Chapter 2
Exploring Color Pattern Diversification in Early Lineages of Satyrinae (*Nymphalidae*)

Carla M. Penz

Abstract Based on the most recent nymphalid phylogeny, the Satyrinae can be tentatively organized into the species-rich tribe Satyrini plus a clade that includes the Morphini, Brassolini, Haeterini, Elymniini, Melanitini, Dirini, Zetherini, and Amathusiini. Members of the latter eight tribes have the largest body sizes within Satyrinae and also show extraordinary wing pattern variation. Representatives of these tribes are illustrated herein, and pattern elements of the nymphalid ground plan are identified. Five themes are briefly discussed in light of their pattern diversification: (1) central symmetry system dislocations, (2) variation in ventral hind wing ocelli, (3) the color band between elements f and g, (4) sexual dimorphism and mimicry, and (5) transparency. Within an ecological and evolutionary standpoint, selected genera are provided as examples to explore wing patterns involved in male mating displays, camouflage, and mimicry.

Keywords Pierellization • Ocelli • Sexual dimorphism • Mimicry • Camouflage • Transparency • Mating behavior

2.1 Introduction

The evolution of adult diurnal activity in Lepidoptera paved the way for the widespread use of color for intra- and interspecific signaling (Grimaldi and Engel 2005; Kemp et al. 2015). Following approximately 90 million years of morphological and species diversification (Wahlberg et al. 2009), butterflies in the family Nymphalidae have played an important role in our understanding of how wing color patterns mediate intraspecific interactions and also the evolution of aposematism, mimicry, and camouflage (Vane-Wright and Ackery 1984; Chai 1990; Nijhout 1991; Rutowski 1991). Whether they target conspecifics or other animals, the evolutionary diversification of butterfly color signals involved impressive modifications of wing pattern elements (WPEs hereafter).

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The characterization of a ground plan that identifies individual pattern components across butterfly wings provided a useful framework for research on development, genetics, and evolution (Schwanwitsch 1924; Süffert 1927; Nijhout 1991 and references therein). Border ocelli are the best studied of all individual WPEs possibly because they are conspicuous and ubiquitous in the family Nymphalidae. The Satyrinae constitutes an excellent group to study variation in the border ocelli alone and also how different WPEs can become integrated to produce particular visual effects.

Most Satyrinae species are small bodied and relatively uniform in appearance, such as members of the tribe Satyrini (85% of the species in the subfamily, Peña and Wahlberg 2008). There are, however, noticeable exceptions. Large-bodied species are grouped in a clade that includes the Brassolini (Fig. 2.1), Morphini (Fig. 2.2), Haeterini (Fig. 2.3), Elymniini (Fig. 2.4), Melanitini (Fig. 2.4), Dirini (Fig. 2.5), Zetherini (Fig. 2.6), and Amathusiini (Fig. 2.7; Wahlberg et al. 2009). Exhibiting remarkable color diversification, these butterflies form the focus of this chapter to provide the first detailed comparison among early satyrine tribes. Representatives were selected for an examination of both ventral and dorsal WPEs (see Nijhout 1991 for terminology), and a list of examined species is given in Appendix. Five themes are briefly described and illustrated and, as much as possible, discussed within the context of the natural history and behavior of the butterflies. More detailed accounts will be presented elsewhere (Penz in prep.).

2.2 Central Symmetry System Dislocations in Forewing and Hind Wing

The term pierellization (Schwanwitsch 1925) refers to the dislocation of elements that pertain to the central symmetry system in such a way that distal elements below vein M_3 align themselves with proximal ones located above such vein. This is visible in the ventral forewings of several species in the Brassolini, Morphini, Haeterini, and Dirini (Figs. 2.1c, e, 2.2d–e, 2.3b and 2.5a), and it varies within and between genera. Taking the genus *Pierella* as an example, the anterior dislocation of element *f* below forewing vein M_3 is found in species with rather plain ventral coloration (e.g., *P. lamia* in Fig. 2.3b; also *luna* and *hortona*, not illustrated). Such dislocation disrupts the interplay between *f* and *g*, which seem to serve as boundaries for a light-colored band that occurs in their congenerics (see below). In *Pierella* species that show ventral forewing pierellization of *f*, elements *f* and *g* are also broadly separated on the ventral hind wing (Fig. 2.3b).

Although pierellization seems to be less common on the ventral hind wing, it occurs in some species that display dead leaf camouflage (e.g., *Caerois gerdrudtus*, Fig. 2.2a) or parallel bars (*Morpho marcus*, Fig. 2.2d–e). Some camouflaged species, however, do not show hind wing dislocation of element *f* (e.g., *Amathuxidia amythaon*, Fig. 2.7b), suggesting that ventral camouflage evolved
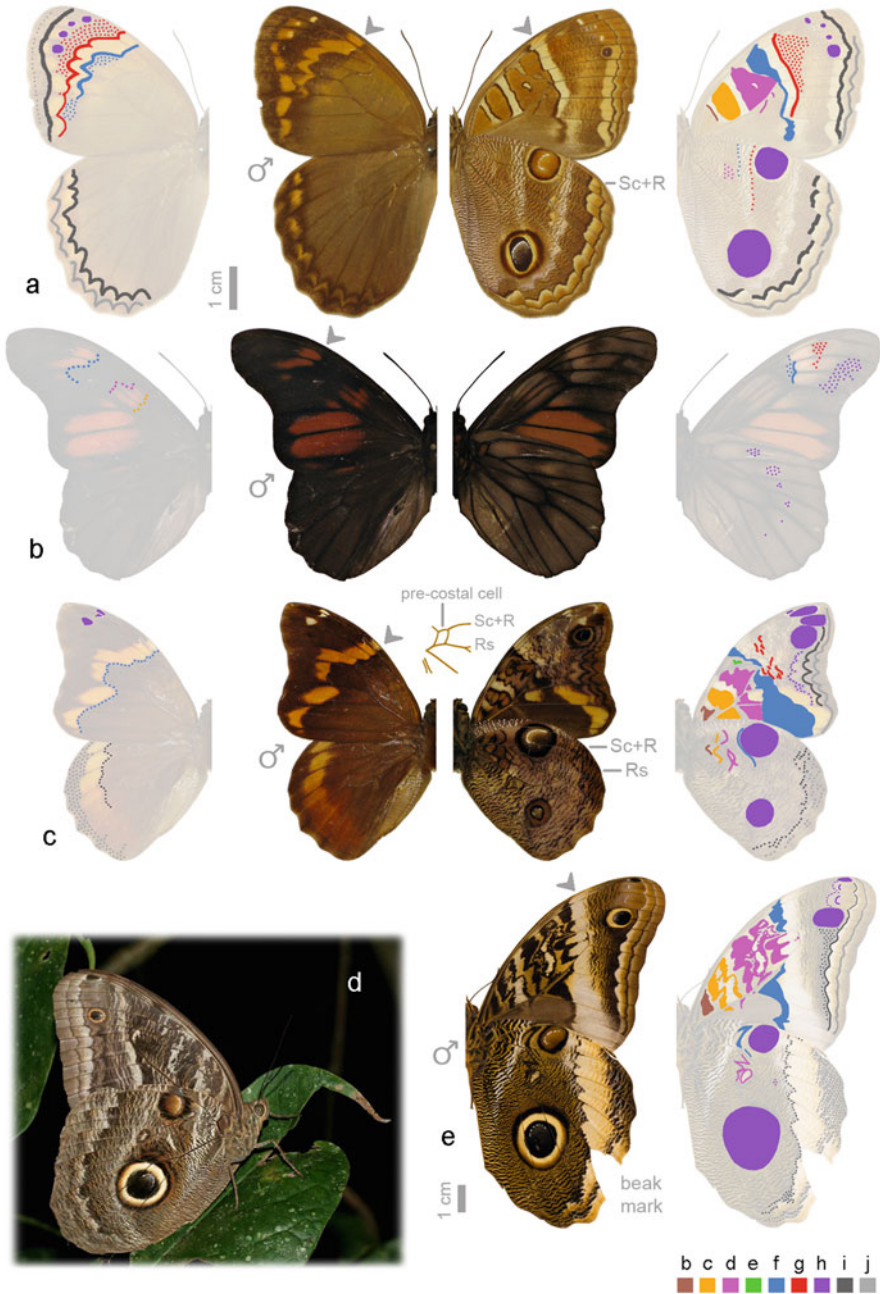
Fig. 2.1 Color-coded wing pattern elements in selected Brassolini. Left side of butterfly image in dorsal view, right side in ventral view. Gray arrows indicate colorful band associated with element *f*. (**a**) *Opoptera syme*. (**b**) *Penetes pamphanis*. (**c**) *Opsiphanes sallei*, note venation detail showing precostal cell present at the base of the hind wing. (**d**) *Caligo illioneus* male perched on leaf (photo by David Powell). (**e**) *Caligo atreus*. All butterflies at the same scale except *C. atreus*
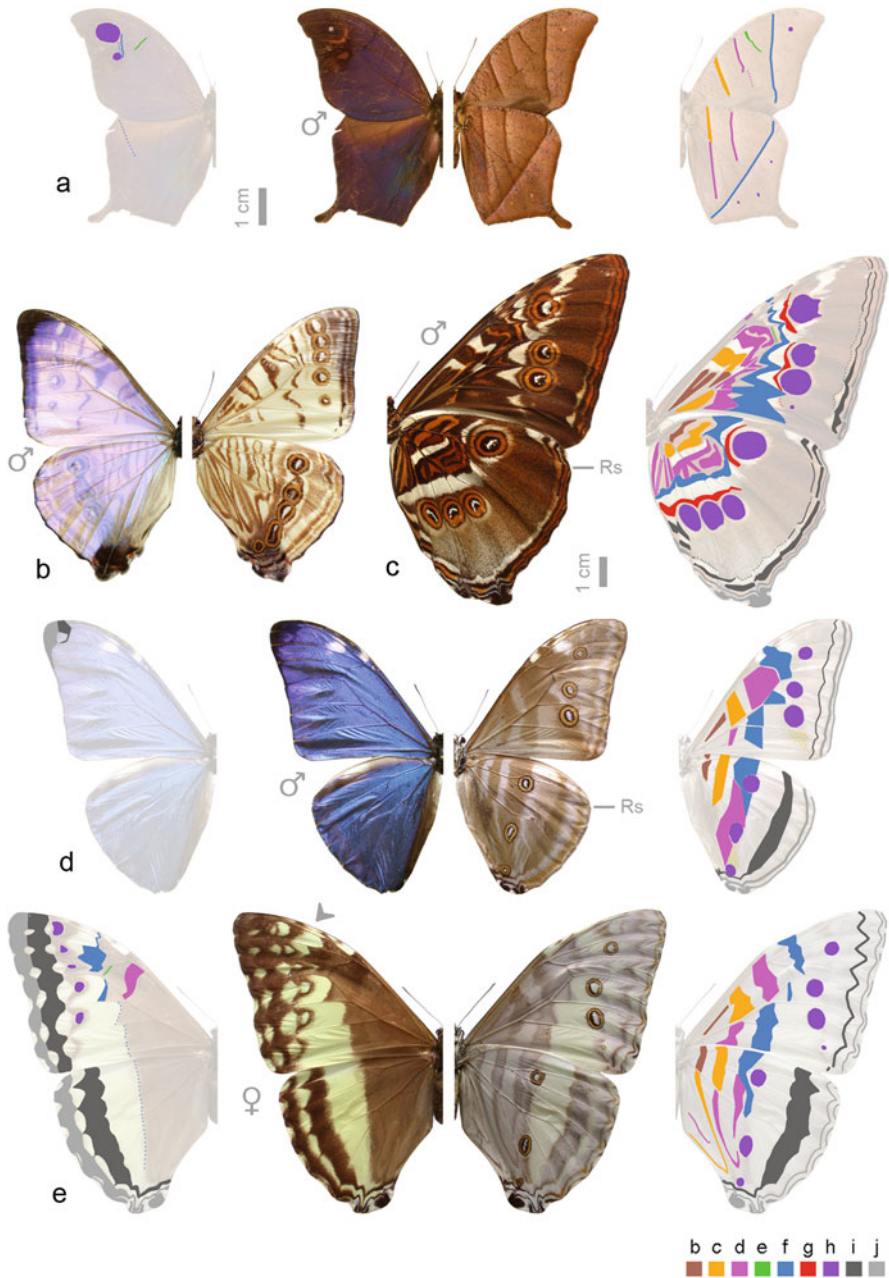
Fig. 2.2 Color-coded wing pattern elements in selected Morphini. Left side of butterfly image in dorsal view, right side in ventral view. Gray arrow indicates colorful band associated with element *f*. (**a**) *Caerois gerdrudtus*. (**b**) *Morpho sulkowskyi*, ventral pattern elements are visible in dorsal view in this semitransparent species. (**c**) *Morpho hecuba*. (**d**) and (**e**) *Morpho marcus*. All butterflies at the same scale except *M. hecuba*

independently multiple times. In the case of *M. marcus*, the comparison of male and female ventral hind wing patterns was helpful to identify the alignment and amalgamation of elements *f* and *d* to produce broad bars (compare Fig. 2.2d–e to *Amathusia phiddippus* in Fig. 2.7e). When *M. marcus* butterflies are at rest, the hind wing bars visibly converge toward an enlarged tornus where the eye-catching parfocal elements seem to be forming a deflection point for predator attack (Fig. 2.2d–e; also present in other species, Fig. 2.2b–c), a pattern that evolved independently in members of the Amathusiini (Fig. 2.7b, e).

2.3 Variation in Ventral Hind Wing Ocelli

Ocelli can take many forms within the Nymphalidae (Nijhout 1991). Species in the eight studied tribes show a broad range of variation, while some species display a complete series at the postmedial area of the wing stereotypical of the nymphalid ground plan (e.g., *Ethope himachala*, Fig. 2.6e; *Faunis eumeus*, Fig. 2.7c); in others the ocelli are markedly reduced (e.g., *Penetes pamphanis*, Fig. 2.1b). Although various types of ocelli are found in members of all tribes, here I limit my discussion to three aspects of the ventral hind wing ocelli: the location of the first ocellus of the series, proximal dislocation of the ocelli, and their use in signaling.

In most members of the eight tribes, the first conspicuous ocellus of the ventral hind wing series is located below vein Rs (Figs. 2.2c, 2.4b–d, 2.5a and 2.7a–b), but there are notable exceptions. In all Brassolini species with well-developed ocelli, the first ocellus is found below Sc + R (Fig. 2.1a, c). All members of Brassolini have a precostal cell (Fig. 2.1c), which increases the distance between Sc + R and Rs, and provides physical space for a well-developed ocellus. Although the function of the precostal cell is unknown, this points to a possible association between wing venation and color pattern in Brassolini. Furthermore, in some Brassolini species this ocellus expands beyond the cell where it originates, suggesting selection for larger size (Fig. 2.1a, c, e). Some members of the Dirini also have a well-developed ocellus below Sc + R, and that of *Paralethe dendrophilus* is particularly large (Fig. 2.5b). In this species the base of Rs is separated from Sc + R, which increases cell height in an analogous way to what is found in Brassolini. Finally, in the transparent Haeterini *Dulcedo*, *Pseudohaetera*, *Haetera*, and *Cithaerias* the first ocellus is located below M_1 (Fig. 2.3e–f), a pattern unique to these taxa.

Border ocelli are usually located in the postmedial area, but dislocations occur in several taxa. Proximal dislocations are more common than distal ones, and the former are associated with a corresponding shift of central symmetry system WPEs. Notable proximal dislocations are found in taxa of Brassolini, Morphini, and Amathusiini (Figs. 2.1, 2.2 and 2.7). In many Brassolini and also *Morpho*, the hind wing ocelli are clearly positioned in the medial area of the wing, which can produce a striking visual effect depending on their size (Penz and Mohammadi 2013; Figs. 2.1d–e and 2.2c). Ocelli dislocations can be uneven with the first, or first and second, ocelli taking a more proximal position than the remaining of the series
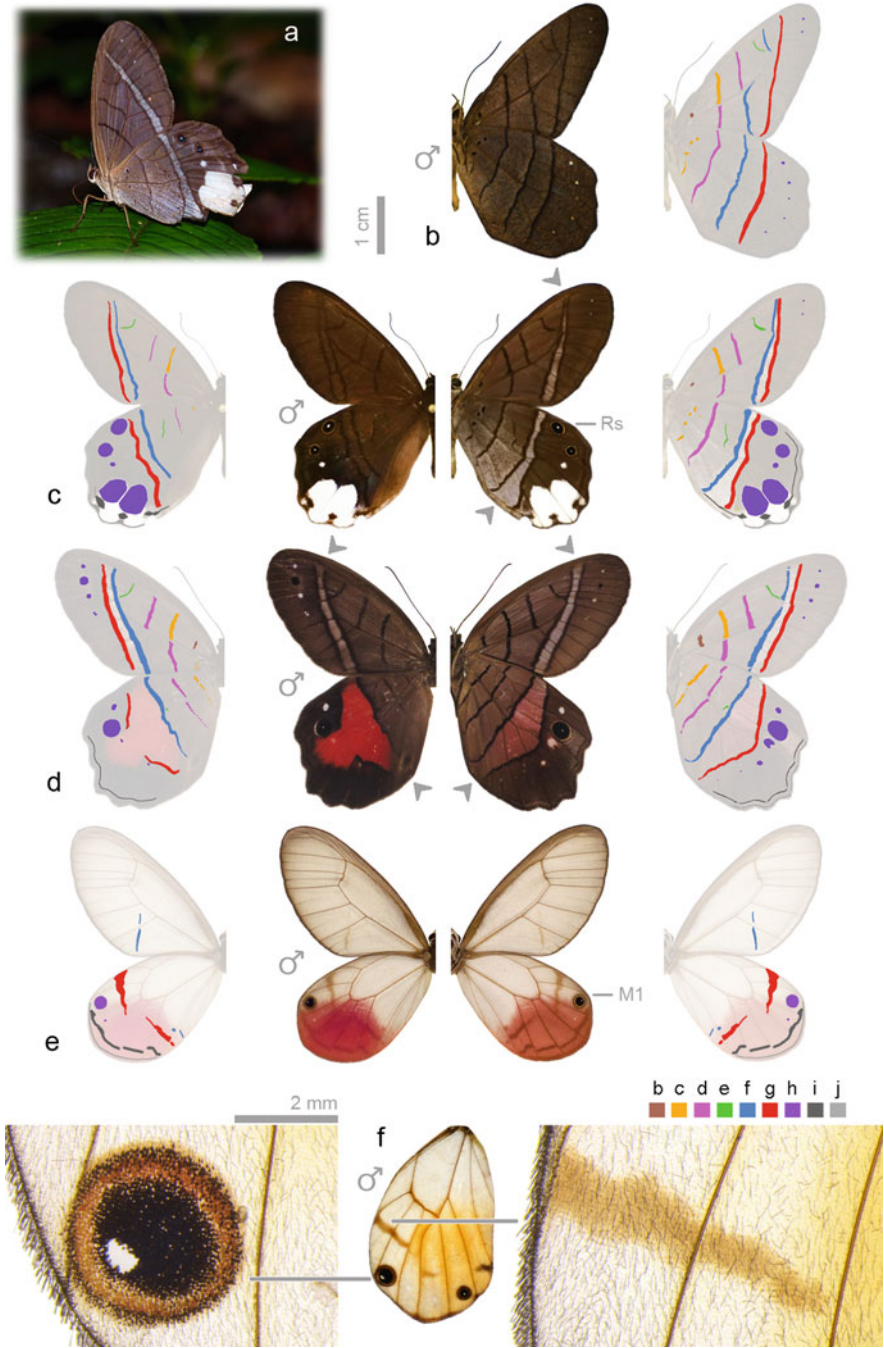
Fig. 2.3 Color-coded wing pattern elements in selected Haeterini. Left side of butterfly image in dorsal view, right side in ventral view. Gray arrows indicate colorful band associated with element

(Figs. 2.6e and 2.5b). Finally, the hind wing ocelli are uniquely dislocated distally in the transparent Haeterini genera by being positioned very near the wing margin (Fig. 2.3e–f). The ocellus below M_1 becomes highly visible when these transparent butterflies alight with their wings closed.

The ventral ocellus located at the hind wing tornus has been hypothesized to function as a defense, either a deflection point in the event of a predator attack or a startle mechanism that prevents or delays attacks (DeVries 2002, 2003; Hill and Vaca 2004; Stevens 2005). Although these hypotheses are compelling, my field observations suggest that in some taxa, ventral hind wing ocelli might have an additional function. Males of some *Caligo* species aggregate at leks along forest edges to wait for virgin females (Freitas et al. 1997, Srygley and Penz 1999; Fig. 2.1d). As they fly into the lek, the large ventral ocelli appear to help airborne females locate perched males (pers. obs.), suggesting a potential function in male-female interactions. *Pierella lucia* has two large white ocelli at the hind wing tornus that show perfect dorsoventral correspondence, likely enhancing light reflection (Fig. 2.3a, c). Hill and Vaca (2004) demonstrated that the hind wing tornus of *Pierella lucia* is weaker than surrounding wing areas, thus supporting the deflection hypothesis (see beak marks in Fig. 2.3a). Nonetheless I once observed the complex courtship behavior of this species. While a female was perched on a leaf, a male hovered in her view, beating the forewings only and keeping the hind wings open and motionless. The male clearly displayed the ventral hind wing ocelli to the female as he repeatedly dipped closer and closer to her. Dorsal ocelli have been considered more important during mating displays (e.g., Oliver et al. 2009), but my observations suggest that ventral ocelli may also be used in this context. In the case of both *Caligo* and *Pierella lucia*, it is possible that both natural and sexual selection could be operating concomitantly on the ventral hind wing ocelli. This is perhaps the case in other species as, for example, male *Faunis phaon leucis* that has larger ventral ocelli than the female (Fig. 2.7d; note that dorsal ocelli are absent in *Faunis*).

2.4 The Color Band Between Elements *f* and *g*

Many nymphalid butterflies have a conspicuous, forewing band that constitutes a highly visible component of the dorsal, and sometimes ventral, coloration (e.g., *Melanitis amabilis*, Fig. 2.4d). This band is common among the species studied here

Fig. 2.3 (continued) f. (**a**) *Pierella lucia*, note multiple beak marks on the hind wing tornus (photo by Andrew Neild). (**b**) *Pierella lamia*. (**c**) *Pierella lucia*. (**d**) *Pierella helvina*. (**e**) *Cithaerias aurora*. (**f**) details of the dorsal hind wing of *Haetera piera*: the ventral orange scales in the ocellus are visible dorsally through transparency; element *g* is expressed on the wing membrane. All butterflies are at the same scale

Fig. 2.4 Color-coded wing pattern elements in selected Elyminiini and Melanitini. Left side of butterfly image in dorsal view, right side in ventral view. Gray arrows indicate colorful band associated with element *f*. (**a**) and (**b**) *Elymnias hypermnestra*. (**c**) *Elymnias patna*. (**d**) *Melanitis amabilis*. All butterflies are at the same scale
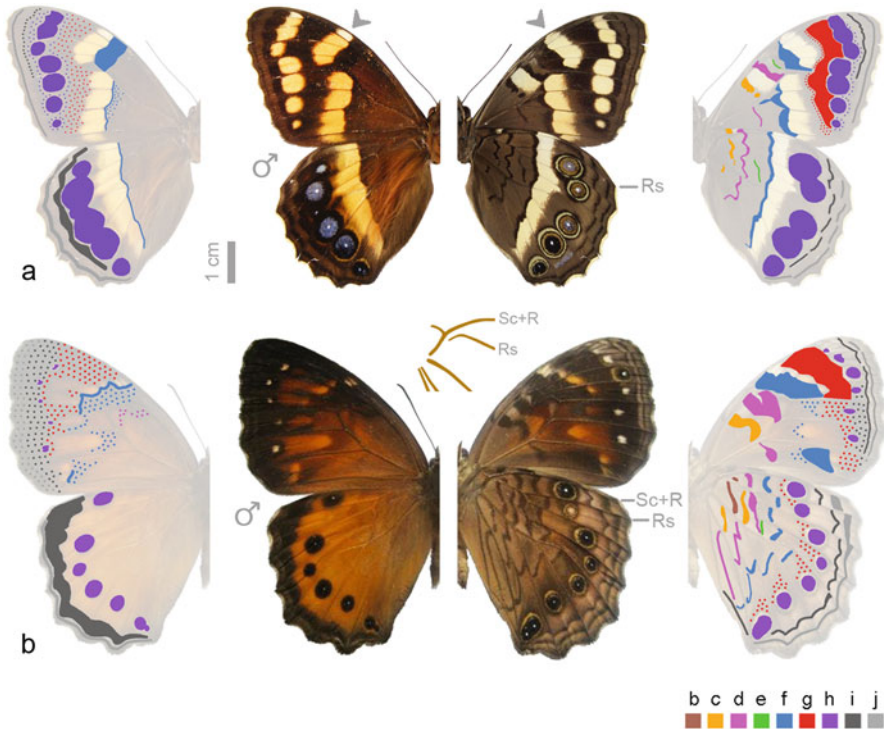
Fig. 2.5 Color-coded wing pattern elements in selected Dirini. Left side of butterfly image in dorsal view, right side in ventral view. Gray arrows indicate colorful band associated with element *f*. (**a**) *Aeropetes tulbaghia*. (**b**) *Paralethe dendrophilus*, note venation detail showing separation of Rs from Sc + R at the base of the hind wing. All butterflies are at the same scale

(see gray arrows in Figs. 2.1, 2.2, 2.3, 2.4, 2.5, 2.6, 2.7, and 2.8). It appears to be associated with element *f* (or bounded between *f* and *g*) and varies between and within the studied tribes. For instance, this band differs noticeably in color, width, and extent of fragmentation between the closely related *Aeropetes tulbaghia* and *Paralethe dendrophilus* (Fig. 2.5a–b). The dorsal forewing band can also vary in orientation (vertical or transverse). A vertical band is found in species where *f* is positioned straight across the medial area of the wing (e.g., Fig. 2.2e). In contrast, a transverse band results from element *f* being slightly diagonal (displaced distally toward the wing tornus, e.g., Fig. 2.7b). Members of the Brassolini, for example, vary in the orientation of this band (compare *Catoblepia* and *Caligo*; Fig. 2.8a–b).

Within the same species and sex, the expression of the band associated with *f* usually differs between the forewing and hind wing and may also show dorso-ventral variation. This is readily apparent in *Pierella helvina* (Fig. 2.3d), where elements *f* and *g* are clearly visible and appear to function as developmental boundaries. Ventrally, the pale-colored band of *P. helvina* is much narrower on the forewing than on the hind wing. Although element *g* forms a continuous line in
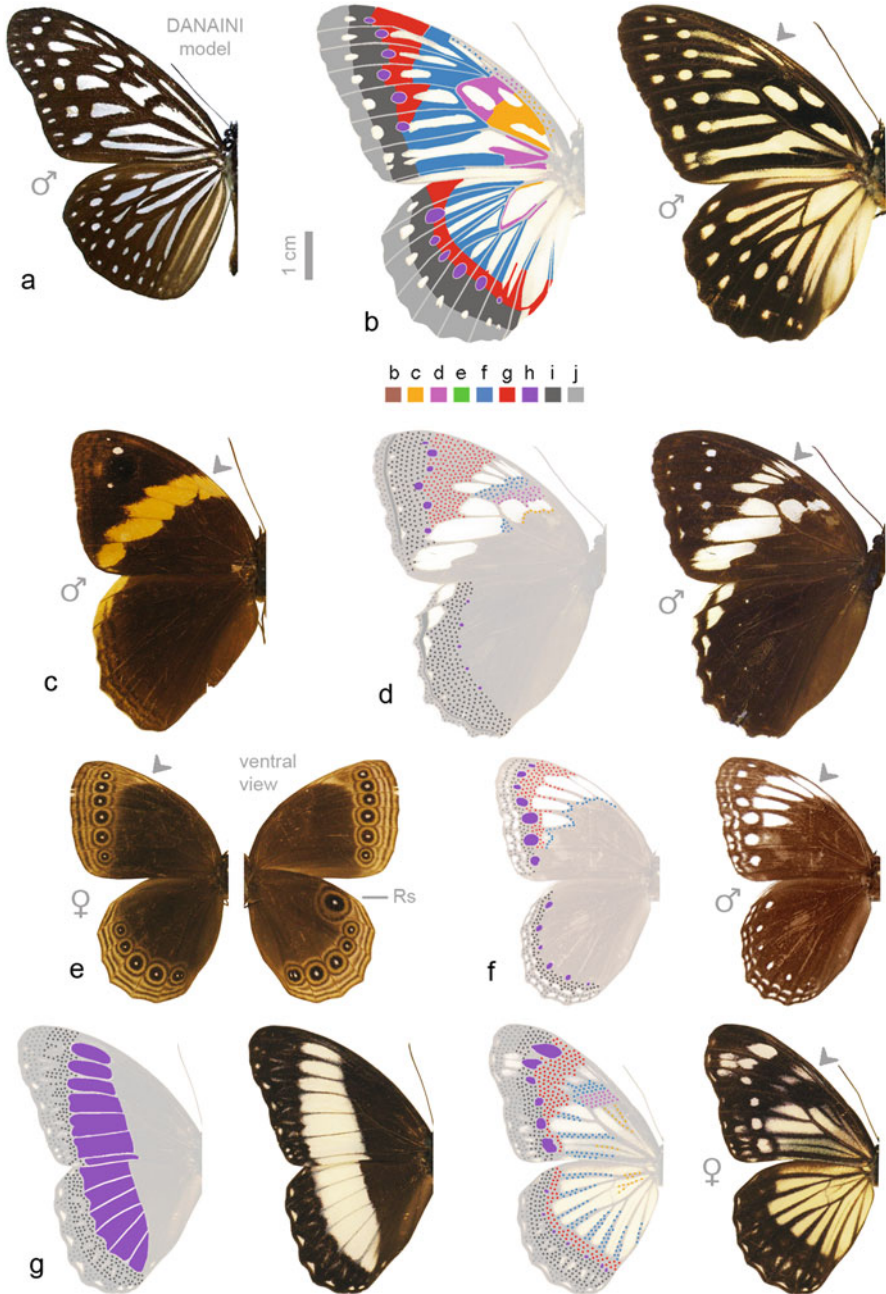
Fig. 2.6 Color-coded wing pattern elements in selected Zetherini. Left side of butterfly image in dorsal view, right side in ventral view. Gray arrows indicate colorful band associated with element *f*. (**a**) *Ideopsis vulgaris* (Danaini) model. (**b**) *Penthema lisarda*, hypothesized delimitation of pattern elements based on Nijhout (1991) plus tentative identification of pattern elements (dotted) for species of nonmimetic or intermediate patterns. (**c**) *Neorina hilda*. (**d**) *Penthema adelma*.

the ventral hind wing, it is not expressed dorsally between M_2 and CuA_1, allowing the bright red band to expand distally. For comparison, note that f and g are also clearly visible on the hind wing of *Pierella lucia* (Fig. 2.3c), where a pale band is expressed ventrally only. The genus *Pierella* constitutes an excellent example of how different WPEs and associated bands can be modified by evolution to give rise to broadly distinctive species-specific patterns (Fig. 2.3b–d).

2.5 Sexual Dimorphism and Mimicry

The species studied here range from sexually monomorphic to slightly or strongly dimorphic, and color pattern divergence implies that selection can operate independently on males and females. When there is little divergence between sexes, both dorsal and ventral WPEs are more conserved in females (Figs. 2.2d–e and 2.4c). In contrast, strong sexual dimorphism can result from simple modifications in few WPEs and the colorful bands associated with them (e.g., *Mielkella singularis*, Penz and Mohammadi 2013) or more complex changes involving a larger number of WPEs (Fig. 2.2d–e).

Strong sexual dimorphism can arise through sexual selection operating on male pattern or natural selection on female pattern (see Kunte 2008 and Oliver and Monteiro 2010 for reviews). Here I confine my discussion to potential natural selection on female pattern. Females could diverge from males to become less conspicuous to potential predators, as might have been the case in five species of *Morpho* (see example in Fig. 2.2e). Furthermore, the evolution of mimetic convergence can be limited to the female sex, although not always the case. Female-limited mimicry has evolved independently in members of various tribes (e.g., Fig. 2.4a–b), and depending on the model, it required simple or complex changes in WPEs. For instance, the convergence of female *Catoblepia orgetorix* with monomorphic *Caligo atreus* (Fig. 2.8a–b) involved a relatively simple set of color pattern modifications. When compared to other species of *Catoblepia*, the band associated with element f is dislocated proximally on the dorsal forewing of *C. orgetorix*, its color changed from orange to white, and it acquired purple iridescence. On the dorsal hind wing, the band associated with i became wider and changed color from orange to yellow. Mimicry is rare in neotropical Satyrinae, and this example is peculiar as neither *Caligo* nor *Catoblepia* are known to possess chemical defenses.

In contrast, mimicry (female-limited or both sexes) is common in the old-world tribes Zetherini and Elymniini and the Amathusiini genus *Taenaris*. In their case, evolution took two distinctive paths. Figure 2.8c–e shows cross-tribal convergence that resulted from an extreme reduction in the expression of most WPEs plus the

Fig. 2.6 (continued) (**e**) *Ethope himachala*. (**f**) *Ethope noirei*. (**g**) *Zethera pimplea*, note that males of other *Zethera* species have small, dorsal ocelli on both wings. All butterflies are at the same scale
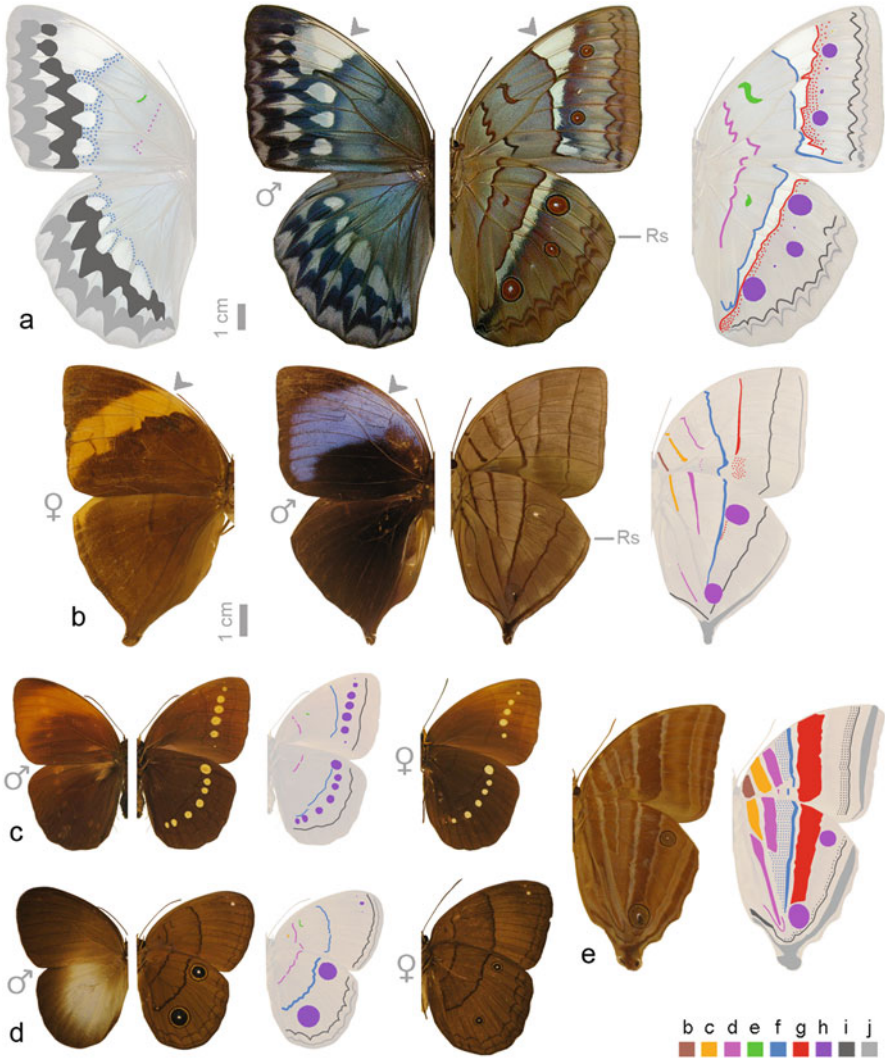
Fig. 2.7 Color-coded wing pattern elements in selected Amathusiini. Left side of butterfly image in dorsal view, right side in ventral view. Gray arrows indicate colorful band associated with element *f*. (**a**) *Stichopthalma godfreyi* (photo by Saito Motoki). (**b**) *Amathuxidia amythaon*. (**c**) *Faunis eumeus*. (**d**) *Faunis phaon leucis*. (**e**) *Amathusia phidippus*. All butterflies are at the same scale except *S. godfreyi*

increase in size of some ocelli to create a similar visual appearance. In other taxa, mimicry involved complex modifications of most WPEs. Nonmimetic and intermediate patterns can help interpret WPE modifications that lead to mimetic convergence of zetherines onto chemically protected danaines (e.g., *Ideopsis vulgaris*, Fig. 2.6a). Figure 2.6c, d, f, and g exemplify a series of such modifications, which
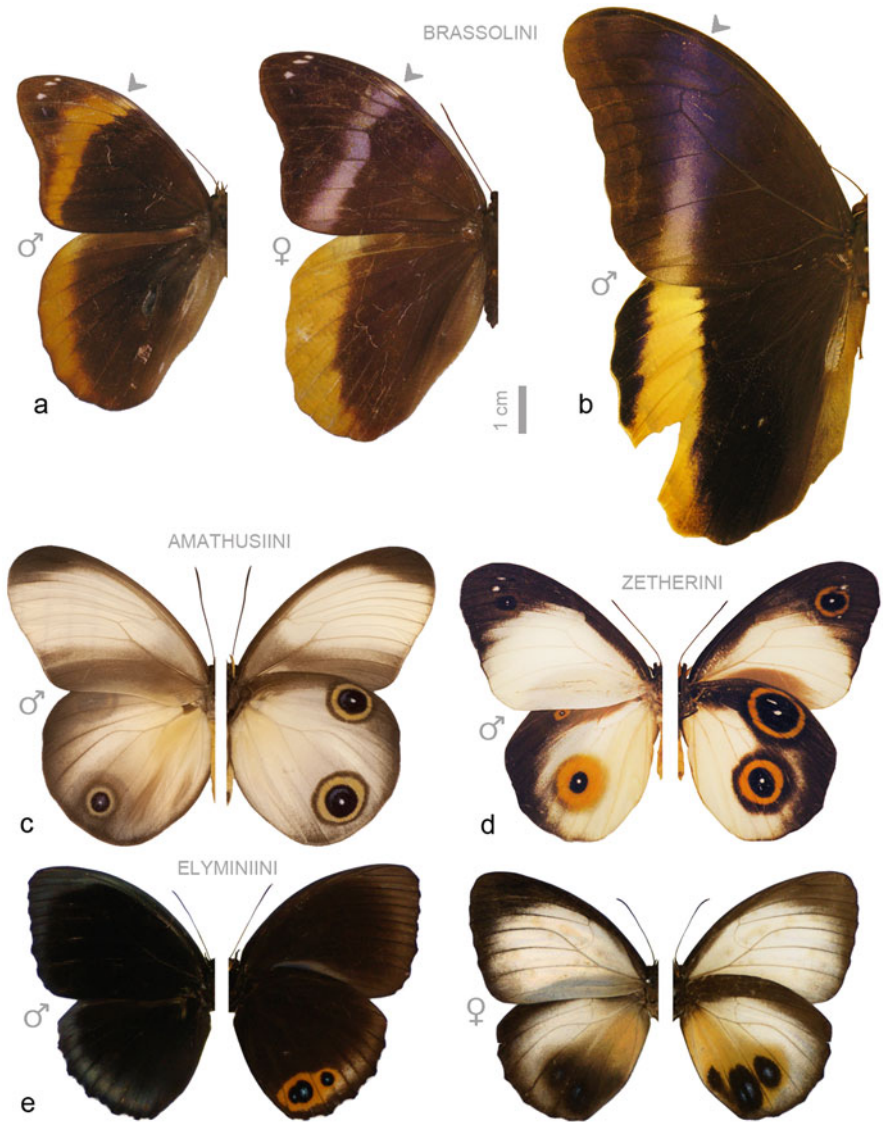
Fig. 2.8 Examples of mimetic convergence. Gray arrows indicate colorful band associated with element *f*. (**a**) nonmimetic male and mimetic female of *Catoblepia orgetorix*. (**b**) *Caligo atreus* model. (**c**) *Taenaris artemis*. (**d**) *Hyanthis hodeva*. (**e**) nonmimetic male and mimetic female of *Elymnias agondas*. All butterflies are at the same scale

can be used to hypothesize the WPE configuration of *Penthema* (Fig. 2.6b; see also Nijhout 1991). Notably, male and female of the sexually dimorphic *Zethera pimplea* have brown and off-white dorsal coloration, but the female pattern is

more intricate and Danaini-like than the male (Fig. 2.6g). Although some WPEs can be identified in *Elymnias* species that have complex Danaini-like dorsal patterns, they are generally difficult to interpret (Fig. 2.4a–c).

2.6 Transparency

Layers of scales make butterfly wings generally impenetrable to light. Nevertheless, some members of Satyrinae have evolved partial or complete transparency. In *Morpho sulkowskyi*, the dorsal scale size and pigmentation are reduced to such a degree that the ventral WPEs are visible through the wing (Fig. 2.2b). Partial transparency has evolved in more than one species of *Morpho*, but its function within the context of their natural history is unknown.

Scale cover is dramatically reduced in *Dulcedo*, *Pseudohaetera*, *Haetera*, and *Cithaerias* (Haeterini; Fig. 2.3e–f), and this possibly evolved ca. 29 million years ago (Cespedes et al. 2015). Transparency makes these butterflies nearly invisible in the forest understory and can be considered a defense against predation. Despite the extensive absence of scales, some WPEs are conserved, and this suggests they serve a function in the behavior of these butterflies. For example, their hind wing ocellus below M_1 is highly visible (Fig. 2.3e–f), and it might be involved in signaling. In the forest, male *Cithaerias* that are perched on the ground repeatedly flash their vivid dorsal hind wing colors (pers. obs.), which can likely be seen by other males or potential mates flying nearby.

The interplay between lost versus conserved wing color patterns is an interesting attribute of transparent Haeterini for two reasons. First, some pattern elements are expressed directly onto the wing membrane to form scale-less bands (Fig. 2.3e–f). This shows that the loss of scales does not necessarily lead to a loss of pattern. Membrane-level expression of WPEs can also be seen in areas that have scales, for example, the ocellus in Fig. 2.3f. To my knowledge, *Dulcedo*, *Pseudohaetera*, *Haetera*, and *Cithaerias* are the only butterflies in which WPEs are expressed on the wing membrane. Second, these butterflies show differential dorsoventral regulation of scale formation. For instance, in most transparent Haeterini, the ocellus below M_1 has a complete set of rings on the ventral hind wing surface, but the dorsal one lacks the orange ring (Fig. 2.3f). In *Cithaerias*, colorful scales are present on the dorsal hind wing only, and WPEs expressed at the wing membrane are thus more visible on the ventral surface (Fig. 2.3e). The colorful dorsal vestiture does not seem to correspond to a given WPE, and it spreads across the hind wing surface unaffected by elements *g*, *i*, and *j*. This begs the question of whether these WPEs are expressed on the ventral surface only (C. M. Penz, work in progress).

2.7   Concluding Remarks

The butterflies that form the focus of this chapter provide remarkable examples of color pattern variation. The significant changes in ocelli size and shape observed in *Bicyclus* selection experiments (e.g., Monteiro et al. 1997) suggest that butterflies can undergo rapid adaptive evolution. As a result, lineages might accumulate substantial wing pattern element modifications in relatively short evolutionary time scales. This is consonant with the observation that every tribe studied here includes species with nearly complete to highly reduced wing pattern elements—evolution repeats itself. Convergent appearance resulting from different pattern element modifications could reflect similarities in natural history or microhabitat use, e.g., ventral stripes in species of neotropical *Caerois* and old-world *Amathuxidia* (Figs. 2.2a and 2.7b). Field observations on mating behavior suggest the ventral hind wing ocelli may be used in male-female interactions in species of *Caligo* and *Pierella* (Figs. 2.1d and 2.3a), and this adds a new dimension to previous work. In the tribes studied here, pattern reduction is intriguing because it is accomplished in exceptionally different ways—pattern elements might not be expressed, or the scale vestiture may disappear almost completely (Figs. 2.8c–e and 2.3e–f). Transparency evolved independently in various ecologically and behaviorally distinct groups of Lepidoptera, the Haeterini being an example. How is scale loss adaptive in different taxa, what are the developmental mechanisms involved, and is it reversible? To further our understanding of the role wing coloration plays within the Satyrinae, the work presented here advocates baseline research on two fronts: documentation of pattern variation and field studies aimed at placing wing color diversification in a behavioral and evolutionary context.

Appendix: List of Examined Taxa

Note that most, but not all, tribes within the focal clade are monophyletic (Wahlberg et al. 2009), and the classification used here is therefore tentative and expected to change (e.g., Zetherini). Genera and species are listed in alphabetic order, and those marked with an asterisk were examined from images only.

Brassolini: *Aponarope sutor*; *Bia actorion*, *B. peruana*; *Blepolenis batea*, *B. bassus*; *Brassolis dinizi*, *B. sophorae*; *Caligo atreus*, *C. idomeneus*, *C. martia*,

C. oberthuri; *Caligopsis seleucida*; *Catoblepia berecynthia*, *C. orgetorix*, *C. xanthus*; *Dasyophthalma creusa*, *D. rusina*; *Dynastor darius*; *Eryphanis aesacus*, *E. automedon*, *E. bubocula*; *Mielkella singularis*; *Narope cyllastros*, *N. panniculus*; *Opoptera aorsa*, *O. fruhstorferi*, *O. syme*; *Opsiphanes cassiae*, *O. invirae*, *O. sallei*; *Orobrassolis ornamentalis*; *Penetes pamphanis*; *Selenophanes cassiope*, *S. josephus*, *S. supremus*. See Penz and Mohammadi (2013) for additional species. Morphini: *Antirrhea archaea*, *A. avernus*, *A. philoctetes*; *Caerois chorineus*, *C. gerdrudtus*; *Morpho aega*, *M. anaxibia*, *M. aurora*, *M. catenarius*, *M. cypris*, *M. hecuba*, *M. helenor*, *marcus*, *M. menelaus*, *M. rhetenor*, *M. theseus*. Haeterini: *Cithaerias andromeda*, *C. aurora*, *C. aurorina*, *C. bandusia*, *C. pireta*, *C. pyritosa*, *C. pyropina*; *Dulcedo polita*; *Haetera piera*; *Pierella helvina*, *P. hortona*, *P. hyalinus**, *P. lamia*, *P. lena*, *P. lucia*, *P. luna*, *P. nereis*; *Pseudohaetera mimica*. Elymniini: *Elymnias agondas*, *E. cumaea*, *E. hypermnestra*, *E. nessaea*, *E. patna*; *Elymniopsis bammakoo*. Melanitini: *Melanitis amabilis*, *M. constantia*, *M. leda*. Dirini + Manataria: *Aeropetes tulbaghia*; *Dingana dingana**; *Dira clytus**; *Paralethe dendrophilus*; *Torynesis mintha**; *Manataria maculata*. Zetherini: *Ethope diademoides*, *E. himachala*, *E. noirei**; *Hyantis hodeva*; *Morphopsis albertisi*, *M. biakensis*, *M. meeki*, *M. ula*; *Neorina crishna*, *N. hilda*, *N. lowi*, *N. patria*; *Penthema adelma*, *P. darlisa*, *P. formosanum*; *Xanthotaenia busiris*; *Zethera incerta*, *Z. musa*, *Z. musides*, *Z. pimplea*. Amathusiini: *Amathusia binghami*, *A. phidippus*, *A. plateni*; *Amathuxidia amythaon*; *Discophora bambusae*, *D. sondaica*, *D. timora*; *Ensipe cycnus*, *E. euthymius*; *Faunis canens*, *F. eumeus*, *F. menado*, *F. stomphax*, *F. phaon leucis*; *Melanocyma faunula*; *Morphotenaris schoenbergi*; *Stichophthalma camadeva*, *S. godfreyi**, *S. howqua*, *S. louisa*, *S. nourmahal*, *S. sparta*; *Taenaris artemis*, *T. butleri*, *T. catops*, *T. myops*, *T. onolaus*; *Thaumantis diores*, *T. noureddin*, *T. odana*; *Thauria aliris*; *Zeuxidia amethystus*, *Z. aurelius*, *Z. doubledayi*.

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