correction). [#]Chi Square = 18.293, df = 2, $p < 0.001$. ^{*}Chi Square = 14.802, df = 2, $p = 0.001$.

populations, even though significant differences occur between them (Fig. 6; Table 7). This is because of an even greater variation in the Sumatran males.

Females differ more than males between the two populations. The most diagnostic characters in the female are the ground colour of the distal areas of both wings on the upperside in relation to the forewing cell (Fig. 5; Table 4), the extent of green in space 4 of the hindwing upperside and the extent of green along vein 2 of the forewing upperside (Tables 2–3). Males of the two populations only differ on average but cannot be reliably distinguished. The extents of the green markings on the uppersides of both wings (Tables 5–6) and consequently the shape of the discal margin of the green hindwing patch (Table 7) are the most indicative characters in the male.

Comparative extent of morphological differences in other subspecies

Differences between the various subspecies of *brookiana* are generally slight. They are based on the females, because the males resemble each other and differ very little. Similar cases of subspecies based

mainly on the female sex are found in other butterfly species, such as *Troides aeacus* (C. & R. Felder, 1860), in which the mainland subspecies *aeacus*, the Taiwanese subspecies *formosanus* Rothschild, 1899 and the Peninsular subspecies *malaiianus* Frühstorfer, 1902 differ mainly in the female, the males having no consistent distinctive characters, differing mainly in overall size (see plates in Rumbucher & von Knötgen 1999; Matsuka 2001; d’Abrera 2003).

Among females of *T. brookiana*, subsp. *mollumar* has the least prominent whitish streaks on the forewing apex, which start from vein 7. The subspecies *trogon* has more prominent streaks, starting from either vein 6 or 7, while in the subspecies *brookiana* from Borneo the white is even more prominent. The subspecies *albescens* from western Peninsular Malaysia has the most extensive white markings of all the subspecies. Ground colour differences are also an important distinguishing character between the subspecies *albescens* and *brookiana* (d’Abrera 2003).

Available molecular data

Based on a comparison of six DNA sequences of *Trogonoptera* available in GenBank, differences between taxa at the molecular level are very small ranging from 0.2 to 1.3 % in the ND5 and COI genes. Even differences between *T. brookiana* (Sumatra, GenBank EF514439, photograph in BOLDSYSTEMS) and *T. trojana* (Staudinger, 1889) are extremely small, that is six to eight base pairs within 596 base pairs in the COI gene, while different specimens of *T. trojana* (Philippines, EF514444 and EF514436, photographs in BOLDSYSTEMS) differ by four base pairs. Two specimens of *T. brookiana* from Cameron Highlands, Peninsular Malaysia (AB084428; AB044648, photograph made available to us by S. Morinaka) differ from each other in three out of 877 base pairs in the ND5 gene but differ from a

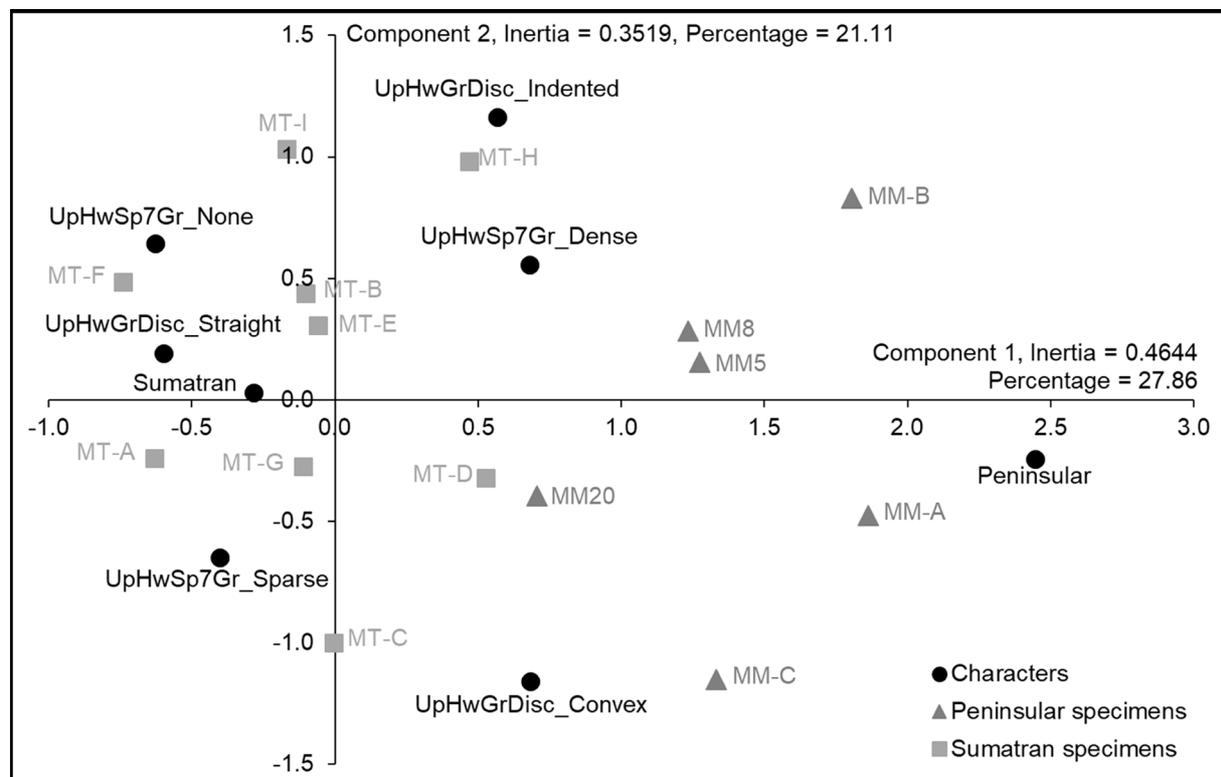


Fig. 6. Two-dimensional plot of correspondence analysis components 1 and 2 for males. Specimens with identical coordinates are grouped together (e.g., MT-A = male, Sumatra, group A; MM-A = male, Peninsular Malaysia, group A).

specimen listed as *T. brookiana* from Padang, Sumatra (AB044647) in only two to three base pairs out of 813. These can be inferred from their localities of origin to be subsp. *albescens* and subsp. *trogon*, respectively. The very slight differences within and between species therefore make it highly unlikely that common molecular techniques will provide sufficient resolution to answer questions about the subspecific status of populations of *T. brookiana*.

Ecological differences

The males of the Sumatran population have been reported to regularly visit a hot sulphur spring (Nicéville & Martin 1895). However, they do not congregate in numbers (Haugum & Low 1982). Judging from the disproportionate numbers of Sumatran males in collections, the habit of visiting wet ground must be very well developed even though they do not congregate in groups like the males of the western peninsular subspecies *albescens*, which has a similar composition of the sexes in collections.

The behaviour of the Sumatran population described by Nicéville & Martin has neither been reported in the eastern population in the Peninsula nor seen in the first and second authors' extensive observations in its habitat, along rivers or other suitable puddling sites. However, we have occasionally observed it landing and sometimes circling and landing multiple times, always briefly, along rivers or on wet ground along forest roads. A similar behaviour has been seen by other field observers (C.Y. Chong pers. com.; S.K. Khew pers. com.). Therefore, the eastern peninsular population differs greatly from the Sumatran population in this behavioural character.

Taxonomic status of *mollumar*

Considering the morphological differences between both sexes and especially the females of the two populations, as well as the comparative differences between other populations already recognised as subspecies, we consider the eastern peninsular population a valid subspecies, *mollumar*, distinct from the Sumatran subspecies *trogon*. This conclusion is also supported by differences in behaviour and a geographical separation of the two subspecies.

Diagnoses: *mollumar* and *trogon*

Like the males of most subspecies of *T. brookiana*, the males of the subspecies *mollumar* and *trogon* are not readily differentiable. The females of both subspecies *mollumar* and *trogon* are differentiable from other subspecies by the very much reduced subapical white streaks on the forewing and by more extensive green scaling on the upperside of the forewing and hindwing, resulting in at least five long green arrow-shaped markings on the forewing upperside (Figs 2A, C, 4A–B), in comparison to two or three, or sometimes four in most other subspecies. A sixth green arrow-shaped marking is sometimes reduced to just streaks above and below vein six (Figs 2A, C, 4A–B), and a seventh, if present, is reduced to a green streak below vein seven (Figs 2A, G, 4A). The females of the subspecies *cardinaali* Haugum & Low, 1982 and *jikoi* Kobayashi, 1986 have a fifth green arrow-shaped marking but of much shorter length as these subspecies have more reduced green markings on the upperside than the subspecies *mollumar* and *trogon*.

The following diagnoses separate *mollumar* and *trogon*.

Trogonoptera brookiana mollumar d'Abbrera, Doggett & Parker, 1976
Figs 2A–B, 3A, 4A, C

Trogonoptera brookiana mollumar d'Abbrera, Doggett & Parker, 1976: 22–23; genitalia figured, p. 24.

Ornithoptera brookeana – Distant 1882–1886: 330–331 (*pro parte*: Johore). — Fickert 1889: 749–753 (*pro parte*: Johore).

Trogonoptera brookiana trogon – Corbet & Pendlebury 1956: 92. — Eliot 1959: 372. — Eliot 1973: 175–176. — Fleming 1975: 15; female figured, pl. 2. — Haugum & Low 1982: 56–60; genitalia figured, text-fig. 19B, p. 45, text-fig. 29D–F, p. 57, text-fig. 30, p. 58; distribution, p. 56 (*pro parte*: Peninsular Malaysia; synonymy inferred, considered to be a locality form). — Eliot 2006: 5.

Trogonoptera brookeana – Rippon 1906: 2–4 (*pro parte*: Johore).

Trogonoptera brookiana mollumar – Eliot in Corbet & Pendlebury 1978: 67; checklist, p. 421. — d’Abreu 1982: 4; holotype and allotype figured, p. 5. — Tsukada & Nishiyama 1982: 235–236; male and female figured, pl. 32, p. 56. — Fleming 1983: 15; female figured, pl. 2, P1B. — Matsuka 2001: 210; checklist, p. 347; male and female figured, p. 210. — d’Abreu 2003: 172–174; holotype, allotype and one male figured, p. 175; genitalia figured, p. 314 (status formally revised).

Troides (Trogonoptera) brookiana trogon – Eliot in Corbet & Pendlebury 1992: 59–60; checklist, p. 394; female figured, pl. 1 (formal synonymy).

Material examined

Holotype

MALAYSIA • ♂; Peninsular Malaysia, Johore, Ulu Sedili; 17 Feb. 1974; V. Doggett leg.; BMNH(E) 1420520.

Paratype (allotype)

MALAYSIA • 1 ♀; same collection data as for holotype; 29 Aug. 1971; N. Parker leg.; BMNH(E) 1420526.

Additional material*

MALAYSIA – **Peninsular Malaysia, State of Johor**** • 3 ♂♂; Johor; NHMUK • 1 ♀; same locality; ZRC • 6 ♂♂, 3 ♀♀; Ulu Sedili Forest Reserve; Chong-Arshad • 3 ♀♀; Lombong; NHMUK • 3 ♂♂, 2 ♀♀; Kangkar, Dohol; NHMUK; 1 ♂; same locality; ZRC • 1 ♀; Endau Rompin National Park; FRIM • 1 ♀; same locality; Kirton • 1 ♀; Endau Forest Reserve; MZUM; • 1 ♂, 1 ♀; Mersing Forest Reserve; Chong-Arshad • 2 ♂♂; Mersing Road; NHMUK • 3 ♂♂, 2 ♀♀; Pantii Forest Reserve; FRIM • 1 ♀; same locality; Chong-Arshad • 1 ♂; Kota Tinggi; NHMUK. – **Peninsular Malaysia, State of Pahang** • 1 ♀; Rompin Endau; FRIM. – **Peninsular Malaysia, State of Terengganu**** • 1 ♂; Jengai Permanent Forest Reserve, near Bukit Lentur; Chong Arshad.

*Label data is shortened for brevity and may vary in detail between specimens from the same general locality. Localities have been georeferenced where possible and are grouped regionally to show geographical coverage, based on the distribution shown in Fig. 1. Regional groupings in bold typeface are not necessarily part of the label data.

**Johor and Terengganu: also spelt Johore and Trengganu, respectively, especially in older labels and literature.

Female

Almost always identifiable by the entirely black ground colour on the upperside in which the outer areas of both wings barely contrast with the veins and with the black forewing cell (Figs 2A, 4A). Hindwing upperside with more extensive green scaling than in the subspecies *trogon*, extending to about half to two thirds of the length of space 4 (Figs 2A, 4A). Forewing upperside with more extensive green scaling than in the subspecies *trogon*, the green arrow-shaped markings slightly longer and reaching nearer the wing margin, especially along vein 2, and with the black ground colour behind the arrowheads sometimes just perceptibly narrower than in *trogon* (Figs 2A, 4A). Forewing underside green scales in space 4 always present, forming a broken patch (Fig. 2E) or sometimes entire patch (Figs 2B, D) of green scales. Forewing upperside with a green streak below vein 7, its scaling usually dense (Figs 2A, G, 4A).

Male

Upperside hindwing green disc on average more extensive than in the subspecies *trogon* (Figs 3A, 4C), with the outer margin usually convex (Figs 3A–B, 4C) or slightly indented (Fig. 3C–D). Forewing upperside with more extensive green scaling than in *trogon* as in the female (Figs 3A, 4C). Green scales always present in space 7 of the hindwing upperside, and usually dense (Figs 3A, F–G, 4C). Not reliably distinguishable from males of the subspecies *trogon*.

Range

Eastern Johor northward to southernmost Pahang, and central to southern Terengganu in Peninsular Malaysia (Fig. 1).

Trogonoptera brookiana trogon (Vollenhoven, 1860)

Figs 2C, 4B, D

Papilio trogon Vollenhoven, 1860: 69–70; male figured, pl. 6.

Ornithoptera brookiana ♀-variety *eleanor* Walker, 1889: 75–77 (locality not stated).

Papilio brookeanus – C. & R. Felder 1864: 292, 334 (*pro parte*: Sumatra; *Papilio trogon* synonymised with *Papilio brookeanus*).

Ornithoptera brookeana – Distant 1882–1886: 330–332 (*pro parte*: Sumatra). — Fickert 1889: 749–753 (*pro parte*: Sumatra). — Hagen 1894: 18 (*pro parte*: Sumatra).

Papilio brookeana – Snellen & Snelleman 1892: 6, 24.

Troides brookianus brookianus – Rothschild 1895: 198–199 (*pro parte*: Sumatra).

Troides brookianus brookianus ♀-aberration *eleanor* – Rothschild 1895: 199.

Trogonoptera brookeana – Kirby 1896: 259–263 (*pro parte*: Sumatra). — Rippon 1906: 2–4 (*pro parte*: Sumatra).

Trogonoptera brookeana ♀ var. *eleanor* – Rippon 1906: 1, 4 (redescription); distribution mentioned, p. 127 (“Sumatra”); female figured, pl. 26, figs 5–6; distribution map erroneously figured as Borneo, map 6, pl. 43.

Papilio brookiana trogon – Jordan 1908: 17–18 (status revised).

Papilio brookiana trogon, syn. *eleanor* – Jordan 1908: 17–18 (synonymised, “*trogon* Voll. (♀-*eleanor* Walk.)”, misspelled); female figured (pl. 7c).

Trogonoptera brookiana trogon – Tsukada & Nishiyama 1982: 235–236; male and female figured, pl. 32, p. 56; genitalia figured, p. 237. — d’Abrera 1982: 4; male figured, p. 5. — Haugum & Low 1982: 51–56; male figured, pl. 1, no. 2; female figured, pl. 2, no. 4; larva figured, text-fig. 18, p. 42; male genitalia figured, text-fig. 19D, p. 45, text-fig. 27, p. 54, text-fig. 29A–C, p. 57, text-fig. 30A, C, p. 58; distribution map figured, text-fig. 25, p. 51 (Sumatra). — Matsuka 2001: 210; checklist, p. 347; male and female figured. — d’Abrera 2003: 170; male and female figured, p. 171; genitalia figured, p. 314.

Trogonoptera brookiana trogon, syn. *eleanor* – Haugum & Low 1982: 54–55 (*nomen dubium* recommended, but regarded as synonym of *trogon* for ‘convenience’). — Matsuka 2001: 347 (checklist).

Trogonoptera brookiana brookiana ♀-f. *eleanor* – d’Abrera 2003: 168.

Material examined

Syntypes

INDONESIA • 2 ♂♂; Sumatra; 1859; Ludeking leg.; RMNH.

Additional material*

INDONESIA – **North Sumatra** • 1 ♂; Aceh; RMNH • 1 ♂; same locality; MZB • 1 ♂; Aceh, Perlak; MZB • 4 ♂♂, 1 ♀; Balimbingan; RMNH • 7 ♂♂; Batak Mount; NHMUK • 1 ♀; Bedagei; NHMUK • 1 ♀; Berastagi town, Karo Batak village; RMNH • 1 ♂; Bohorok; NHMUK • 1 ♂; Deli; NHMUK • 2 ♂♂; same locality; RMNH • 4 ♂♂, 3 ♀♀; Gedung Biara; RMNH • 1 ♂; Langkat; MCZ • 4 ♂♂; Selesseh; NHMUK • 2 ♂♂, 3 ♀♀; Seumanjam, Meulaboh; RMNH • 1 ♂; Silau Dunia; RMNH • 1 ♂; Tanjung Morawa; RMNH. – **Central West Sumatra** • 2 ♂♂; Anai; RMNH • 1 ♂, 1 ♀; Harau; MZB • 1 ♀; Kuala Simpang; RMNH • 1 ♂; Lubuk Sikapang; RMNH • 3 ♂♂, 2 ♀♀; same locality; MZB • 3 ♂♂; Batang Proepoe, Padang Bovenland; NHMUK • 1 ♀; Padang Beneden; NHMUK • 55 ♂♂; Padang; RMNH • 1 ♂; same locality; MZB • 1 ♂; same locality; MCZ • 1 ♂; Padang, Balun; RMNH • 1 ♂; Padang, Sidempuan; NHMUK • 1 ♂; same locality; RMNH • 1 ♂; Silago; RMNH • 46 ♂♂; Solok; RMNH • 1 ♂; Surian; RMNH. – **South West Sumatra** • 2 ♂♂; Bengkulu; RMNH • 2 ♂♂; Kaba Mount; NHMUK • 2 ♂♂; Lebong Tandai; NHMUK • 2 ♂♂; Tanjung Sakti; RMNH • 3 ♂♂; Koprass; NHMUK. – **Central East Sumatra** • 1 ♂; Inderagiri; MZB. – **South Sumatra** • 1 ♂; Teluk Betung Bay, Kalianda; RMNH. – **Sumatra (not georeferenceable)** • 2 ♀♀; NE Sumatra; NHMUK • 6 ♂♂; Sumatra; NHMUK • 3 ♂♂; same locality; RMNH • 2 ♂♂, 1 ♀; Sumatra, East coast; RMNH • 3 ♂♂; Sumatra, Bila; NHMUK • 2 ♂♂; Sumatra, West coast; RMNH • 6 ♂♂; W. Sumatra; NHMUK • 2 ♂♂; Kuala Lemui-Rak; NHMUK.

* See note for additional material of *T. brookiana mollumar*, which is also applicable here for *T. brookiana trogon*.

Female

Almost always identifiable by the brown to dark brown ground colour of the outer areas on the upperside of both wings, which are paler than the base of the dark forewing cell and dark veins, and especially contrasting at the forewing cell end and the distal end of the forewing (Figs 2C, 4B). Hindwing upperside with less extensive green scaling than in the subspecies *mollumar*, extending to about one third to half the length of space 4 (Figs 2C, 4B). Forewing upperside with less extensive green scaling than in the subspecies *mollumar*, the green arrow-shaped markings slightly shorter and ending further from the wing margin, especially along vein 2, and with the dark brown ground colour behind the arrowheads sometimes just perceptibly wider than in *mollumar* (Figs 2C, 4B). Forewing underside space 4 usually with just sparse green scaling (Fig. 2F) and sometimes without green scales, but occasionally with a broken patch of scales (Fig. 2E). Forewing upperside without green scaling below vein 7 or, more commonly, with sparse scaling (Fig. 2H), and sometimes with a densely-scaled green streak (Fig. 2G).

Male

Green disc on hindwing upperside on average less extensive than in the subspecies *mollumar*, with the outer margin variable, but straight (Figs 3E, 4D) in about half of males. Forewing upperside with less extensive green scaling (Fig. 4D) than in *mollumar*, as in the female. Green scaling in space 7 on the hindwing upperside variable, not always present, often sparse (Fig. 3H–I). Not reliably distinguishable from males of the subspecies *mollumar*.

Range

Sumatra Island, excluding small neighbouring islands, occurring in the foothills, especially in the north-east and central to south-central west, but with occasional coastal occurrences in the south, south-central east and north (Fig. 1).

Discussion

Status of the taxon *mollumar*

Haugum & Low (1982) examined many males from Sumatra but only 10 of the more rarely collected females and just a few males and females from the Peninsula. They gave exclusive forewing length

ranges for Sumatran and Peninsular males but inexplicably said they fully overlap. We found a significant difference among males, but a large overlap. They also examined other characters by subjective judgement without quantification. Perhaps because of this and limited availability of specimens from the Peninsula, they did not perceive adequate differences between the Sumatran and Peninsular specimens.

In the current study, we examined a larger sample and larger number of characters quantitatively using measurements and scores. Discriminant function analysis, correspondence analysis and significance tests all showed that Sumatran and Peninsular specimens differ morphologically in both sexes, but especially in the female. Females could almost always be diagnosed by their distal ground colour (Figs 2A, C, 4A–B) and, where there was doubt, could be diagnosed by a combination of characters. The differences between the Sumatran and eastern Peninsular populations, though small, are comparable in magnitude and consistency to differences between other subspecies of *T. brookiana* of undisputed status. We therefore conclude that *mollumar* merits the status of a subspecies distinct from *trogon*, a conclusion supported by differences in their ecology and behaviour, which, as pointed out by Parsons (1996), can be useful in differentiating taxa.

Status of the taxon *eleanor*

The nominal taxon *eleanor* was described by Walker (1889). It was described as a female variety of *Trogonoptera brookiana* (“*Ornithoptera brookiana*”), without information on type locality, and conforms in the description of its morphology with the females of subsp. *trogon* and subsp. *mollumar*. Rippon (1906: 1, 4, pl. 26, figs 5–6), who later received two females from Walker, redescribed and figured the taxon, but it is not possible to ascertain the locality of origin from the description or illustrations. Rippon (1906: 127), however, listed the locality as Sumatra, and his account of the specimens he received suggests that he received from Walker what would appear to be the only specimen on which Walker based his description, which lacked antennae (cf. Walker 1889: 77). Inexplicably, the maps of Rippon (1906: map 6, pl. 43) show *eleanor* in Borneo and absent from Sumatra, but no other specific mention is made of Borneo as a locality for *eleanor*, contrary to what is stated by Haugum & Low (1982). Our view is that *eleanor*, which is senior to *mollumar*, is best treated as a synonym of *trogon* to which it is junior, just as it has been treated by Jordan (1908) and Ohya (in Matsuka 2001). All available evidence suggests that it is from Sumatra. No forms resembling *trogon* or *mollumar* have ever been recorded from Borneo. The absence of *eleanor* from Rippon’s Sumatran map and its inclusion in his Bornean map is clearly a mix-up on his part, and may have led d’Abrera (2003) to treat *eleanor* as a female-form of the nominate Bornean race *brookiana*. Therefore, we do not think it necessary to regard *eleanor* as a *nomen dubium* as suggested by Haugum & Low (1982), even though we are also unable to trace the type of *eleanor*. Rippon’s collection in the National Museum of Wales, Cardiff does not have specimens that could correspond with Walker’s (M. Wilson pers. com.). The type may remain in Walker’s collection, for which we have been unable to find information on its whereabouts.

Recognised subspecies of *Trogonoptera brookiana*

The following subspecies of *T. brookiana* are recognised:

Trogonoptera brookiana (Wallace, 1855)

T. b. brookiana (Wallace, 1855) – Borneo

T. b. haugumei Parrott, 1991 – East Kalimantan

T. b. bosuangi Schäffler, Rumbucher & Dufek, 2014 – Banggi Island

T. b. natunensis (Rothschild, 1908) – Natuna Island

T. b. albescens (Rothschild, 1895) – Western Peninsular Malaysia

T. b. mollumar d’Abrera, Doggett & Parker, 1976 – Eastern Peninsular Malaysia

T. b. trogon (Vollenhoven, 1860), syn. *eleanor* (Walker, 1889) – Sumatra

T. b. cardinaali Haugum & Low, 1982 – Lingga Islands

T. b. jikoi Kobayashi, 1986 – Tuangku Island

T. b. toshikii Kobayashi, 1991, syn. *apolloniae* Neukirchen, 1992 – Mentawai Islands

T. b. mariae Neukirchen, 1993, syn. *akikoe* Morita, 1994 – Batu Islands

Status of the taxa *walshi* and *walshoides*

Haugum & Low (1982) described two male ‘forms’ under the subspecies *trogon* namely *walshi* and *walshoides* with ‘types’ designated in the RMNH, Leiden. In the specimens on which the descriptions are based, “*walshi*” has the basal half of the veins of the forewing bordered by semi-translucent dull brown scales instead of the usual black. The form “*walshoides*” has a similar colouration but more extensive, covering the whole basal halves of the forewing and hindwing, instead of occurring only around the basal veins of the forewing. However, the extent and intensity of the abnormal colouration is variable between several specimens in RMNH, sometimes being restricted to the basal veins or extreme base and sometimes extending to over two thirds of the wings, and may even be asymmetric. The iridescent blue scales described by Haugum & Low (1982) around the outer margins of the abnormally coloured area were not seen in the specimens examined. The characters used in describing these ‘forms’ are actually artefacts of chemically induced discolouration. When examined under a microscope, the antero-lateral margins of the scales in the discoloured areas of the wings can be seen to be curled or rolled inwards, sometimes with the scales raised and rolled to a conical point, instead of lying flat as in normal scales. The distribution of the scales in the basal half of the wings and sometimes surrounding only the basal veins of the forewing, its variability and sometimes asymmetric pattern, is consistent with a chemical killing agent or preservative that was absorbed by the body and dispersed into the wings through the veins from which it would have seeped into adjacent wing membranes and scales. Chemicals such as ether, chloroform, carbon tetrachloride, hydrogen cyanide, ammonia and ethyl acetate have been used in the past as killing agents and some are known to produce chemically-induced wing discolouration after prolonged exposure (Salmon 2000). We therefore view that “*walshi*” and “*walshoides*” are not valid biological forms. Since infra-subspecific names are not regulated by the ICZN, these named forms do not become available names and are not included in the synonymy.

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References

CITES. 2017. *Convention on International Trade in Endangered Species of Wild Flora and Fauna: Appendix II*. Available from <http://www.cites.org/eng/app/appendices.php> [accessed 22 Dec. 2017].

- Cognato A.I. 2006. Standard percent DNA sequence difference for insects does not predict species boundaries. *Journal of Economic Entomology* 99: 1037–1045. <https://doi.org/10.1093/jee/99.4.1037>
- Corbet A.S. & Pendlebury H.M. 1956. *The Butterflies of the Malay Peninsula*. 2nd ed. Oliver and Boyd, Edinburgh and London.
- Corbet A.S. & Pendlebury H.M. 1978. *The Butterflies of the Malay Peninsula*. 3rd ed. Revised by Eliot J.N. Malayan Nature Society, Kuala Lumpur.
- Corbet A.S. & Pendlebury H.M. 1992. *The Butterflies of the Malay Peninsula*. 4th ed. Revised by Eliot J.N. Malayan Nature Society, Kuala Lumpur.
- d’Abrera B. 1982. *Butterflies of the Oriental Region. Vol. Part 1: Papilionidae, Pieridae and Danaidae*. Hill House, Victoria, Australia.
- d’Abrera B. 2003. *Birdwing Butterflies of the World*. New and revised edition. Hill House Publishers Pty Ltd, Victoria, Australia.
- d’Abrera B., Doggett V. & Parker N. 1976. A new race of *Trogonoptera brookiana* Wallace (Lepidoptera: Papilionidae) from West Malaysia. *The Victorian Naturalists* 93: 21–24.
- Distant W.L. 1882–1886. *Rhopalocera Malayana: A Description of the Butterflies of the Malay Peninsula*. West, Newman and Co., London. <https://doi.org/10.5962/bhl.title.8806>
- Eliot J.N. 1959. New or little known butterflies from Malaya. *Bulletin of the British Museum (Natural History) Entomology* 7: 371–391.
- Eliot J.N. 1973. Letters to the editor: Rajah Brooke’s Birdwing in Trengganu. *Malayan Nature Journal* 26: 175–176.
- Eliot J.N. 2006. Updating The Butterflies of the Malay Peninsula. Edited, enlarged and prepared for publication by Barlow H., Eliot R., Kirton L.G. & Vane-Wright R.I. *Malayan Nature Journal* 59: 1–49.
- Felder C. & Felder R. 1864. Species Lepidopterorum hucusque descriptae vel iconibus expressae in seriem systematicam digestae. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien* 14: 289–378.
- Fickert C. 1889. Ueber die Zeichnungsverhältnisse der Gattung *Ornithoptera*. *Zoologische Jahrbücher. Abtheilung für Systematik, Geographie und Biologie der Thiere* 4: 692–770.
- Fleming W.A. 1975. *Butterflies of West Malaysia and Singapore*. Vol. 1. Longman Malaysia Sdn. Berhad, Kuala Lumpur.
- Fleming W.A. 1983. *Butterflies of West Malaysia and Singapore*. 2nd ed. Revised by Mc Cartney A. Longman Malaysia Sdn. Berhad, Selangor.
- Hagen B. 1894. Verzeichniss der von mir auf Sumatra gefangenen Rhopalocera. *Deutsche Entomologische Zeitschrift* 7: 1–41.
- Haugum J. & Low A.M. 1982. *A Monograph of the Birdwing Butterflies, the Systematics of Ornithoptera, Troides and Related Genera. Vol. 2, Part 1: The Genera Trogonoptera, Ripponia and Troides*. E.J. Brill/Scandinavian Science Press Ltd., Leiden and Copenhagen.
- Jordan K. 1908. Family Papilionidae. In: Seitz A. (ed.) *Macrolepidoptera of the World* (9 ed.): 11–118. E. Le Moût, Paris.
- Kirby W.F. 1896. *A Handbook to the Order Lepidoptera*. Part I, vol. II. Edward Lloyd, Limited, London. <https://doi.org/10.5962/bhl.title.23911>
- Kirton L.G. 1991. Butterflies in Peninsular Malaysia. In: Kiew R. (ed.) *The State of Nature Conservation in Malaysia*: 105–110. Malayan Nature Society, Kuala Lumpur.

- Kirton L.G. 2014. *A Naturalist's Guide to the Butterflies of Peninsular Malaysia, Singapore and Thailand*. John Beaufoy Publishing Limited, Oxford.
- Matsuka H. 2001. *Natural History of Birdwing Butterflies*. Matsuka Printing Co, Tokyo. (Checklist of Birdwing Butterfly authored by T. Ohya).
- Nicéville L. de & Martin L. 1895. A list of the butterflies of Sumatra with especial reference to the species occurring in the north-east of the Island. *Journal of the Asiatic Society of Bengal* 64: 357–555.
- Panchen A.L. 1980. Notes on the behaviour of Rajah Brooke's birdwing butterfly, *Trogonoptera brookiana brookiana* (Wallace), in Sarawak. *The Entomologist's Record and Journal of Variation* 92: 98–102.
- Parsons M.J. 1996. Gondwanan evolution of the Troidine swallowtails (Lepidoptera: Papilionidae): Cladistic reappraisals using mainly immature stage characters, with focus on the birdwings *Ornithoptera* Boisduval. *Bulletin of the Kitakyushu Museum of Natural History* 15: 43–118.
- Phon C.-K. & Kirton L.G. 2009. Conservation of the Rajah Brooke's birdwing, one of Malaysia's natural wonders. *Conservation Malaysia Bulletin* 10: 2–3.
- Phon C.-K., Kirton L.G. & Wong S. 2011. A glimmer of hope for the Rajah Brooke's birdwing. *Malaysian Naturalist* 65-1: 24–25.
- Rippon R.H.F. 1906. *A Monograph of the Papilionine Tribe Troides of Hübner, or Ornithoptera* [birdwing butterflies] of Boisduval. Vol. 2. London. <https://doi.org/10.5962/bhl.title.60897>
- Rothschild W. 1895. A revision of the *Papilios* of the eastern hemisphere, exclusive of Africa. *Novitates Zoologicae* 2: 167–463.
- Rumbucher K. & von Knötgen B. 1999. *Butterflies of the World. Part 6, Papilionidae III, Troides I*. Bauer E. & Frankenbach T. (eds). Goeke & Evers, Keltern.
- Salmon M.A. 2000. *The Aurelian Legacy – British Butterflies and their Collectors. With Additional Material by Marren P. and Harley B*. University of California Press, Berkeley and Los Angeles, California.
- Snellen P.C.T. & Snelleman F. 1892. Lepidoptera. *Natuurlijke Historie* 4: 4–92.
- Tsao W.-C. & Yeh W.-B. 2008. DNA-based discrimination of subspecies of Swallowtail butterflies (Lepidoptera: Papilioninae) from Taiwan. *Zoological Studies* 47: 633–643.
- Tsukada E. & Nishiyama Y. 1982. *Butterflies of the South East Asian Islands. Vol. 1: Papilionidae*. Plapac Co Ltd, Tokyo, Japan.
- Vollenhoven S.C.S.V. 1860. Description d'une nouvelle espèce de lépidoptère du genre *Papilio*, suivie d'une énumération des espèces de ce genre, qui se trouvent au Musée royal des Paysbas à Leide. *Tijdschrift voor Entomologie* 3: 67–89.
- Walker F.A. 1889. Description of a variety of *Ornithoptera brookiana* (female). *The Transactions of the Entomological Society of London*: 75–77. <https://doi.org/10.1111/j.1365-2311.1889.tb02697.x>

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