WING VARIATION IN TRIBE LIMENITIDINI (NYMPHALIDAE: LIMENITIDINAE) FROM SARAWAK, MALAYSIA

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ABSTRACT

This study describes and compares the wing pattern variation among species of the tribe Limenitidini. A total of 34 species representing 13 genera of the tribe Limenitidini wing were examined and illustrated, where pattern elements of the nymphalid ground plan (NGP) are labelled in color. In general, the ventral wing surface tends to have more visible pattern elements than the dorsal wing surface. Elements *c* (basal symmetry system), *d* (proximal band of central symmetry system), *f* (discal band of central symmetry system) and *I* (parafocal element) are the common pattern elements found among species examined of this tribe. UPGMA were constructed to show the similarity distance between the species of tribe Limenitidini in terms of pattern elements on the ventral wing surface. The sexual dimorphism and colour resemblance among species in this study are also discussed.

Keywords: Automated identification, nymphalid ground plan, trailing band, Sarawak

ABSTRAK

Kajian ini menerangkan dan membandingkan variasi corak sayap antara spesies dalam suku Limenitidini. Sejumlah 37 spesies dari 13 genus telah diperiksa dan diilustrasi, di mana elemen corak pelan asas nymphalid (NGP) telah dilabel menggunakan warna. Secara amnya, lebih banyak elemen corak dapat dikenal pasti pada permukaan sayap ventral daripada permukaan sayap dorsal. Elemen *c* (simetri sistem basal), *d* (jalur proksimal pada pertengahan sistem simetri), *f* (jalur diskal pada pertengaan sistem simetri) dan *I* (elemen parafokal) adalah elemen yang paling banyak dijumpai di kalangan spesies dalam suku yang dikaji ini. Nilai jarak persamaan elemen corak pada permukaan sayap ventral yang terdapat dalam suku Limenitidini ini telah dibentuk menggunakan UPGMA. Dimorfism seksual dan persamaan warna di kalangan spesies dalam kajian ini turut dibincangkan.

Kata kunci: Pengecaman automatik, pelan asas nymphalid, jejak garisan, Sarawak

INTRODUCTION

Tribe Limenitidini is divided into three subtribes, namely subtribe Limenitiditi, Partheniti and Adoliaditi (Corbet & Pendlebury 1992). Subtribe Limenitiditi comprises of 10 genera, which are *Pantoporia, Lasippa, Neptis, Phaedyma, Athyma, Moduza, Pandita, Auzakia, Sumalia,* and *Parasarpa*, subtribe Partheniti is represented by two genera, which are *Lebadea* and *Parthenos,* while subtribe Adoliaditi comprises of five genera, which are *Tanaecia, Euthalia, Dophla, Bassarona,* and *Lexias*, respectively. All these genera are found in Borneo except for genus *Auzakia* (Tsukada 1991).

Wings of butterflies are made up of colourless and translucent membrane covered with overlapping scales. These scales which are arranged more likely of rows are responsible for the colours of the wings (Stavenga et al. 2004). Each wing has their own venation, which forms the pattern arrangement of the wings (Fleming 1975; Fleming & McCartney 1983). These pattern arrangement often play a significant role in the classification of Lepidoptera (Bascombe et al. 1999; Fordyce et al. 2002). The uniqueness of wing patterns make it possible to track the related species across their genera and families (Fordyce et al. 2002; Nijhout 2001). The pigmentation patterns of butterflies had been pointed out as one of the most remarkable and vivid model of pattern formation in biology (Nijhout 2003), and are remarkable for research of butterflies evolutionary and developmental pattern (Jiggins 2017). Other than that, the diverse colour pattern play an important role in facilitating intraspecific interactions as well as protecting the butterflies from predators in the form of mimicry and camouflage (Chai 1990; Nijhout 1991; Rutowski 1991), as well as to attract the opposite gender for mating purposes (Sekimura & Nijhout 2017). The diversities of colour pattern have caught the interest of many researchers to further study on the development and evolution of wing patterns within the butterfly species. Therefore, this study aims to identify the wing pattern variation among species of the tribe Limenitidini of Sarawak.

MATERIALS AND METHODS

Specimens Examined, Illustration, and Coding

A total of 207 specimens comprising of 13 genera and 34 species of the tribe Limenitidini deposited at UNIMAS Insect Reference Collection (UIRC), Faculty of Resource Science and Technology (FRST) were examined and illustrated (Table 1).

Table 1. List of species of the tribe Limenitidini deposited at UIRC

Genus	Species	No. of individuals
Athyma	*Athyma kanwa kanwa*	6
	Athyma nefte subrata	7
	Athyma pravara pravara	5
	Athyma reta reta	4
Bassarona	*Bassarona dunya dunya*	19
	Bassarona dunya monara	7
Dophla	*Dophla evelina magama*	3
Euthalia	*Euthalia godarti vacillaria*	4
	Euthalia iapis ambalika	8
	Euthalia monina bipunctata	4
Lasippa	*Lasippa tiga empat*	5
Lebadea	*Lebadea martha paduca*	1

Lexias	*Lexias canescens canescens*	2
	Lexias cyanipardus sandakanus	1
	Lexias dirtea chalcenoides	16
	Lexias dirtea opicus	10
	Lexias pardalis dirteana	5
Moduza	*Moduza procris agnata*	3
Neptis	*Neptis duryodana duryodana*	3
	Neptis hylas sopatra	11
	Neptis ilira cindia	1
	Neptis leucoporos cresina	4
	Neptis magadha plautia	1
Pandita	*Pandita sinope sinope*	32
Pantoporia	*Pantoporia sandaka sandaka*	4
Parthenos	*Parthenos sylvia borneensis*	1
Tanaecia	*Tanaecia aruna aparasa*	6
	Tanaecia aruna aruna	1
	Tanaecia aruna pardalis	10
	Tanaecia clathrata coerulescens	9
	Tanaecia munda fruhstorferi	3
	Tanaecia munda munda	8
	Tanaecia pelea djataca	1
	Tanaecia pelea lutala	2
	Total number of individuals	207
	Total number of species	34

Photographs of the wing for each species were captured by using a digital compact camera (Olympus TG-4) and the images were processed using Adobe Photoshop (Adobe System Inc.). Methods of examining and illustrating wing pattern diversity in the papilionid butterflies are adapted and follows Penz and Mohammadi (2013). Figures with colour coded key identifying wing pattern elements were prepared using representative of each genus, focusing on the characteristics of their wing patterns based on the nymphalid ground plan (NGP). The images used to describe pattern elements were converted to a similar size while images used to illustrate sexual dimorphism and colour resemblance were converted proportionately to life size to compare the variation.

Homology and Identification of Pattern Elements

Following the NGP framework by Nijhout (1991), the pattern elements have been identified based on the characters expressed and will correspond to the wing background. However, the wing background colour may or may not be homogenous across the wing surface. In addition, the nine pattern elements observed in Limenitidini are indicated by letters *b* to *j* from the wing base to the distal edge, following Nijhout (1991), namely *b,c* = basal symmetry system; *d* = proximal band of central symmetry system; *e* = discal spot; *f* = discal band at central symmetry system; *g* = outer boundary of border ocelli system; *h* = border ocelli; *i* = parafocal element; and *j* = submarginal and marginal bands.

Data Analysis

A dendrogram was constructed with Unweighted Pair-Groups Method Average (UPGMA) clustering method using the Multi-Variate Statistical Package (MVSP) software to show the similarity of wing pattern characters among the species examined in this study.

RESULTS AND DISCUSSION

Pattern elements of the NGP were easily identified in most specimens used in this study, although some species had reduced patterns. Images of wings and colour- coded key figures for identifying wing pattern elements across genera were represented in Figures 1-12, while images that show sexual dimorphism and colour resemblance across genera were represented in Figures 13-18.

Ventral Wing Surface

The diversity of ventral wing pattern elements within tribe Limenitidini is illustrated in Figures 1-6. The number of visible wings colour and pattern elements varies between and sometimes within genera. Ventral forewing (VFW) usually shows more visible elements than the ventral hindwing (VHW).

Most of the butterflies' VFW contains pattern elements of *b* to *j*. Elements *b, c* and *d,* are sometimes connected in a few genera on VFW, such as genus *Athyma* (Figures 1(a) & 1(c)), *Lasippa* (Figure 2(e)), *Neptis* (Figures 4(b)-(f)) and *Pantoporia* (Figure 5(b)), thus making element *d* or *c* vestigial or absent. Elements *e, g* and *h* are reduced in several genera while the other two pattern elements, *i* and *j* or sub-marginal bands are mostly visible in most species but one or both can be absent. For example, *Bassarona dunya dunya* (Figure 1(e)) and *B. dunya monara* (Figure 1(f)) only exhibit pattern element *i* while pattern element *j* is absent on both VFW and VHW. The sub-marginal bands are usually thin and distinctive in most of the species, such as *A. kanwa kanwa* (Figure 1(a)) while some are broad and diffuse, such as *Parthenos sylvia borneensis* (Figure 5(c)).

The VHW usually contains pattern elements *c, d, f, i* and *j* in most of the species examined. Elements *b, e* and *h* might be reduced in most species but present in some genus while element *g* is absent on the VHW in all genera examined. The position and appearance of pattern elements vary between both wing surfaces due to the different shape between VFW and VHW. Commonly, the elements *c* and *d* are located distally on the VFW while element *f* is located proximally on the VFW and VHW.

According to Penz and Mohammadi (2013), element *h* or border ocelli can be absent, fragmented, continuously diffuse or form a uniquely broad band. Most of the species examined do not have element *h* while some of them have element *h*, but only as a small spot, simple spot, and broad band. For example, *Lebadea martha paduca* (Figure 2(f)) have simple spots on the VFW and a broad band of element *h* on the VHW. Most species in genus *Lexias* (Figure 3), also contain simple spots of ocelli on the VFW and VHW.

The colour, width and intensity of trailing bands may vary between genera. Several species have dark wing background, which make the trailing bands more visible, for example, *A. nefte subrata* (Figure 1(b)), while species with lighter wing background and white trailing bands looks pale, such as *L. martha paduca* (Figure 2(f)).

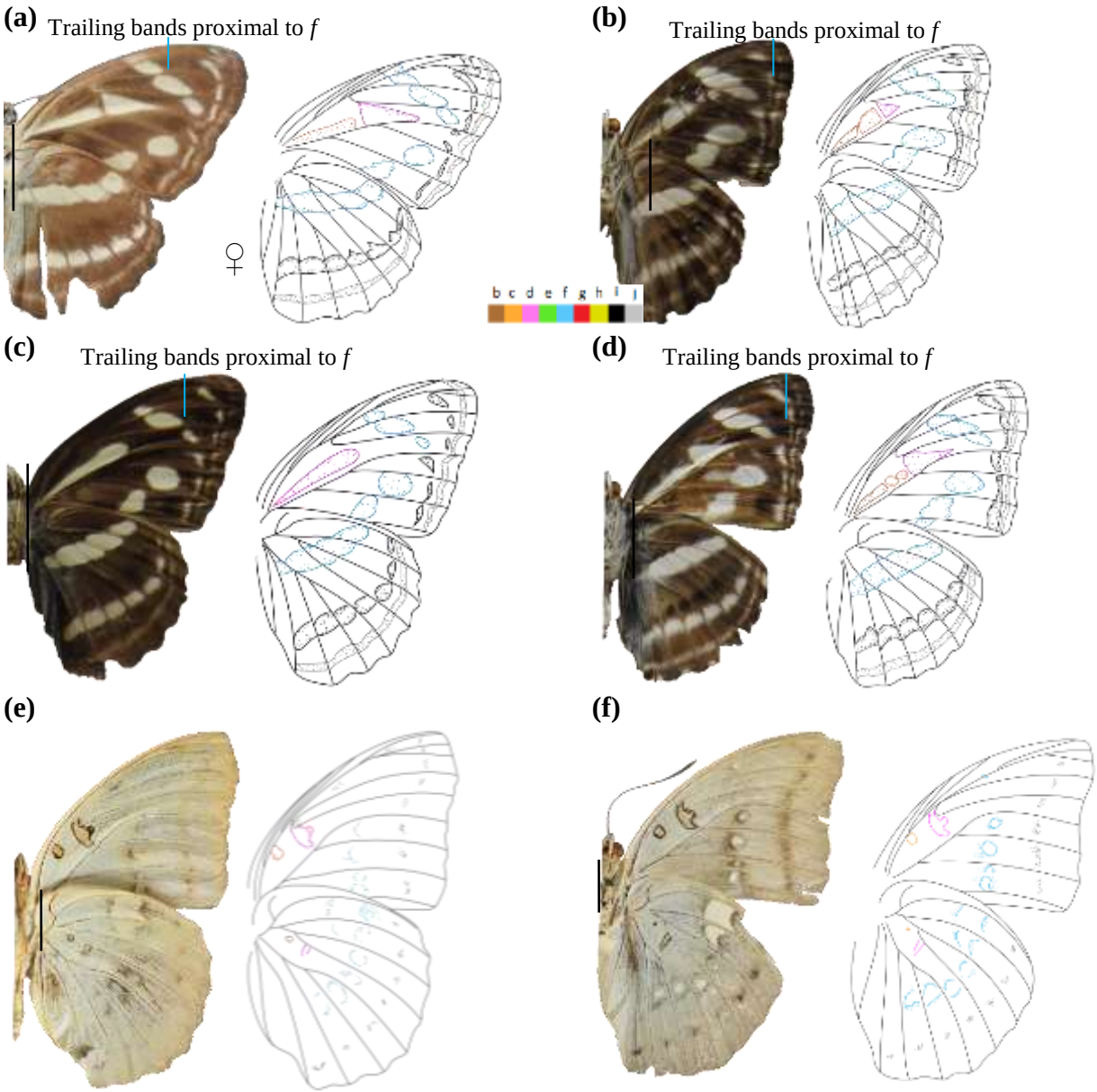


Figure 1. Wings in ventral view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Athyma kanwa kanwa* (Kuching); (b) *A. nefte subrata*, (Lundu); (c) *A. pravara pravara* (Balul); (d) *A. reta reta* (Kuching); (e) *Bassarona dunya dunya* (Miri); (f) *B. dunya monara* (Lundu)

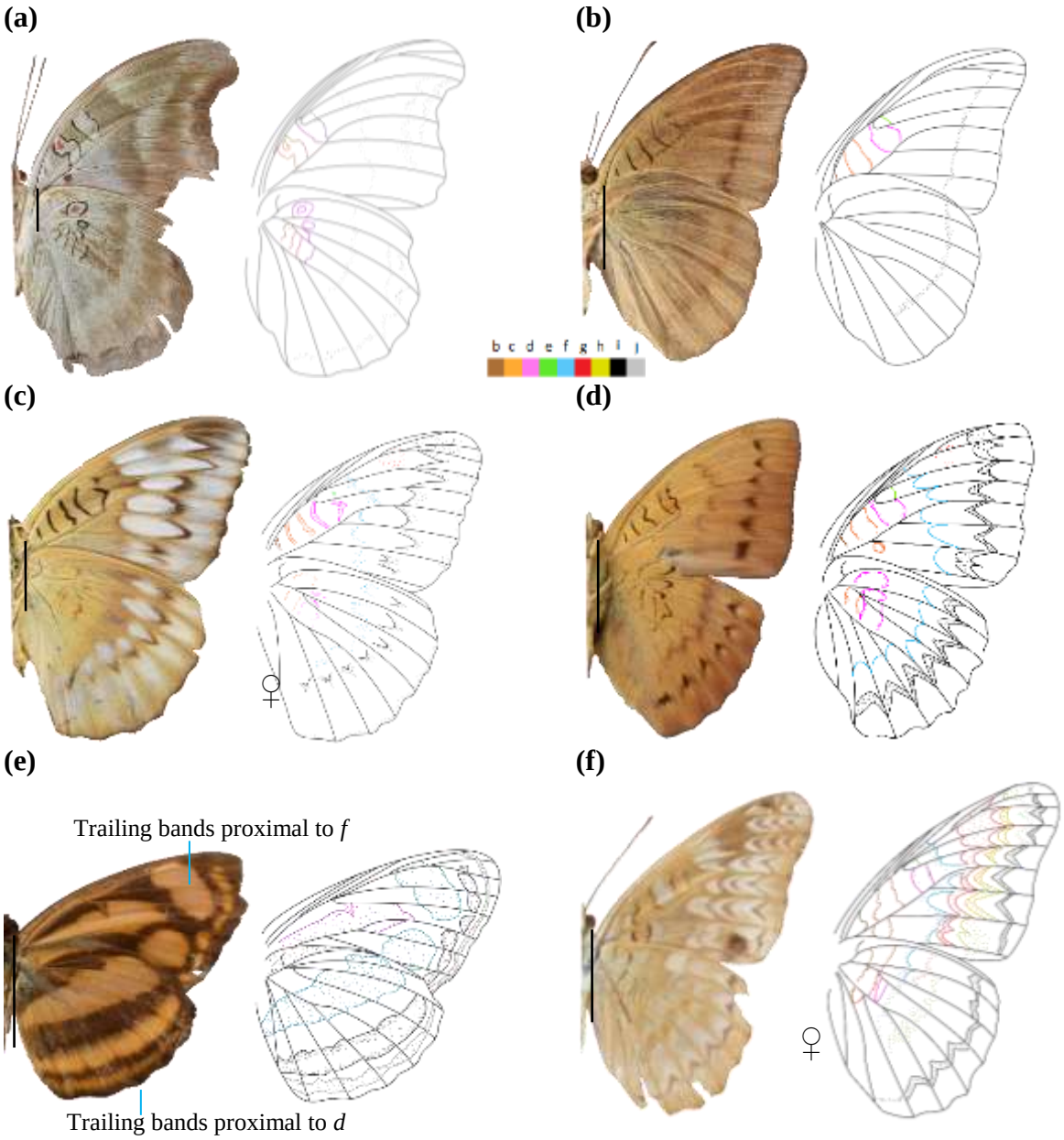


Figure 2. Wings in ventral view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Dophla evelina magama* (Miri); (b) *Euthalia godarti vacillaria* (Kuching); (c) *E. iapis ambalika* (Kuching); (d) *E. monina bipunctata* (Bau); (e) *Lasippa tiga empat* (Kuching); (f) *Lebadea martha paduca* (Lundu)

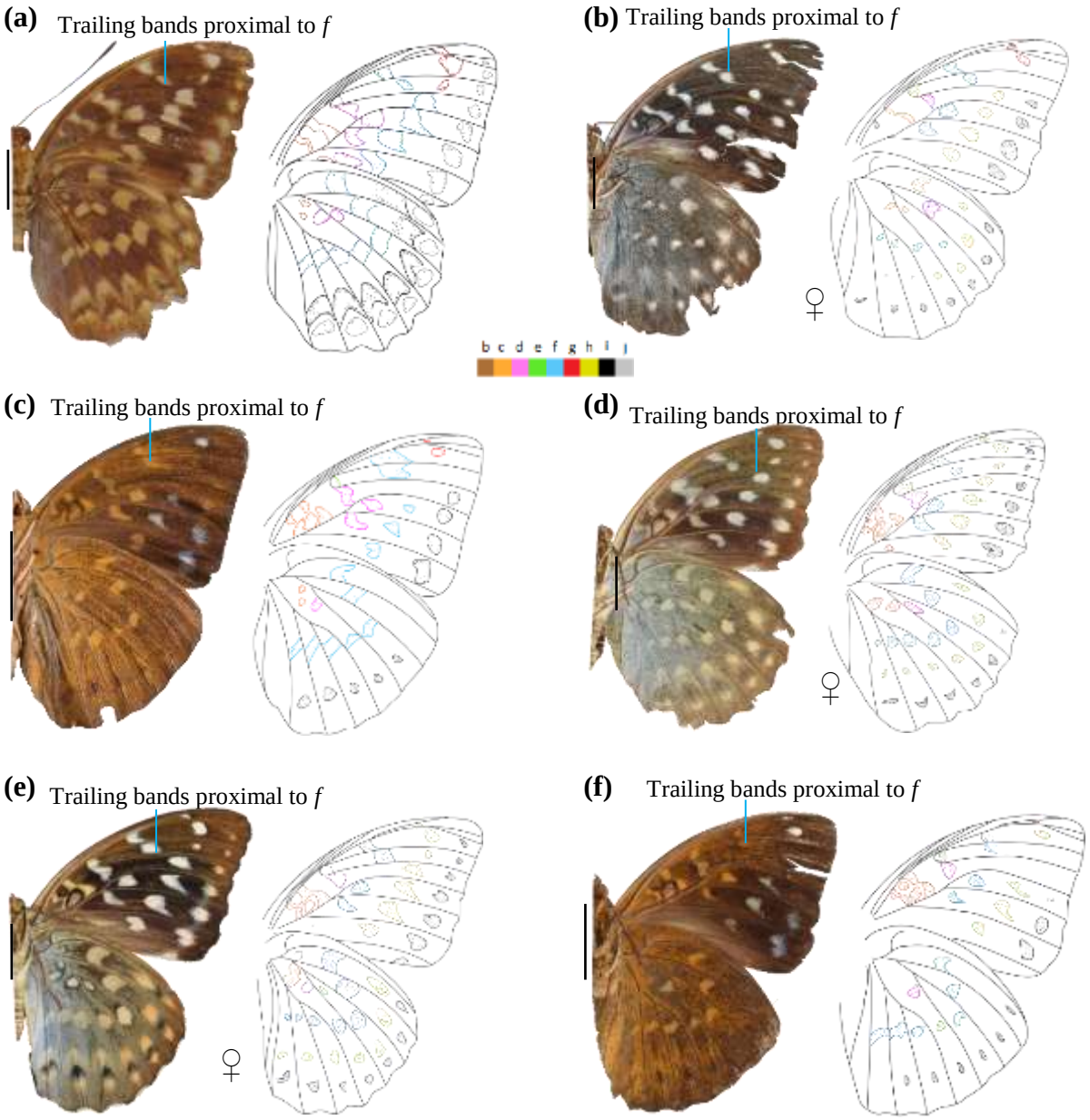


Figure 3. Wings in ventral view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Lexias canesce canescens* (Kuching); (b) *L. cyanipardus sandakanus* (Kota Samarahan); (c) *L. dirtea chalcenoides* (Miri); (d) *L. dirtea chalcenoides* (Kota Samarahan); (e) *L. dirtea opicus* (Kota Samarahan); (f) *L. pardalis dirteana* (Serian)

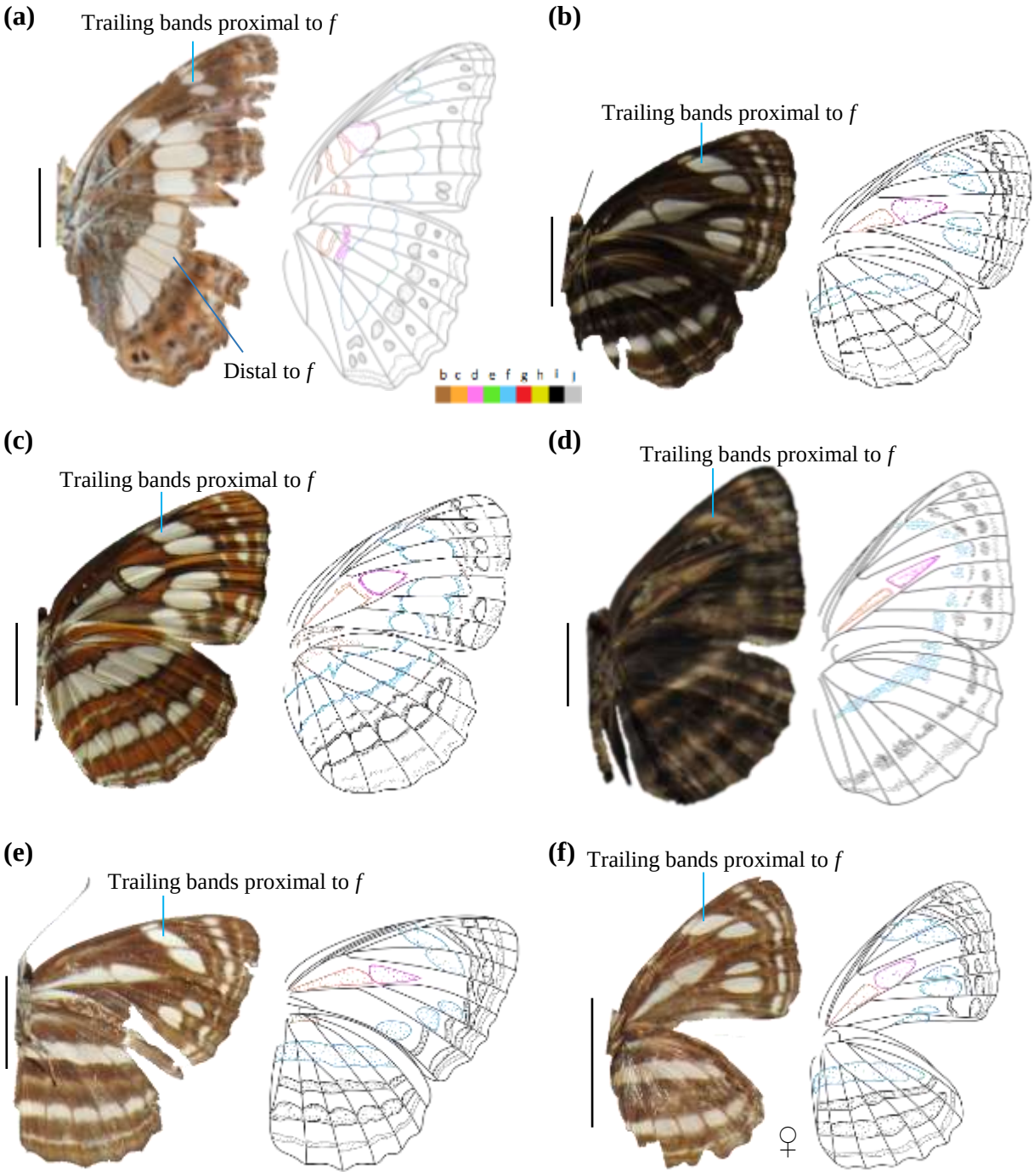


Figure 4. Wings in ventral view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Moduza Procris agnata* (Kota Samarahan); (b) *Neptis duryodana duryodana* (Miri); (c) *N. hylas sopatra* (Kuching); (d) *N. ilira cindia* (Lundu); (e) *N. leucoporos cresina* (Serian); (f) *N. magadha plautia* (Kota Samarahan)

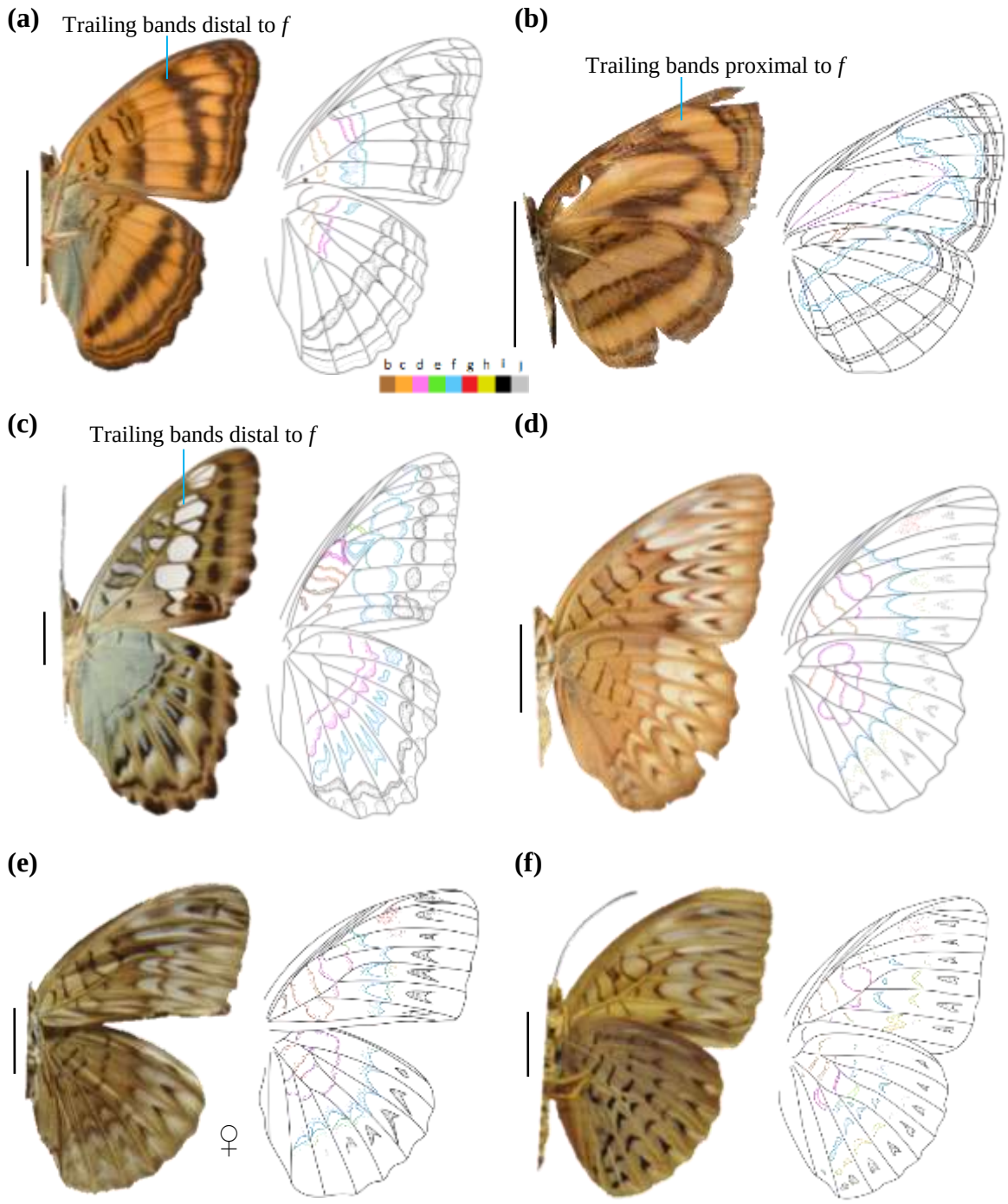


Figure 5. Wings in ventral view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Pandita sinope sinope* (Kota Samarahan); (b) *Pantoporia sandaka sandaka* (Kuching); (c) *Parthenos sylvia borneensis* (Miri); (d) *Tanaecia aruna aparasa* (Kuching); (e) *T. aruna aruna* (Lundu); (f) *T. aruna pardalis* (Kota Samarahan)

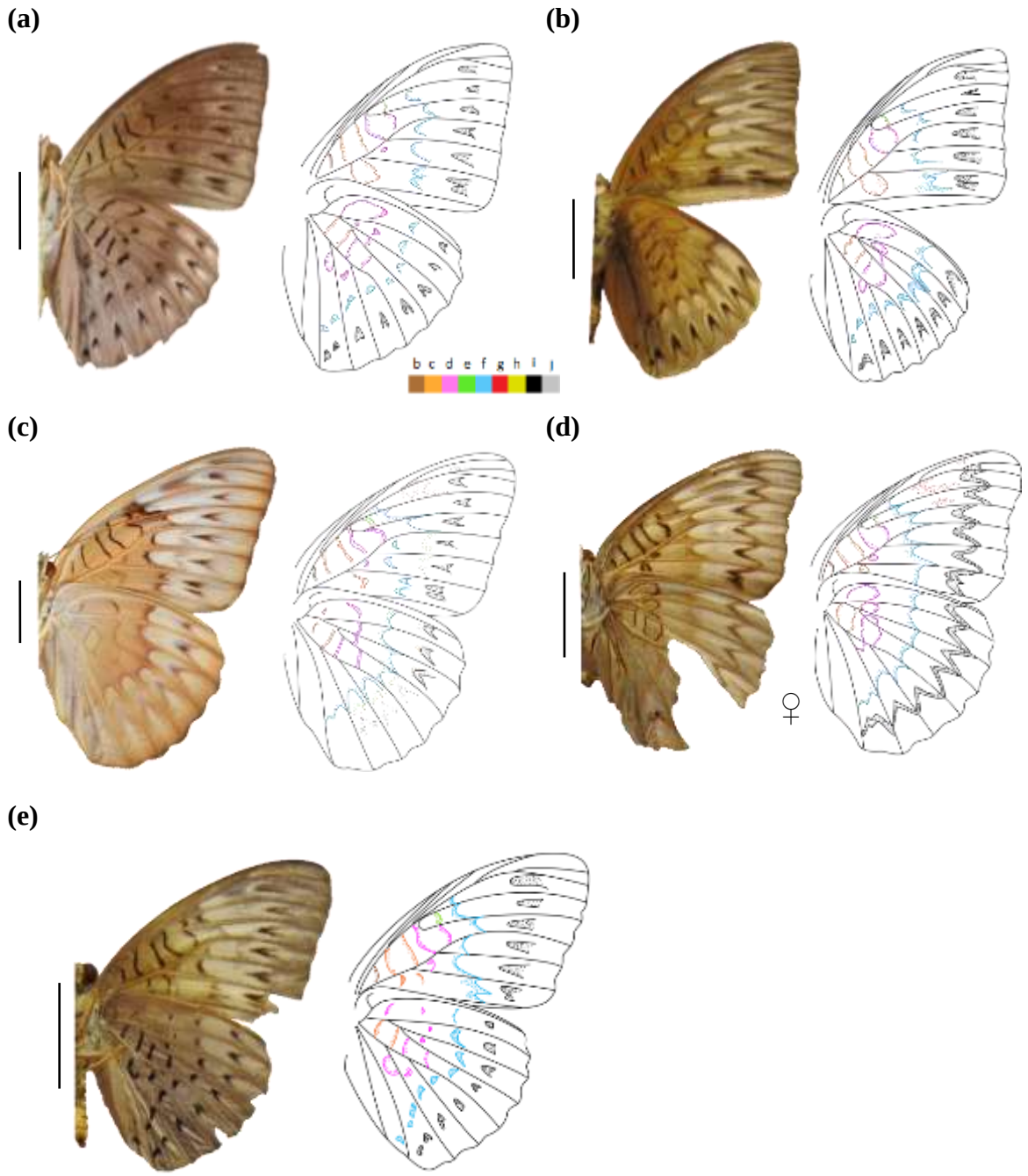


Figure 6. Wings in ventral view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Tanaecia clathrata coerulescens* (Kuching); (b) *T. munda fruhstorferi* (Kota Samarahan); (c) *T. munda munda* (Kuching); (d) *T. pelea djataca* (Kota Samarahan); (e) *T. pelea lutala* (Lundu)

Dorsal Wing Surface

The dorsal colour and pattern elements are simpler than ventral colour and pattern elements. This is because of reducing number of pattern elements and presence of trailing bands, and as well as iridescent patches, which is not part of the nymphalid ground plan (Penz & Mohammadi 2013). Based on the observation, the DFW contains elements *b* to *j* while the dorsal DHW contains *c, d, f, i*, and *j* in most of the species examined. However, elements *b, e, g* and *h* are absent on the DHW in most of the species. Element *e* can only be found in *Lebadea martha paduca* (Figure 9(a)) on the DHW.

Most of the species have darker wing background, which contrasts with the trailing bands colour. The trailing bands are present in all species of genus *Athyma* that were examined (Figure 7). In some species, the sub-marginal bands, elements *f, g* and *h* might be absent but uniquely, iridescent patches are present on the DFW and DHW. Iridescent patches can be seen in males of *Euthalia godarti vacillaria* (Figure 8(c)), *Lexias dirtea chalcenoides* (Figure 9(e)), *L. pardalis dirteana* (Figure 10(b)), *Tanaecia clathrata coerulescens* (Figure 12(c)) and female of *E. iapis ambalika* (Figure 8(d)), *L. cyanipardus sandakanus* (Figure 9(c)) and *L. dirtea opicus* (Figure 9(f)). In contrast, *P. sylvia borneensis* (Figure 11(e)) is the only species that have intervenous stripes on the DHW among the species that were examined.

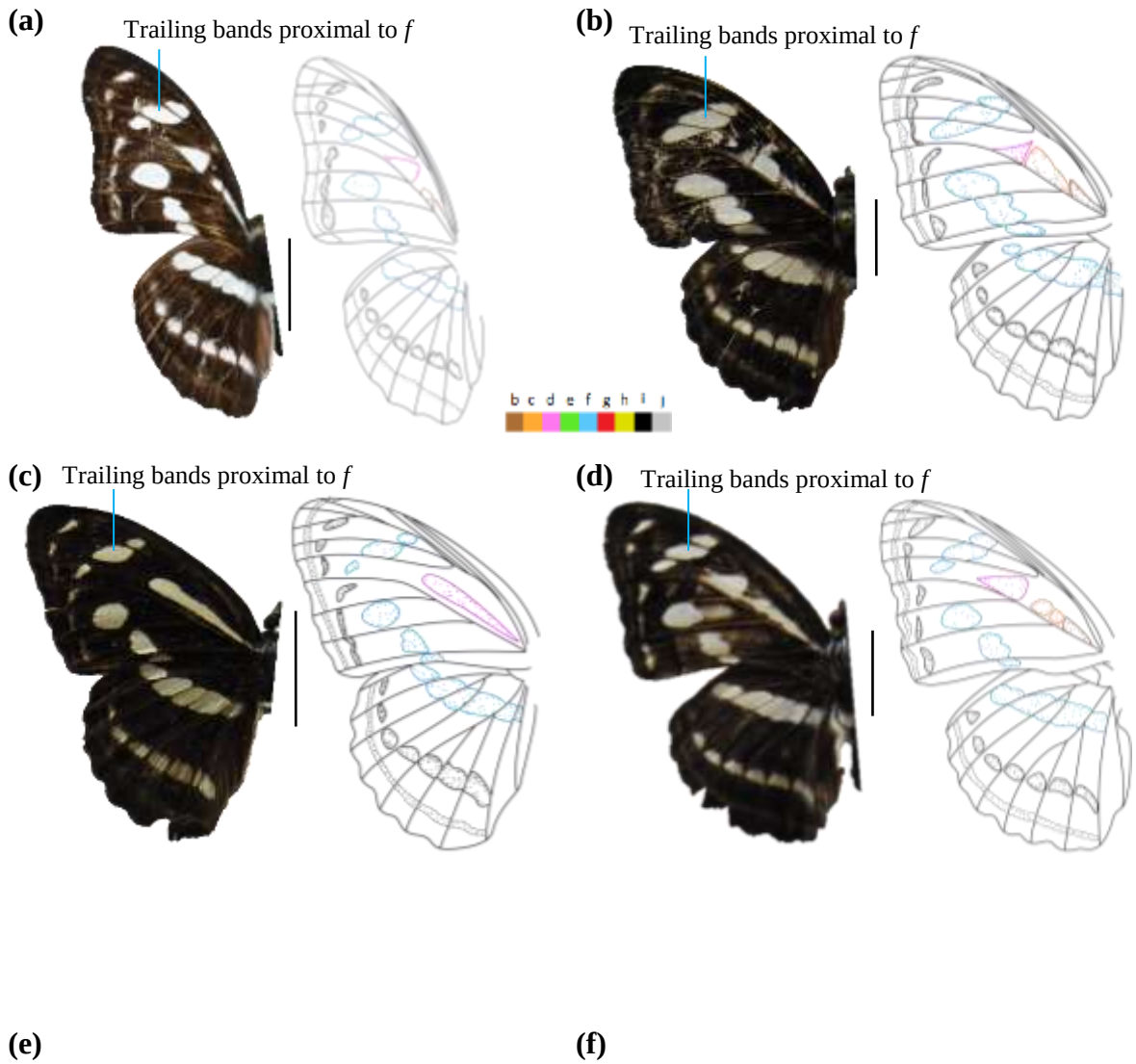
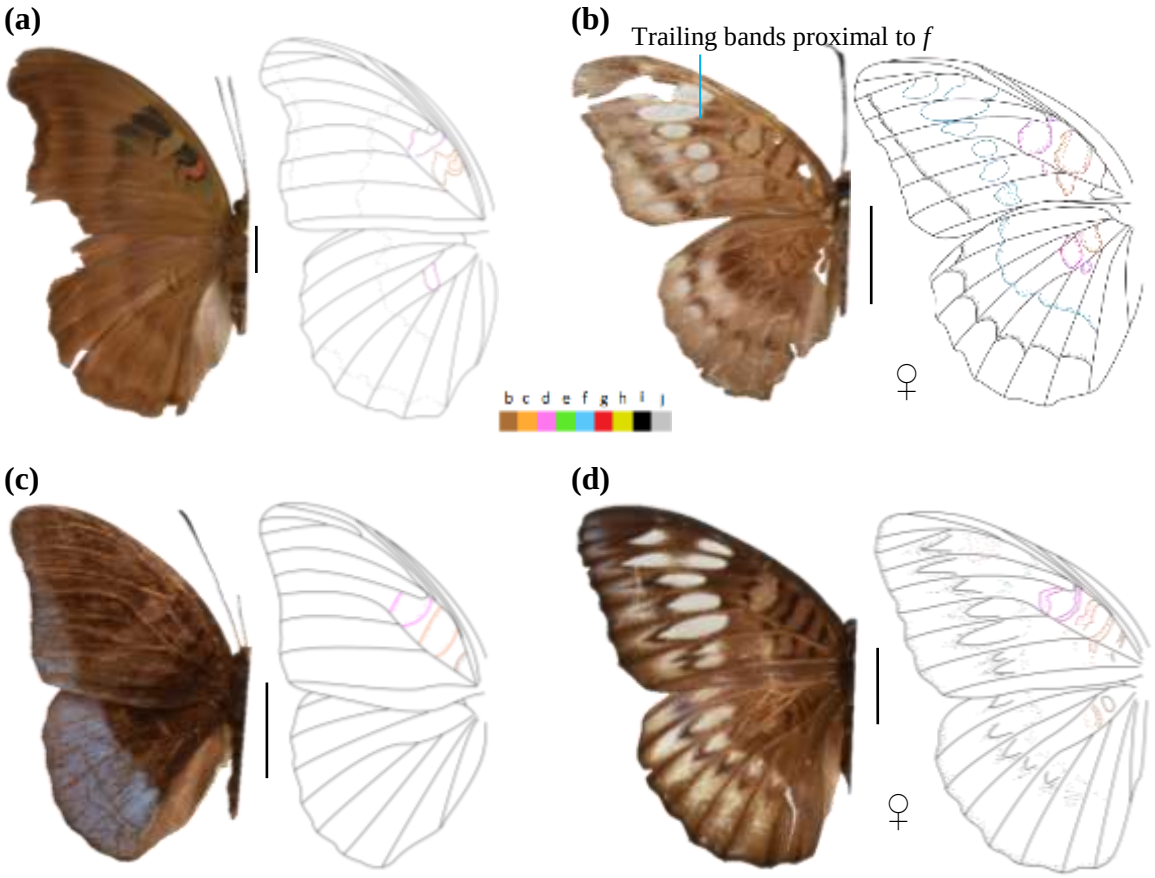


Figure 7. Wings in dorsal view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Athyma kanwa kanwa* (Lundu); (b) *A. nefte subrata* (Lundu); (c) *A. pravara pravara* (Bau); (d) *A. reta reta* (Kuching); (e) *Bassarona dunya dunya* (Kuching); (f) *B. dunya monara* (Lundu)



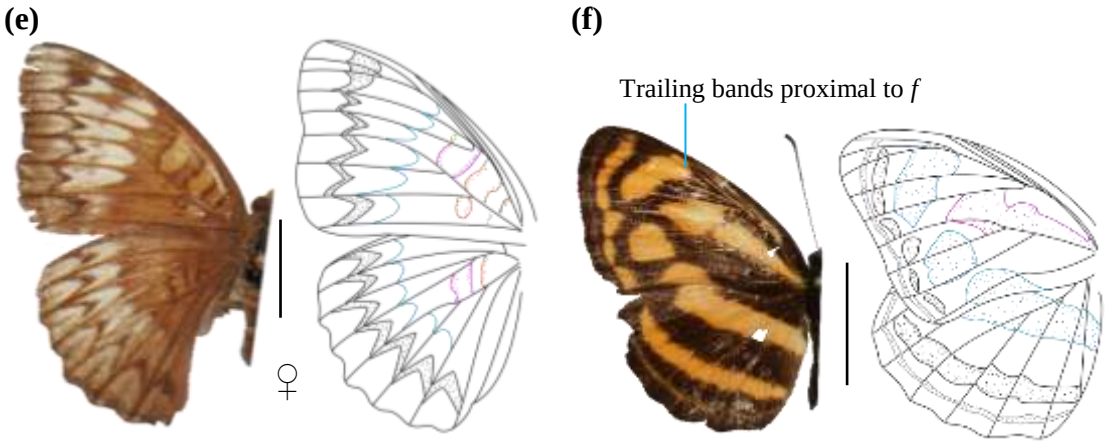
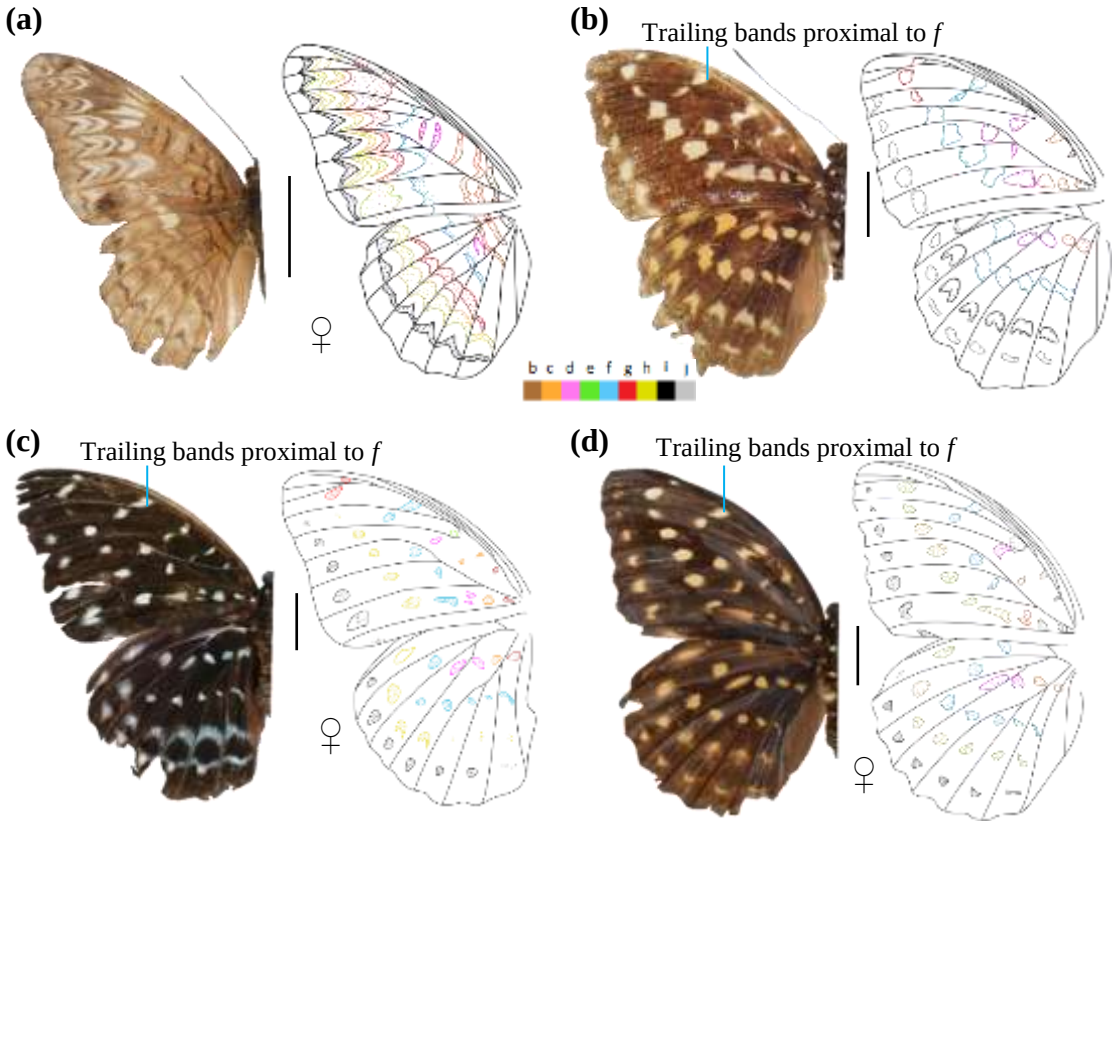


Figure 8. Wings in dorsal view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Dophla evelina magama* (Miri); (b) *Euthalia godarti vacillaria* (Kuching); (c) *E. godarti vacillaria* (Kuching); (d) *E. iapis ambalika* (Kuching); (e) *E. monina bipunctata* (Lundu); (f) *Lasippa tiga empat* (Kuching)



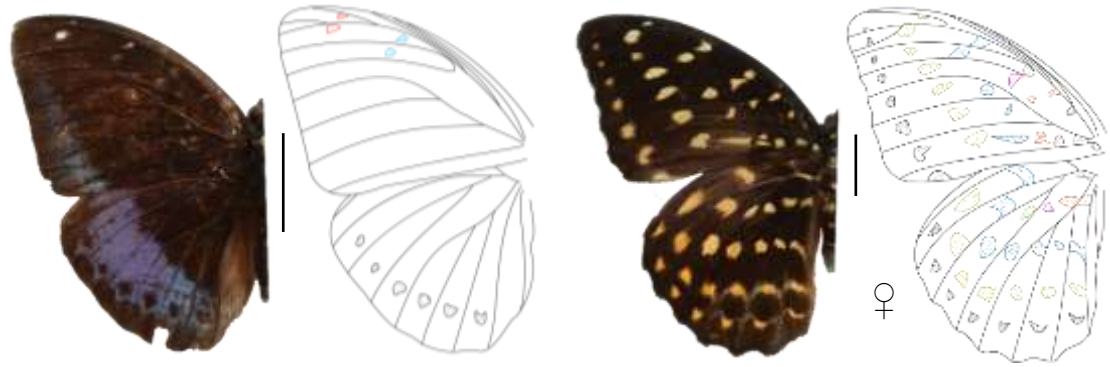
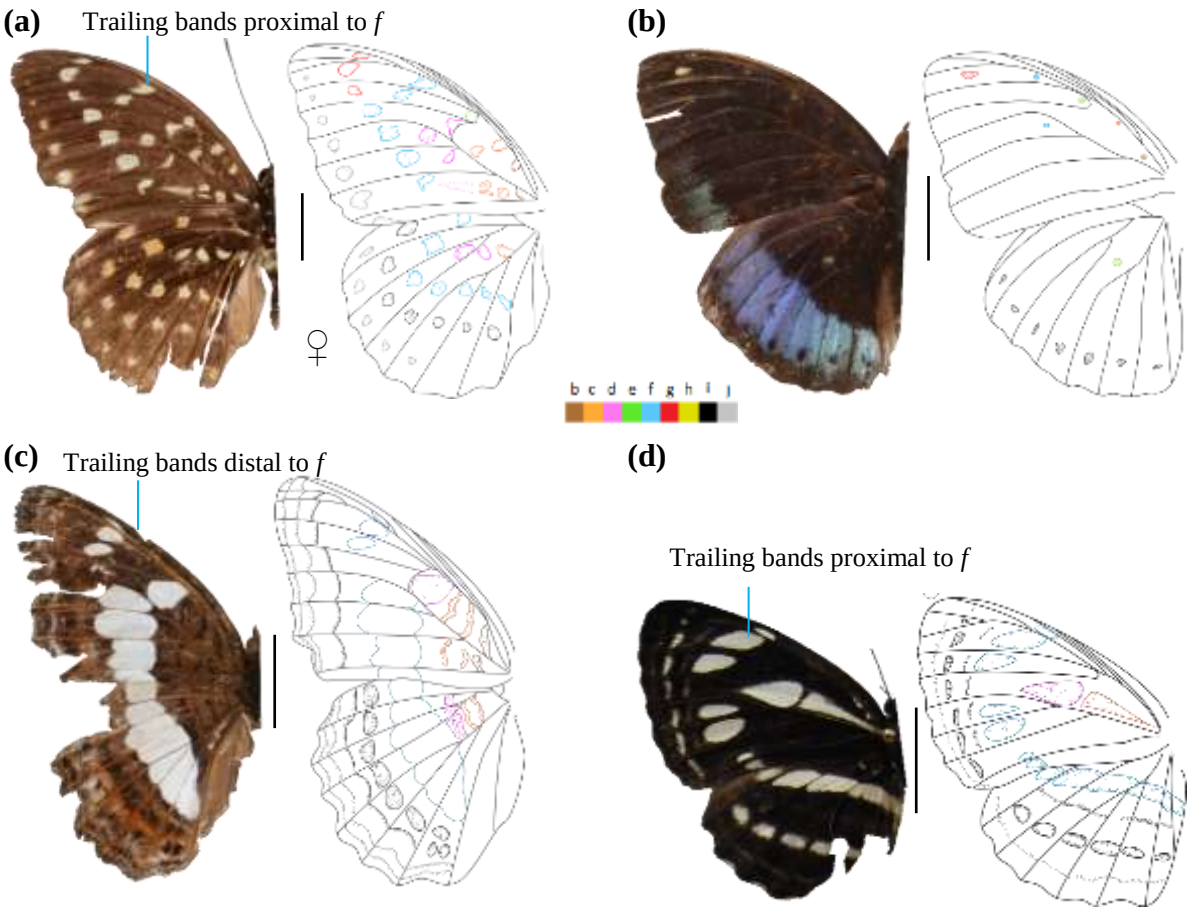


Figure 9. Wings in dorsal view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Lebadea martha paduca* (Lundu); (b) *Lexias canescens canescens* (Kuching); (c) *Lexias cyanipardus sandakanus* (Kota Samarahan); (d) *Lexias dirtea chalcenoides* (Kota Samarahan); (e) *Lexias dirtea chalcenoides* (Miri); (f) *Lexias dirtea opicus* (Kota Samarahan)



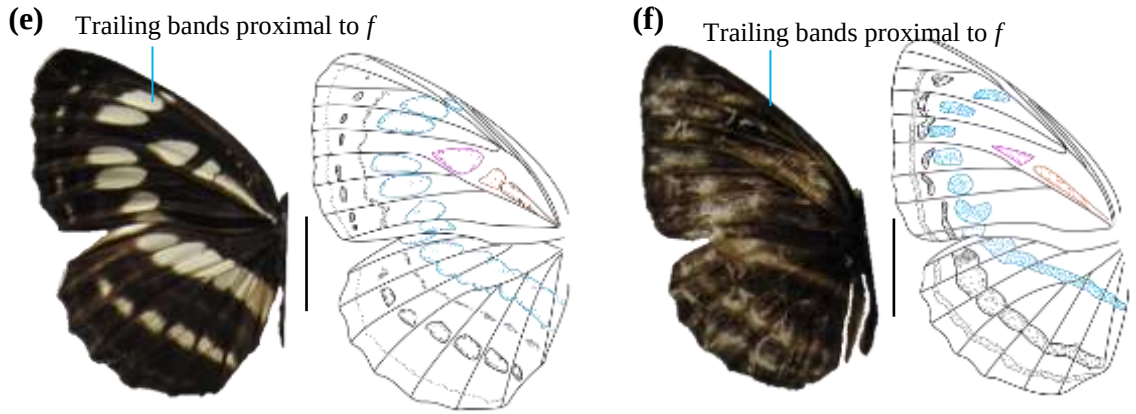
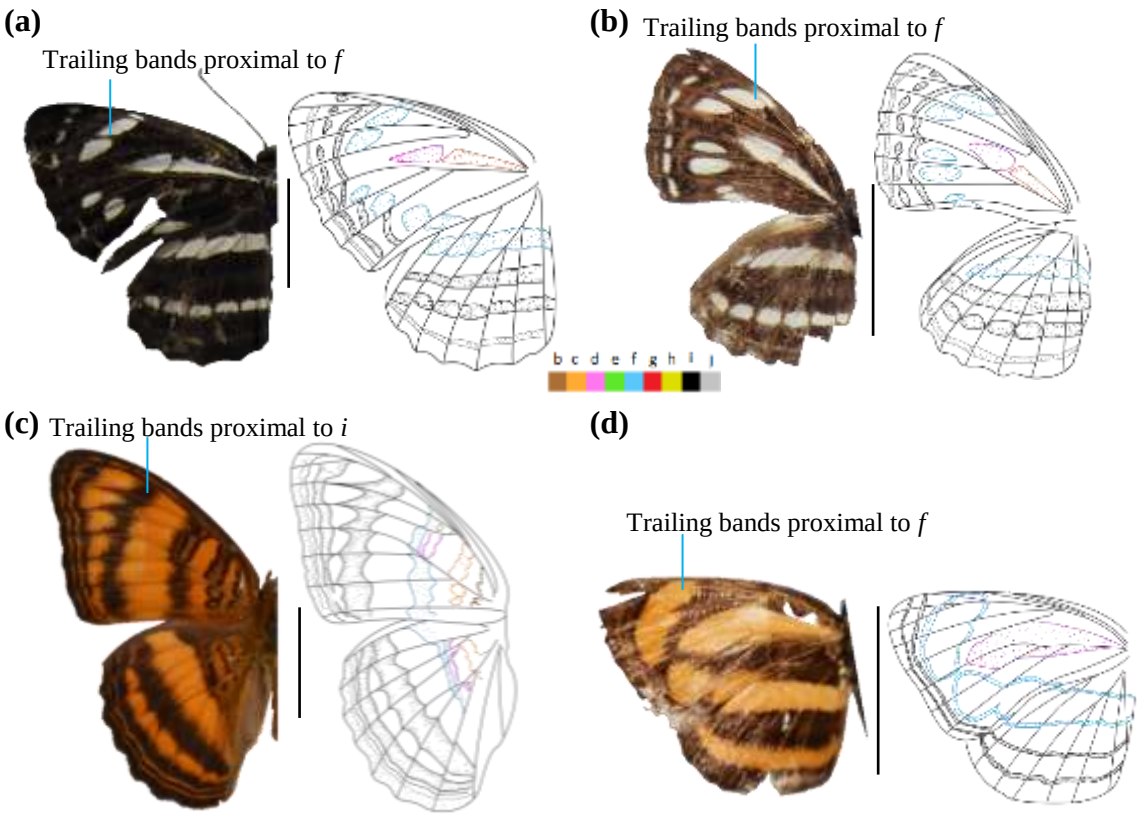


Figure 10. Wings in dorsal view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Lexias pardalis dirteana* (Lundu); (b) *L. pardalis dirteana* (Serian); (c) *Moduza procris agnata* (Kota Samarahan); (d) *Neptis duryodana duryodana* (Miri); (e) *N. hylas sopatra* (Kuching); (f) *N. ilira cindia* (Lundu)



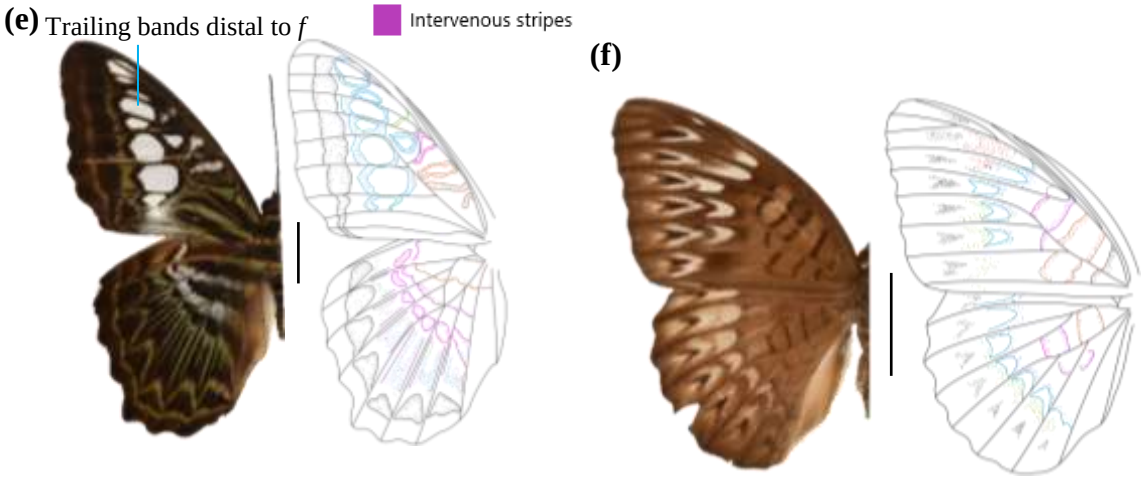
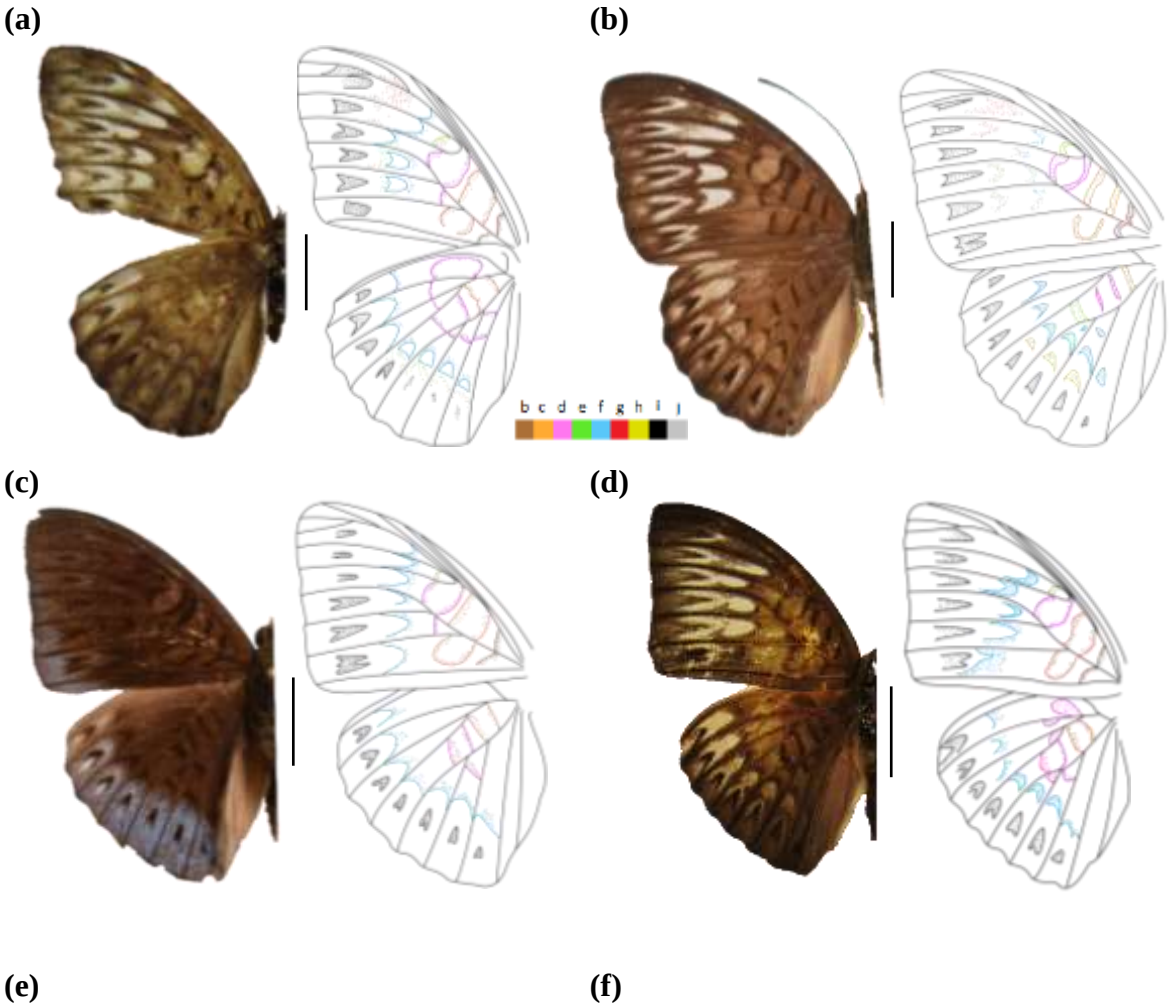


Figure 11. Wings in dorsal view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Neptis leucoporos cresina* (Serian); (b) *N. magadha plautia* (Kota Samarahan); (c) *Pandita sinope sinope* (Kota Samarahan); (d) *Pantoporia sandaka sandaka* (Kuching); (e)*Parthenos sylvia borneensis* (Miri); (f) *Tanaecia aruna aparasa* (Kuching)



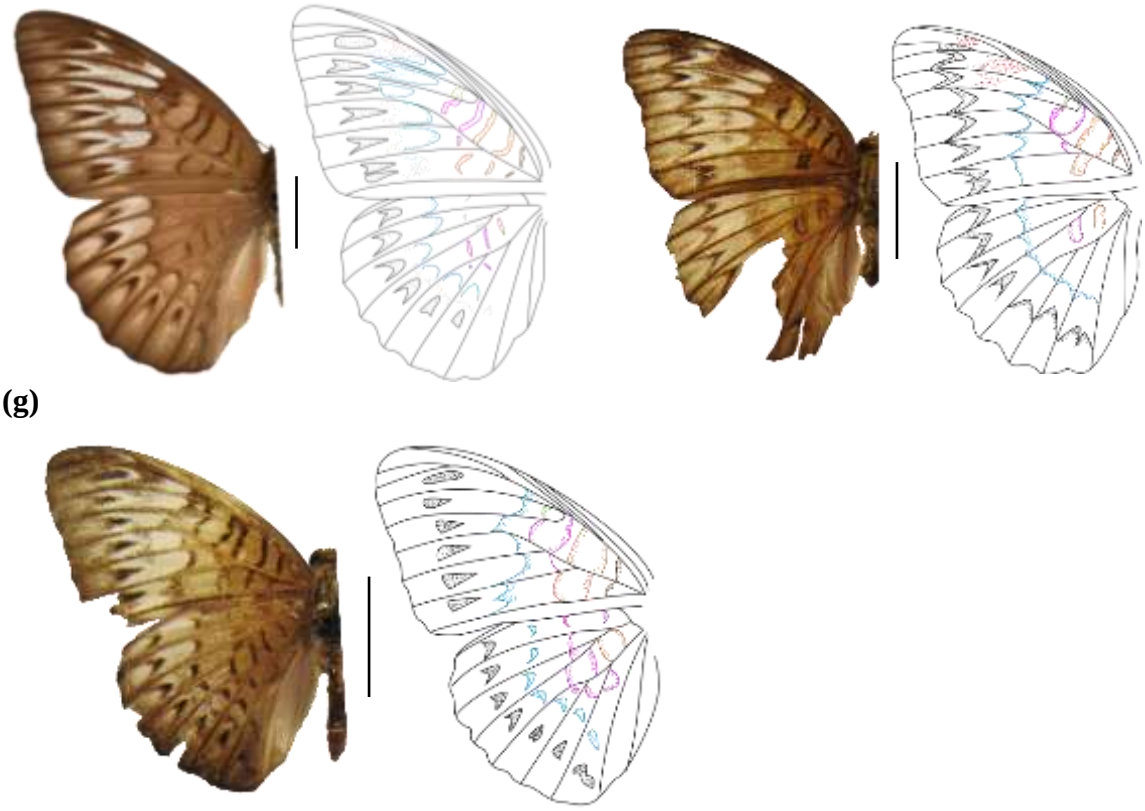


Figure 12. Wings in dorsal view plus a schematic drawing colour-coded pattern elements. Mostly males, except when indicated. Scale bars = 1 cm. (a) *Tanaecia aruna aruna* (Lundu); (b) *T. aruna pardalis* (Kota Samarahan); (c) *T. clathrata coerulescens* (Kuching); (d) *T. munda fruhstorferi* (Kota Samarahan); (e) *T. munda munda* (Kuching); (f) *T. pelea djataca* (Kota Samarahan); (g) *T. pelea lutala* (Lundu)

Sexual Dimorphism and Colour Resemblance

Based on the specimens that were examined, females tend to be larger than males in size although they exhibit similarities in shape. The colour and pattern elements are almost similar between males and females in most species except *Athyma nefte subrata* (Figure 13(b)), *Euthalia godarti vacillaria* (Figure 15(a)), *E. monina bipunctata* (Figure 15(c)), *Lexias dirtea chalcenoides* (Figure 16(a)), *L. pardalis dirteana* (Figure 16(b)), *Tanaecia aruna aparasa* (Figure 17(c)), *T. aruna pardalis* (Figure 17(d)) and *T. clathrata coerulescens* (Figure 18(a)). Females of *A. nefte subrata* have brown wing background with orange pattern while the males have darker wing background and white pattern. These two is easily distinguished because of the colour differences and their elements *b*, *c* and *d*, the male have separated cell streak (Otsuka 1988) while the female cell streak is not separated. The males and females of *E. godarti vacillaria*, *E. monina bipunctata*, *L. dirtea chalcenoides*, *L. pardalis dirteana* and *T. clathrata coerulescens* are completely different because the males tend to have darker wing background, reduced pattern elements and the presence of iridescent patches while the females tend to have brighter wing background and pattern elements. In the case of *E. iapis ambalika* (Figure 15(b)), the females have similar colour pattern elements but exhibit two forms of appearance. Based on the observation of *E. iapis ambalika* in this study, the individuals have slight iridescence at the apex of the DFW and DHW.

The similarities on the wing colour and pattern elements make it hard to distinguish between the sexes unless it has distinguishable pattern elements. For instance, both male and female of *A. kanwa kanwa* (Figure 13(a)) exhibit divided white cell forming a club and a triangle (Otsuka 1988) but the club is divided only in male individuals. On another note, *B. dunya dunya* (Figure 13(e)) and *B. dunya monara* (Figure 14(e)) have almost similar wing colour patterns. However, the shape of the white spots at space 7 and 6 are differ between male and female individuals.

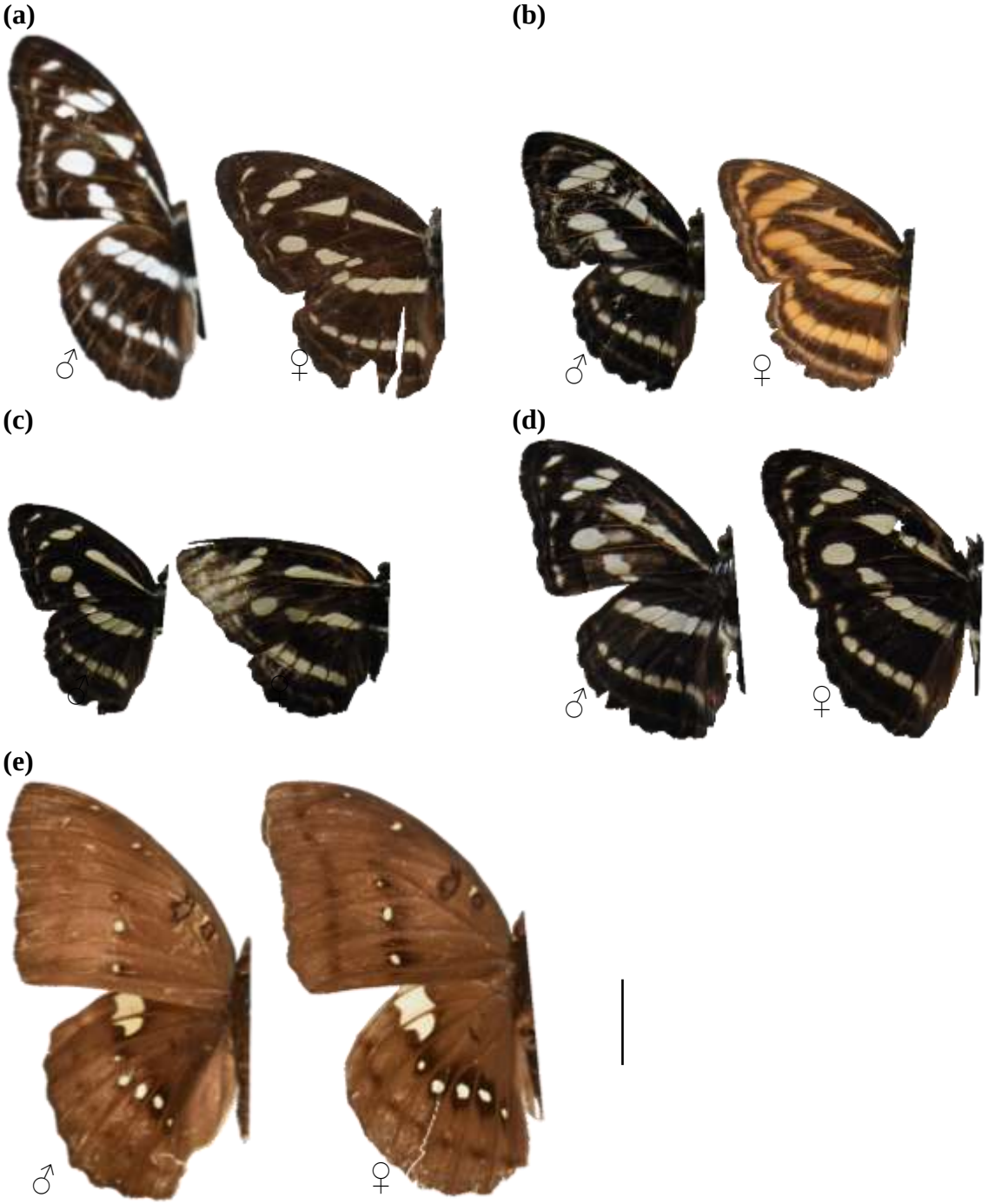


Figure 13. Wings in dorsal view showing sexual dimorphism and colour convergence. Scale bar = 1 cm. (a) *Athyma kanwa kanwa*; (b) *A. nefte subrata*; (c) *A. pravara pravara*; (d) *A. reta reta*; (e) *Bassarona dunya dunya*

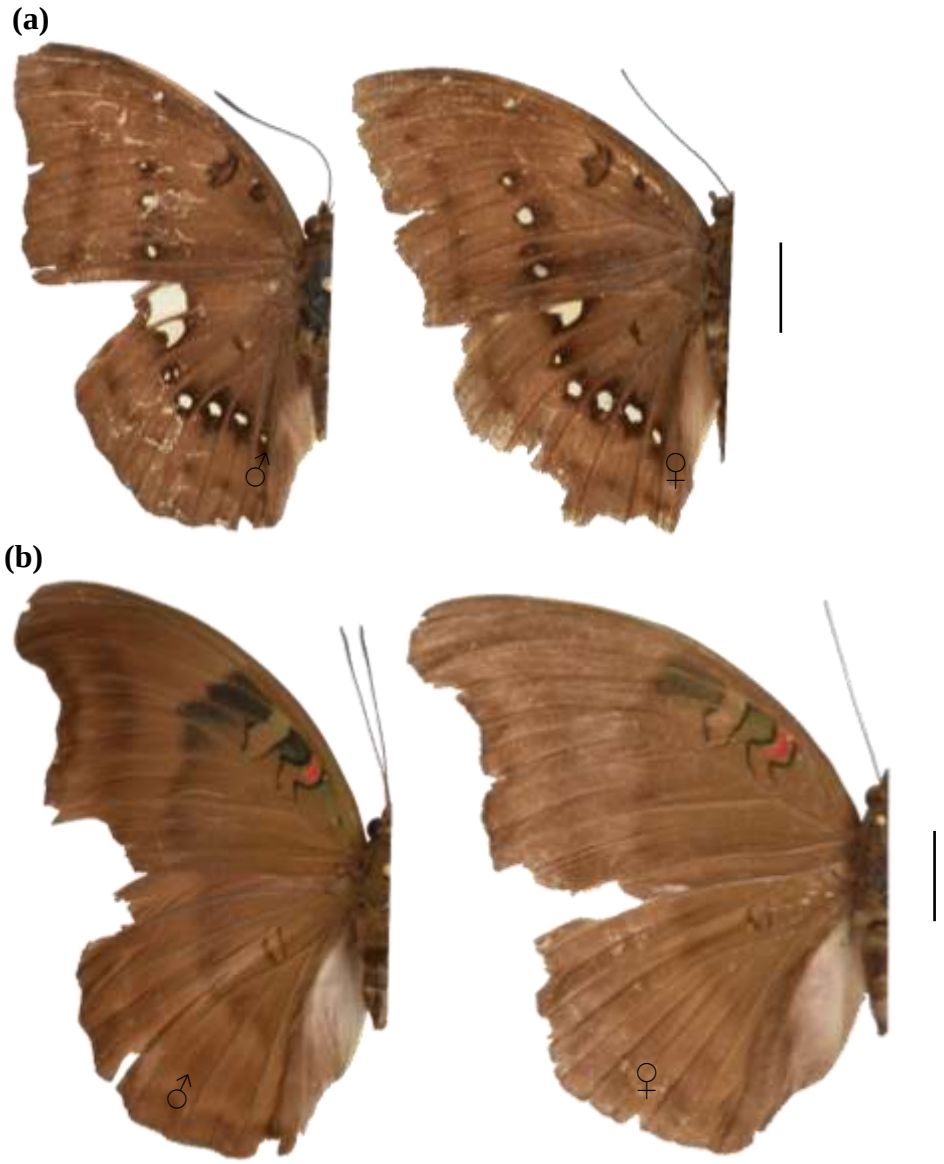
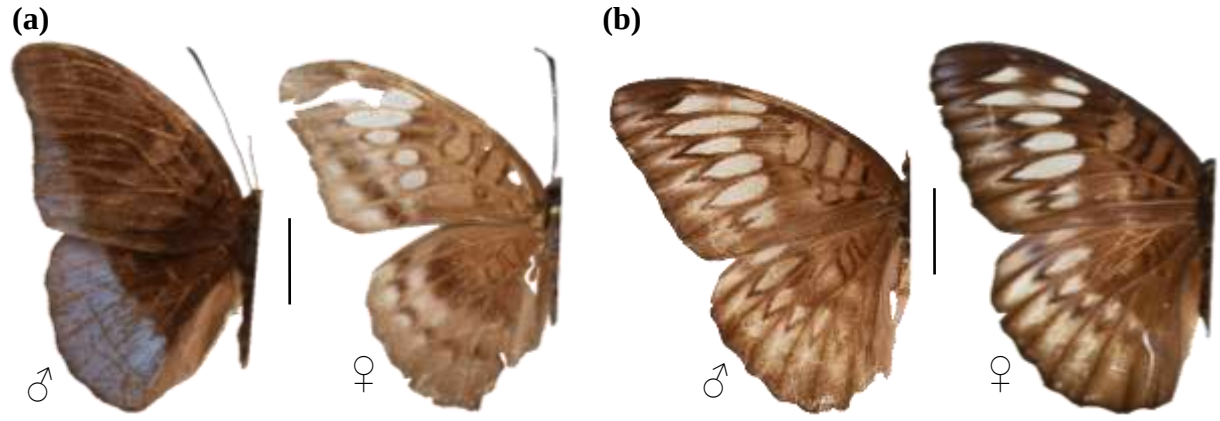


Figure 14. Wings in dorsal view showing sexual dimorphism and colour convergence. Scale bars = 1 cm. (a) *Bassarona dunya monara*; (b) *Dophla evelina magama*



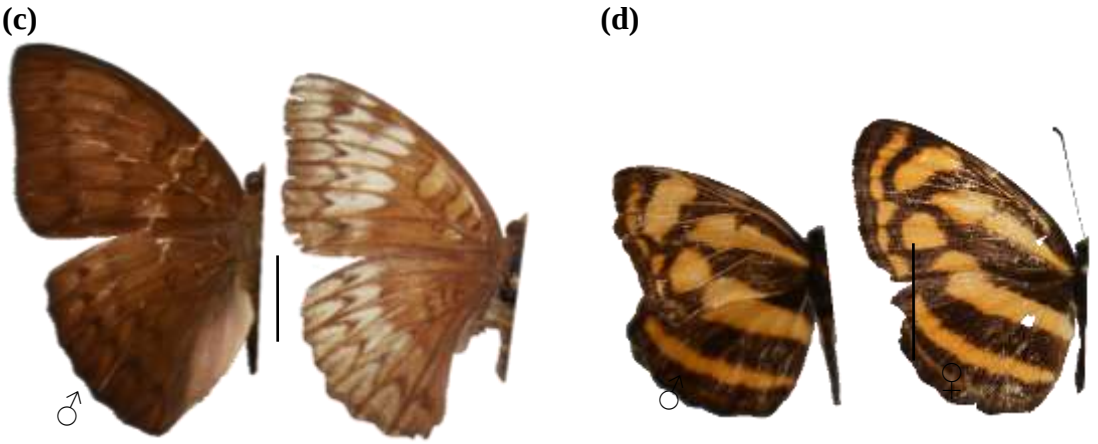


Figure 15. Wings in dorsal view showing sexual dimorphism and colour convergence. Scale bars = 1 cm. (a) *Euthalia godarti vacillaria*; (b) *E. iapis ambalika*; (c) *E. monina bipunctata*; (d) *Lasippa tiga empat*

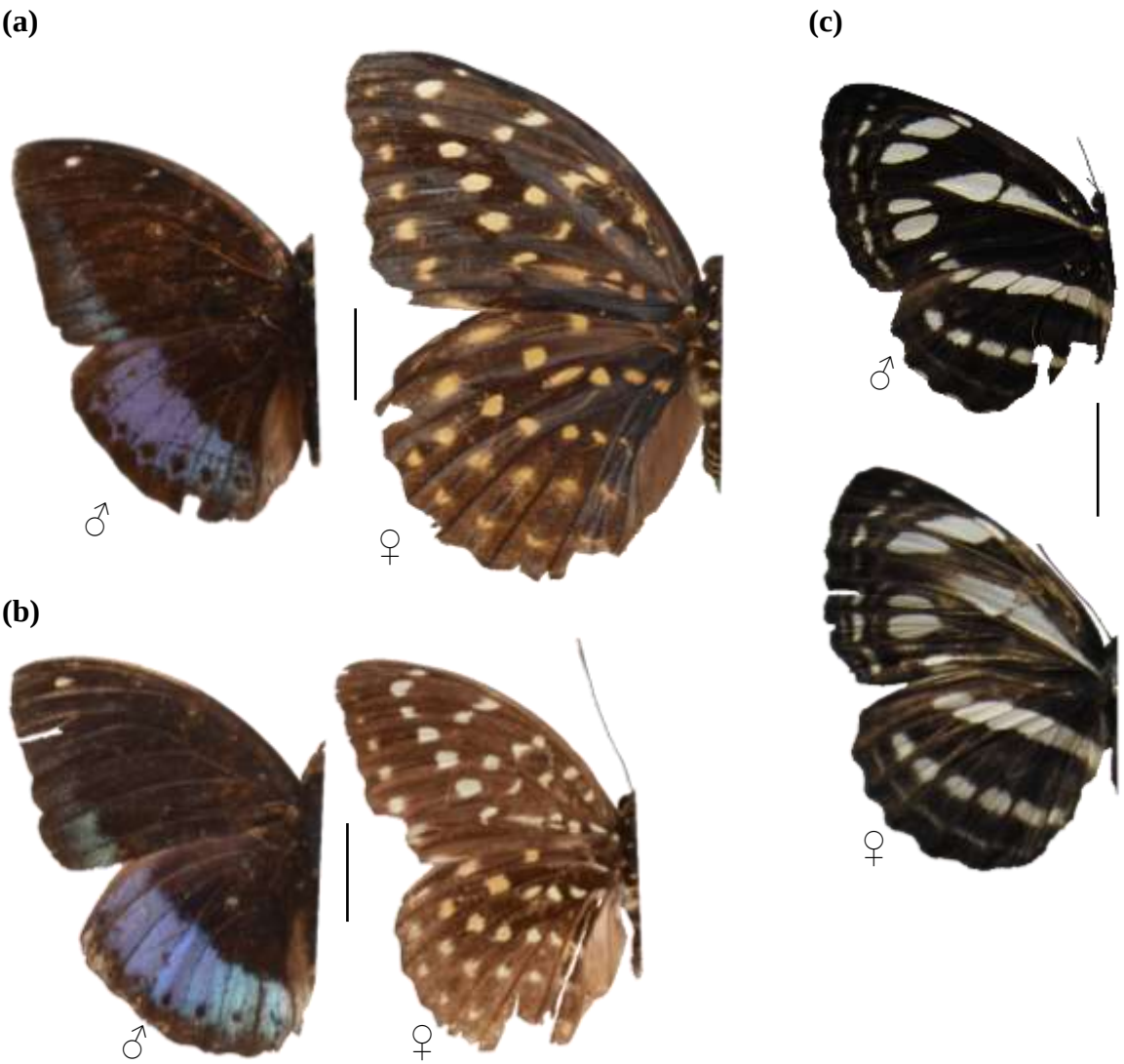


Figure 16. Wings in dorsal view showing sexual dimorphism and colour convergence. Scale bars = 1 cm. (a) *Lexias dirtea chalcenoides*; (b) *L. pardalis dirteana*; (c) *Neptis duryodana duryodana*

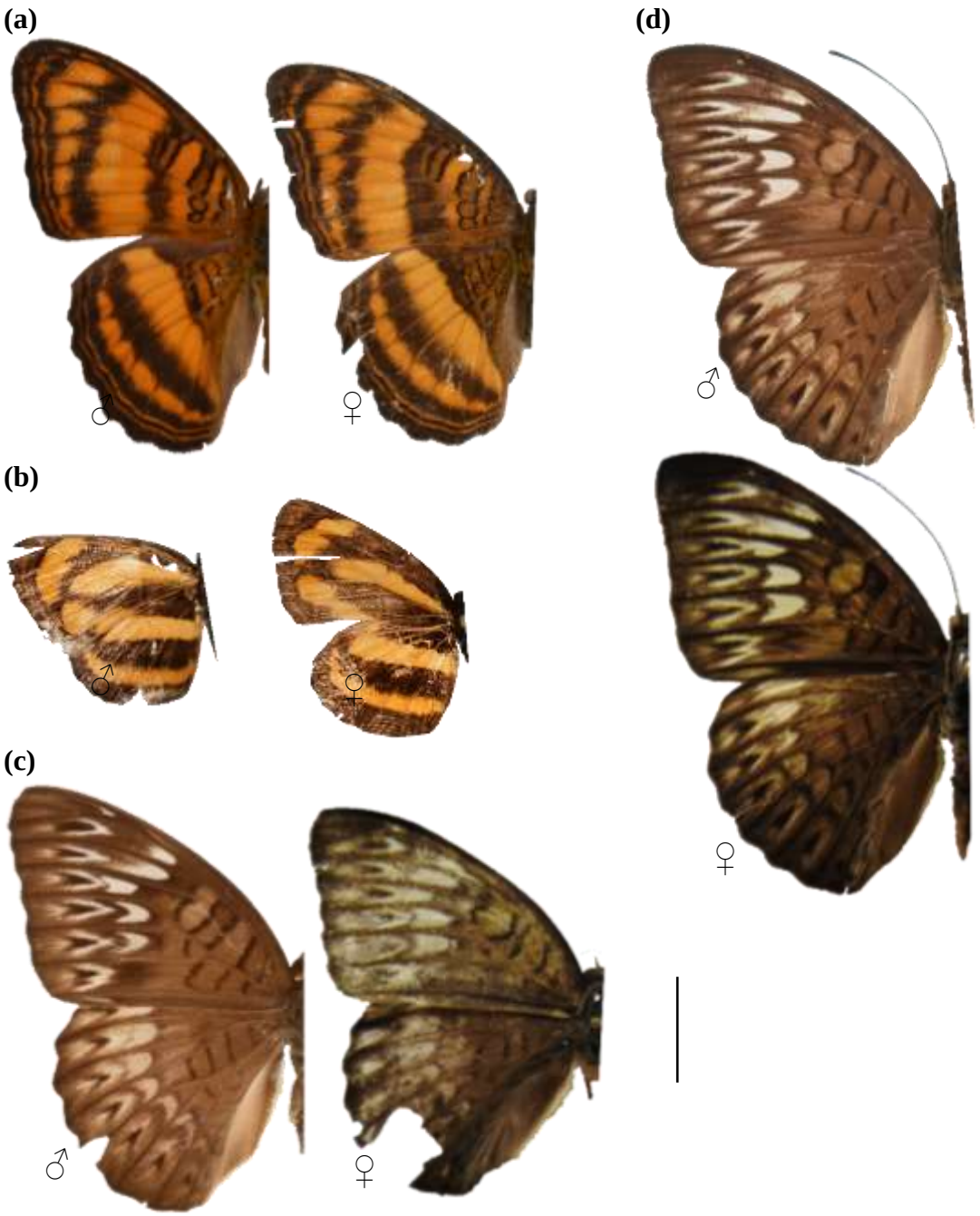


Figure 17. Wings in dorsal view showing sexual dimorphism and colour convergence. Scale bar = 1 cm. (a) *Pandita sinope sinope*; (b) *Pantoporia sandaka sandaka*; (c) *Tanaecia aruna aparasa*; (d) *Tanaecia aruna pardalis*

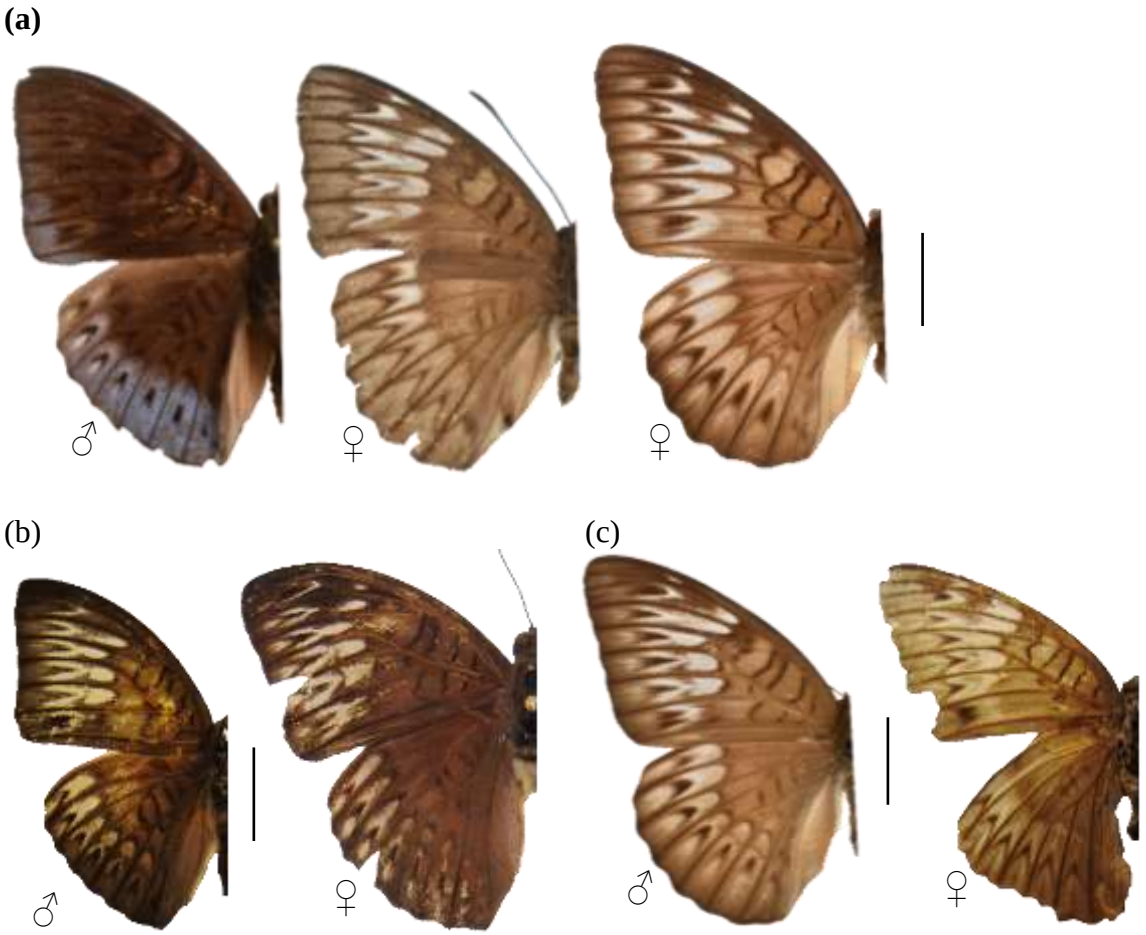


Figure 18. Wings in dorsal view showing sexual dimorphism and colour convergence. Scale bars = 1 cm. (a) *Tanaecia clathrata coerulescens*; (b) *T. munda fruhstorferi*; (c) *T. munda munda*

Similarity of Wing Pattern Elements in Tribe Limenitidini

Key characteristics based on ventral wing surface of the tribe Limenitidini used in this study are tabulated in Table 2. Based on Table 2, elements *c* (basal symmetry system), *d* (proximal band of central symmetry system), *f* (discal band of symmetry system) and *i* (parafocal element) are the most common wing patterns of nymphalid ground plan in tribe Limenitidini on ventral wing surface and followed by trailing bands. Most of the butterflies have reduced elements *g* and *h*. Based on the dendrogram (Figure 19), it shows that almost all species that belong to the same genera are clustered together. The farthest neighbour in the dendrogram is between node 30 and node 32 with Euclidean distance of 2.064. Node 30 consists of one species of genus *Dophla* (*D. evelina magama*), one species of genus *Athyma* (*A. kanwa kanwa*), two species of genus *Bassarona* (*B. dunya dunya* and *B. dunya monara*), four species of genus *Neptis* (*N. magadha plautia*, *N. leucoporos cresina*, *N. ilira cindia* and *N. hylas sopatra*), whereas, node 32 consists of one species of genus *Euthalia* (*E. iapis ambalika*), one species of genus *Lebadea* (*L. martha paduca*), five species of genus *Lexias* (*L. canescens canescens, L. cyanipardus sandakanus, L. pardalis dirteana, L. dirtea chalcenoides* and *L. dirtea opicus*) and six species from genus *Tanaecia* (*T. pelea lutala, T. munda munda, T. aruna aparasa, T. clathrata coerulescens, T. munda fruhstorferi* and *T. aruna aruna*).

Table 2. Key characteristics based on ventral wing surface of the tribe Limenitidini used in this study

No.	Species	Wing Pattern Elements									
		b	**c**	**d**	**e**	**f**	**g**	**h**	**i**	**j**	**Trailing bands**
1	*Athyma kanwa kanwa*		/	/		/			/	/	/
2	*Athyma nefte subrata*	/	/	/		/			/	/	/
3	*Athyma pravara pravara*			/		/			/	/	/
4	*Athyma reta reta*	/	/	/		/			/	/	/
5	*Bassarona dunya dunya*		/	/		/			/		
6	*Bassarona dunya monara*		/	/		/			/		
7	*Dophla evelina magama*		/	/		/			/	/	
8	*Euthalia godarti vacillaria*		/	/	/				/		
9	*Euthalia iapis ambalika*	/	/	/	/	/	/		/	/	
10	*Euthalia monina bipunctata*	/	/	/	/	/	/		/		
11	*Lasippa tiga empat*			/		/			/	/	/
12	*Lebadea martha paduca*	/	/	/	/	/	/	/	/		
13	*Lexias canescens canescens*		/	/	/	/	/	/	/		/
14	*Lexias cyanipardus sandakanus*	/	/	/	/	/	/	/	/		/
15	*Lexias dirtea chalcenoides*		/	/	/	/		/	/		/
16	*Lexias dirtea opicus*		/	/	/	/		/	/		/
17	*Lexias pardalis dirteana*		/	/	/	/		/	/		/
18	*Moduza procris agnata*	/	/	/		/			/	/	/
19	*Neptis duryodana duryodana*		/	/		/			/	/	/
20	*Neptis hylas sopatra*		/	/		/			/	/	/
21	*Neptis ilira cindia*		/	/		/			/	/	/
22	*Neptis leucoporos cresina*		/	/		/			/	/	/
23	*Neptis magadha plautia*		/	/		/			/	/	/
24	*Pandita sinope sinope*	/	/	/	/	/			/	/	/
25	*Pantoporia sandaka sandaka*			/		/			/	/	/
26	*Parthenos sylvia borneensis*	/	/	/	/	/			/	/	/
27	*Tanaecia aruna aparasa*	/	/	/	/	/	/	/	/		
28	*Tanaecia aruna aruna*	/	/	/	/	/	/	/	/		

29	*Tanaecia aruna pardalis*	/	/	/	/	/	/	/	/
30	*Tanaecia clathrata coerulescens*	/	/	/	/	/			/
31	*Tanaecia munda fruhstorferi*	/	/	/	/	/			/
32	*Tanaecia munda munda*	/	/	/	/	/	/	/	/
33	*Tanaecia pelea djataca*	/	/	/	/	/	/		/
34	*Tanaecia pelea lutala*	/	/	/	/	/			/

Note: *b*,*c* = basal symmetry system, *d* = proximal band of central symmetry system, *e* = discal spot, *f* = discal band at central symmetry system, *g* = outer boundary of border ocelli system, *h* = border ocelli, *i* = parafocal element, *j* = submarginal and marginal bands

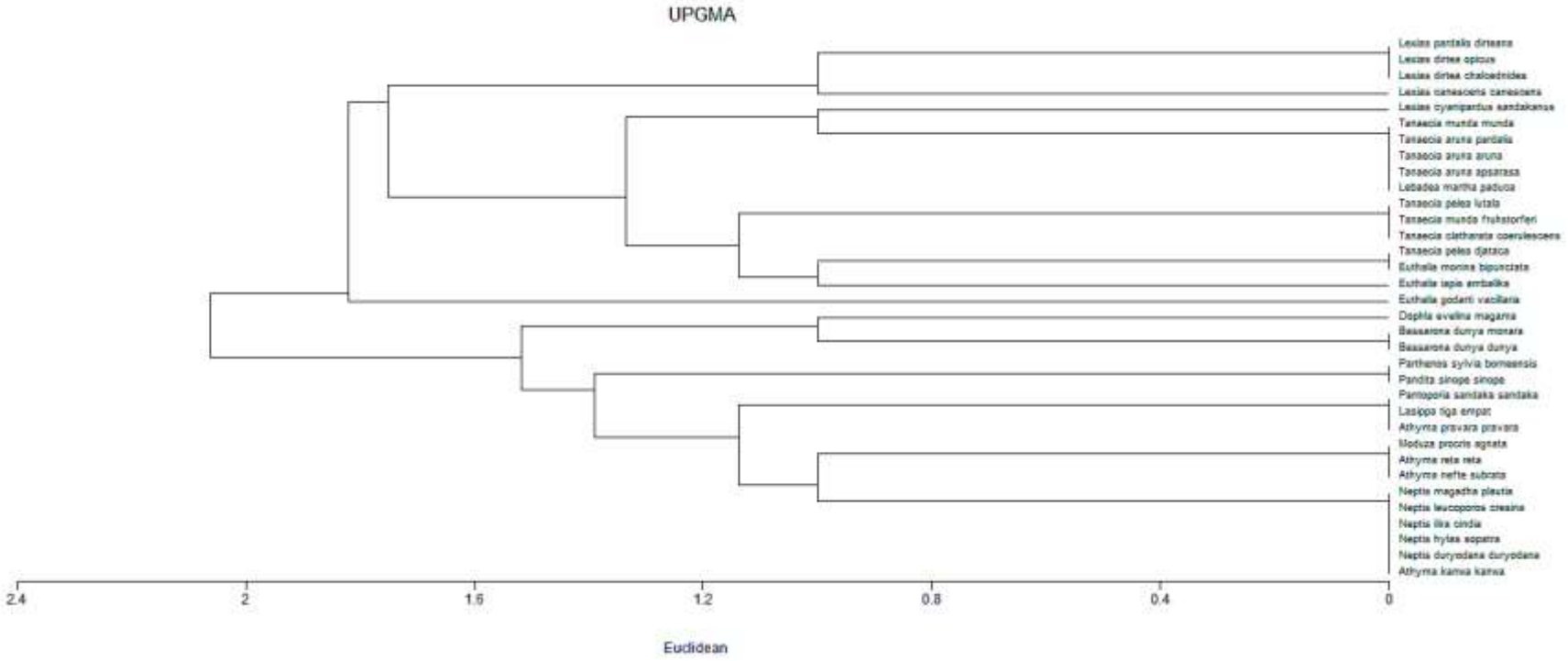


Figure 19. Dendrogram shows the similarity distances between the species based on ventral wing pattern

This study represents the comprehensive examination of colour pattern diversity in the tribe Limenitidini through NGP, the set of pattern elements out of which butterflies build their wing patterns (Nijhout 1991; 2001). This NGP allows for the identification of nymphalid homologous characters within and across species, making it possible to precisely describe the results of experiments designed to interfere with pattern development (Monteiro et al. 2006; Martin & Reed 2014; Mazo-Vargas et al. 2017), and identify large-scale trends in pattern evolution (Monteiro 2008).

Although iridescent pattern is not part of the nymphalid ground plan, this pattern can be seen on the dorsal wing surface in several species of tribe Limenitidini (i.e. species of genus *Lexias*, *Euthalia* and *Tanaecia*). The males tend to have iridescent band at the sub-marginal bands area on DFW and DHW (Figures 15(a), 16(a), 18(a) & 18(b)), while the females of genus *Lexias* tend to have a slight iridescence on DHW (Figures 9(c) & 9(f)). This pattern also varies in intensity and may located at different areas of the wing. Another trait which is not in the nymphalid ground pattern is intervenous stripes. However, intervenous stripes are visible on the HDW of *Parthenos sylvia borneensis* (Figure 11(e)).

Most of the species in tribe Limenitidini tend to have colour resemblance between two genera or more, for example, genus *Athyma* and genus *Neptis* might look similar at the first glance. This is due to similarities on the wing background as well as the pattern elements especially on the DHW, however slight differences can be observed at the element *f* on the DFW. Since some *Athyma* are sexually dimorphic and the females closely match the wing pattern, flight, and seasonality of some *Neptis* species, it could be suggested that they are mimics of the *Neptis*. This is also supported by the UPGMA dendrogram (Figure 19), which shows that the species from these two genera were clustered together. However, more research should be done to reveal the taxonomic placement of these two genera.

CONCLUSION

This study represents the first comprehensive examination of wing variation diversity in the tribe Limenitidini of Sarawak. Generally, individuals among tribe Limenitidini exhibit a variety of colour pattern within the species and genera. Elements *c, d, f* and *i* are the most common pattern elements found in this tribe while elements *g* and *h* are the least common pattern elements. The presence of iridescent pattern and trailing bands, which is not included in the nymphalid ground plan were also observed among examined species. Some instances of color resemblance observed among the species examined in this study might be due to phylogenetic relatedness or male color divergence. Hence, further examination with more samples to be included will help to elucidate this matter.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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