

Light habitats and the role of polarized iridescence in the sensory ecology of neotropical nymphalid butterflies (Lepidoptera: Nymphalidae)

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Summary

The exploitation of polarized light may increase perceived visual contrast independent of spectrum and intensity and thus have adaptive value in forest habitats, where illumination varies greatly in brightness and spectral properties. Here we investigate the extent to which Costa Rican butterflies of the family Nymphalidae exhibit polarized wing reflectance and evaluate the types of habitats in which the trait is commonly found. We also examine the degree of polarized reflectance of wing patterns in representative species belonging to the nymphalid subfamilies Charaxinae, Heliconiinae, Morphinae and Nymphalinae. Polarized reflectance was evaluated using museum specimens illuminated with a light source that simulated the spectrum of ambient sunlight and viewed through a polarized filter. Of the 144 species examined, 75 species exhibited polarized

reflectance patterns. These species were significantly more likely to occupy forest habitats than open habitats. A concentrated changes test performed on a phylogeny of the Nymphalidae, with the Papilionidae as an outgroup, provides further support for the correlated evolution of polarized iridescence and life in a forest light environment. These results are consistent with the hypothesis that the production and detection of polarized light may have adaptive communicative value in those species inhabiting forest habitats with complex light conditions. The potential utility of polarized iridescence and iridescent wing coloration within differing ambient spectral environments is discussed to provide a basis for future investigation of the polarized light ecology of butterflies.

Key words: polarized, iridescence, butterfly, light habitat.

Introduction

In order to locate potential mates and other important natural resources in their environment, organisms must generate, transmit, receive and interpret relevant biological signals. The ambient light environment in which an organism dwells is a particularly important aspect of its sensory ecology, especially if it depends on visual cues to find food and mates (Endler, 1992; Endler, 1993a; Endler, 1993b; Endler, 1997). In particular, the properties of a light environment determine which visual signals can be efficiently transmitted (Endler, 1992; Endler, 1997).

Forests present a particularly diverse array of light environments, which vary greatly in intensity and spectral composition (Endler, 1993a). Endler categorized these environments as open, large gap, small gap, woodland shade, forest shade and early/late. The environments appear white, white, orange, blueish-green, yellowish-green and purple, respectively (Endler, 1992; Endler, 1997). The geometric complexity of forests may force a butterfly to move through many different ambient light spectra in a short period of time,

which may promote adaptations to produce an effective visual signal through these changes.

An optimal visual signal should create a more striking, conspicuous, or otherwise attractive individual to conspecifics or potential mates. Simultaneously, it should signal warning or render an individual less conspicuous to predators (Endler, 1992). Polarized reflectance is one signal production mechanism hypothesized to enhance signal transmission in complex forest light environments, and thus may fulfill the criteria for an optimal visual signal (Shashar et al., 1998; Cronin et al., 2003a).

Polarized light in nature

Light from the sun is depolarized and becomes partially polarized as a result of scattering in the atmosphere. In addition, many naturally occurring objects partially polarize light upon reflectance. Waxy or shiny (specular) biological materials such as leaves and insect cuticle are some of the more common biological light polarizers, with water and wet surfaces being common abiotic light polarizers (Shashar et al., 1998; Horváth and Varjú, 2004). In forested

environments, polarized light may offer additional information about an animal's surroundings that is lost or unreliable due to the complexity of the light environment (Cronin et al., 2003a).

There is evidence that a wide variety of organisms may be able to detect and utilize polarized light. Spiders, crustaceans, cephalopods, insects, and perhaps some echinoderms and vertebrates, may use polarized skylight or other sources of polarized light for purposes such as orientation, feeding and signaling (Johnsen, 1994; Labhart, 1996; Shashar and Cronin, 1996; Kriska et al., 1998; Dacke et al., 1999; Dacke et al., 2001; Dacke et al., 2002; Labhart and Meyer, 1999; Schwind, 1999; Shashar et al., 2000; Reppert et al., 2004; Boal et al., 2004; Mussi et al., 2005). Much of this behavior relies only on reception, and not image formation, of the polarized reflectance pattern of the sky or the ambient polarization in the environment (Können, 1985; Pomozi et al., 2001). However, some organisms, such as butterflies, are known to possess polarization sensitivity in an image forming capacity, making them an ideal model for testing hypotheses about the potential roles of polarized light in biological signaling.

Butterfly signaling and polarized light

Butterflies, like many other insects, use various aspects of vision in nearly all of their ecological undertakings (Silberglied, 1984; Kinoshita et al., 1999; Kelber et al., 2002; Rutowski, 2003; Briscoe, 2003). Location and acquisition of food resources, selection of suitable oviposition sites, and conspecific communication are all dependent on vision in butterfly ecology (Kinoshita et al., 1999; Kelber et al., 2001; Kelber et al., 2002; Weiss and Papaj, 2003). Therefore, attributes of visual ecology are expected to be adapted to light environments specific to a butterfly's niche (Endler, 1992; Endler, 1993a; Endler, 1993b; Endler, 1997).

Butterfly species living within complex forest light environments must, then, evolve mechanisms to generate and propagate effective visual signals in that habitat (Théry, 2001). Within a given light environment, visual signal properties, such as hue and polarization, should be predictable based on efficacy of transmission of the hypothetical signal (Endler, 1993b). It has been proposed that those organisms living in complex and low light environments such as the tropical forest understory, may be more likely than others to utilize polarized light as a signal (Cronin et al., 2003a; Sweeney et al., 2003), because polarized light could provide additional visual information about an organism's surroundings that is independent of light spectrum and intensity (Shashar et al., 1998, Cronin et al., 2003a; Cronin et al., 2003b).

Insects, in general, have morphological predispositions for polarized light reception within each of the ommatidia composing their compound eyes. Nevertheless, many have evolved morphological mechanisms that abolish much of this sensitivity in many ommatidia, while accentuating it in others (Labhart and Meyer, 1999). A specialized and possibly widespread aspect of butterfly visual physiology is the

retention of the ability to detect and exploit polarized light reflectance of objects (Kelber, 1999; Kelber et al., 2001; Reppert et al., 2004; Hegedüs and Horváth, 2004). Akin to color vision, some butterflies are thought to generate a neural image based on the relative percentage of polarization reflectance from its surroundings.

In one butterfly, preserved polarization sensitivity has been shown to cause fluctuations in perceived color, behaviorally and in a model retina (Kelber, 1999; Kelber et al., 2001; Horváth et al., 2002; Hegedüs and Horváth, 2004). These fluctuations, termed false colors, may be used to determine the 'shiny-ness' or 'matte-ness' of a surface and could be helpful in object detection, determining substrate composition, and determining substrate surface orientation (Shashar et al., 1998; Kelber, 1999). This information is of great potential value to foraging and ovipositing butterflies and could be determined independent of hue and intensity of ambient and reflected light (Shashar et al., 1998; Horváth et al., 2002; Hegedüs and Horváth, 2004). Thus, the ability to perceive polarized light potentially provides an additional tool that may be used in conjunction with more typical visual sensory mechanisms (Bernard and Wehner, 1977; Cronin et al., 2003a; Cronin et al., 2003b; Shashar and Cronin, 1996).

Therefore, forest butterflies may use signals containing polarized light to enhance mate visibility where low light levels make production of bright signals difficult. Sweeney and colleagues (Sweeney et al., 2003) have demonstrated that forest dwelling *Heliconius cydno* butterflies utilize polarized reflectance patterns to recognize conspecifics and potential mates, whereas a sister species that lives in open habitats, *Heliconius melpomene*, does not produce or use polarized signals. *H. cydno* butterflies may use polarized light as a private communication channel, minimizing detection by predators while maximizing conspicuousness to potential mates; vertebrate predators of butterflies are unlikely to be able to resolve objects based upon polarized light reflectance (Vos Hzn et al., 1995; Greenwood et al., 2003).

The ubiquity of polarized light throughout natural environments and its potential utility in butterfly ecology has only recently been considered. The adaptive value of reflecting and detecting polarized light is predicted to be greater in complex and changing light environments, such as those encompassed by forests. Polarized light could increase contrast of objects and conspecifics, act in inter- or intraspecific signaling, and provide vital information that might otherwise be lost in low light conditions. Here we present a broad survey of the nymphalid butterflies of Costa Rica, correlating ambient light properties typical within their habitats to the presence/absence of polarized reflectance within their wing patterns (DeVries, 1987; Endler, 1993a). We also conducted a phylogenetic analysis to establish whether there is a statistically significant evolutionary relationship between the forest light habitat of some nymphalid butterflies and their use of polarized reflectance patterns.

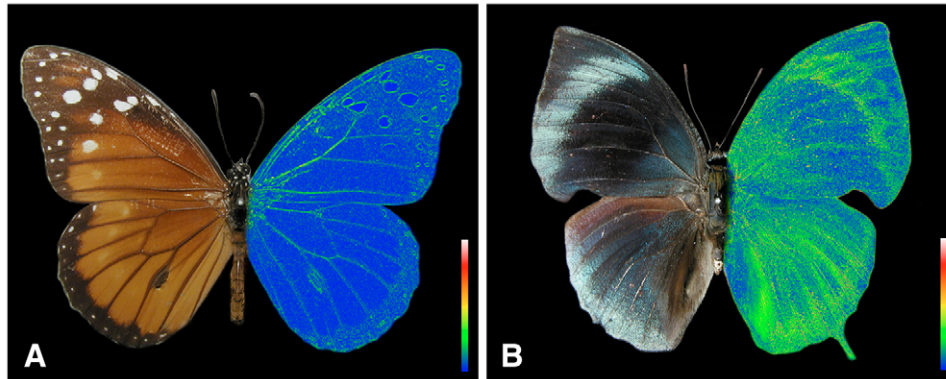


Fig. 1. Composite images of (A) non-polarized (*Danaus erisimus*) and (B) polarized (*Memphis chaeronia*) butterfly wings. Two pattern elements in B are polarized while none are polarized in A. The few instances where polarization exists in A are due to wear on the wings and the shine of the wing veins. False color imaging allowed transformation from a continuous to a binary polarized data set. Color reference keys: blue indicates no polarization while green, yellow, red and white indicate increased polarized reflectance (white=complete polarization).

Materials and methods

Survey of Costa Rican butterflies

Butterfly specimens were obtained from the Field Museum of Natural History in Chicago and the Smithsonian National Museum of Natural History in Washington DC, USA. A list of specimens used can be found in the Appendix. Primary surveys evaluating the presence of polarized light reflectance were conducted utilizing a polarizing filter held approximately 45° relative to the normal of a stationary horizontal wing surface in the direction of the posterior. A white light source similar in spectrum to sunlight (GE plant light 75 W; Fairfield, CT, USA) was situated 45° relative to the normal of the wing in the direction of the anterior, making the angle of incidence 90°.

As almost any butterfly will reflect some polarized light if appropriately illuminated, we distinguished presence and absence of polarized reflectance in two ways. First, if the reflectance intensity of the specimen changed appreciably upon rotating the filter 90°, this indicated that the specimen is a candidate for the polarized category. Second, if this significant change was primarily associated with a pattern element of the wing surface (i.e. band, spot or ground color) as opposed to chance polarization from worn wing veins or random areas of specifically oriented wing scales, then it was placed in the polarized category. The latter means of determining whether a specimen was polarized was reinforced by the false-color reflectance images, as described below (Fig. 1). Butterflies were then separated into two discrete categories to be mapped onto a phylogeny. This division was based upon whether the reflectance of the entire wing or a pattern element was significantly polarized (polarized group) or whether polarization was slight and artefactual or nonexistent (non-polarized group).

False-color polarized reflectance images

False-color photographs encoded to display degree of polarization were produced using the program Image-Pol (developed by T.-H. Chiou) from original color images

obtained using a digital camera fitted with a polarizing filter. For each specimen, three photographs were taken with the filter rotated to three different known e-vectors: 0°, 45° and 90°. The program measured relative intensities of reflected light at each orientation and determined the proportion of reflected light polarized by the butterfly wings. From this information a fourth image was generated in false color. Images are color coded by Image-Pol using an intensity scale where blue indicates no polarized reflectance and green, yellow, red and white indicate increasing degrees of polarization (white=100% polarized reflectance).

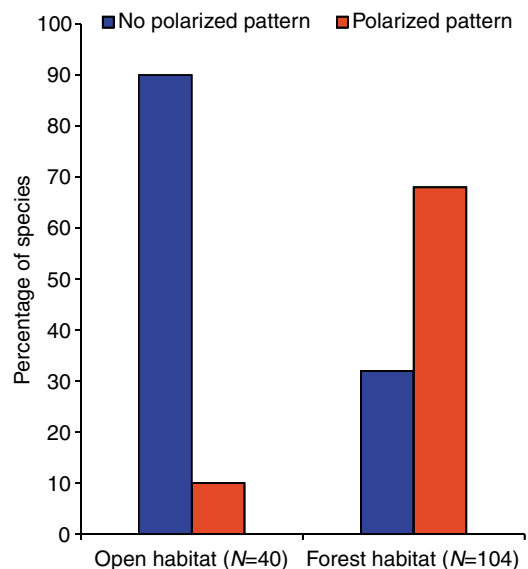


Fig. 2. Graphical representation of the proportion of Costa Rican nymphalid species exhibiting polarized and non-polarized wing patterns in open and forest light environments. 68% of species dwelling within forests ($N=104$) with complex ambient light environments exhibit polarized reflectance patterns. 90% of species flying under open light conditions ($N=40$) display non-polarized reflectance patterns.

Phylogeny and the concentrated changes test

Currently available phylogenies were obtained from the literature and a composite phylogeny of the Nymphalidae was generated, placing a subset of the Papilionidae as the outgroup using MacClade 4.0 (Copyright © 2002 David R. Maddison and Wayne P. Maddison). Evolutionary branch lengths are not comparable among published phylogenies and are not integral for the concentrated changes test; thus, all were presumed to be equal. Butterflies of the nymphalid subfamily Ithomiinae (clearwing butterflies) were excluded from the phylogenetic analysis as they exhibit a polarized reflectance that appears to be an artifact of insect cuticle rather than light reflectance from the wing scales.

A concentrated changes test (1000 simulations) was performed using MacClade to test for a correlation between ambient light habitat and presence of polarized reflectance, while controlling for phylogenetic non-independence. This test determines the probability of finding polarized reflectance as frequently in those branches designated as forest dwelling butterflies compared to the polarized reflectance trait being randomly distributed over the tree. A

low *P*-value indicates a non-random distribution of the polarized reflectance trait in those branches coded as taxa dwelling in forest light, and therefore an evolutionary correlation between the two traits.

Results*Survey and false-color photography*

A significant correlation (Yates $\chi^2=37$; d.f.=1; $P<0.0001$) was found between polarized reflectance patterns of butterfly wings and forest light habitats (Fig. 2). Butterflies with polarized wing reflectance patterns tended to occupy forest understory habitats characterized by highly variable and complex light conditions. Additionally, we found variation among those butterflies with polarized reflectance in the relative area of the wing surface covered, location and shape of the polarization pattern, and the percentage of polarized light reflected from a polarized area of the wing.

Representative polarized patterns of nymphalid butterflies are shown in Fig. 3. These patterns typically are reflected at wavelengths shorter than 550 nm. As the light source used was

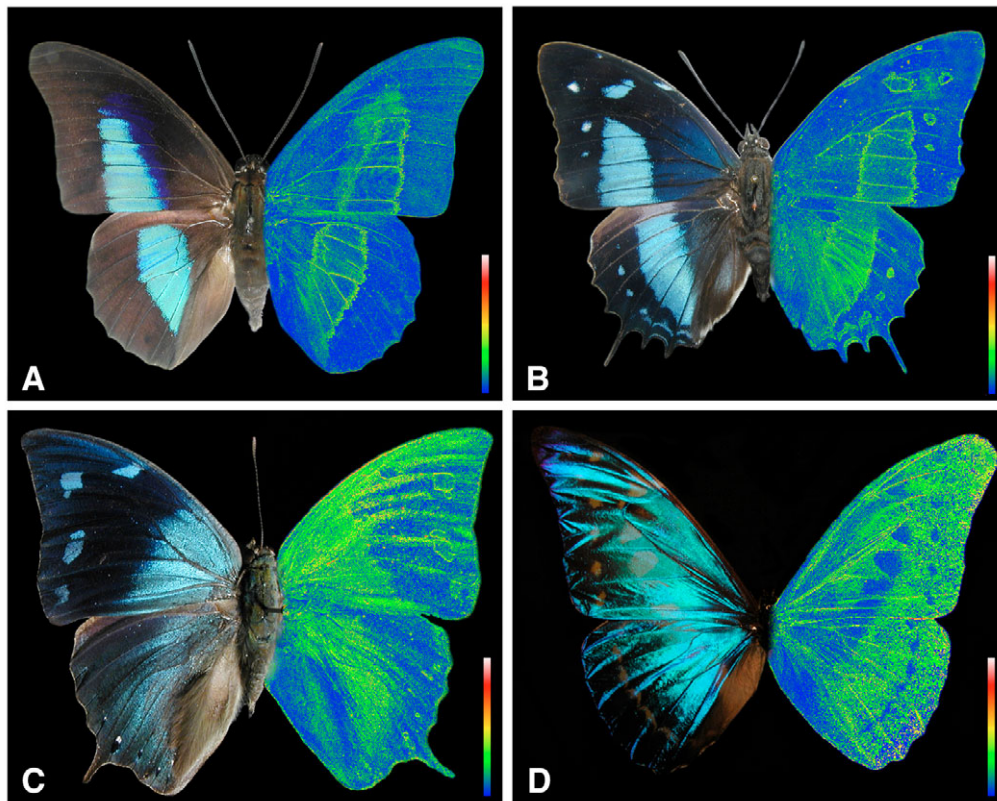


Fig. 3. Composite images of representative species from several nymphalid subfamilies (A) *Prepona gnorima*, (B) *Baeotus baeotus*, (C) *Memphis xenocles* and (D) *Morpho cypris*. A shows two differently colored localized bands of polarized iridescence while B and C exhibit prominent bands of polarized reflectance with an iridescent ground coloration that is polarized to a lesser extent. D presents a nearly uniform polarization pattern over the entire wing surface with the exception of the white diffuse reflecting patches along the midline of both wings. False-colored portions of the composite images are coded for intensity of polarization according to the color bar in the corner of each figure. False-color portions of the images are coded as in Fig. 1.

not rich in the ultraviolet wavelengths, and most polarizing filters absorb ultraviolet light, it was not possible to determine whether there were ultraviolet reflectance patterns and whether or not any of these potential patterns were polarized. Ultraviolet pattern elements in butterflies are often structural in nature and therefore might also be polarized (Silberglied, 1984; Kemp et al., 2005). Furthermore, recent work on the nymphalid butterfly *Danaus plexippus* has shown that the dorsal rim area of their compound eyes is sensitive to ultraviolet polarized light and that this may function in skylight orientation (Sauman et al., 2005; Stalleicken et al., 2005). Due to limitations inherent in the methods of this study, the potential importance of ultraviolet polarized patterns on butterfly wings could not be assessed.

Patterns tend to be banded, instead of spotted, with an exception for the typically spotted biblidine genus, *Hamadryas*. Polarized bands are generally centrally located, running

through the discal cells of the forewing and hindwing. Some species exhibit a polarized background reflectance with depolarized spots situated along the midline of the wings, such as in *Morpho cypris* (Fig. 3). Spots and bands of polarized reflective scales generally are absent from the apical and basal areas of the wings, possibly suggesting different selection pressures for location of polarized and color signals on the wing. In some butterflies of the heliconiine genus *Heliconius*, the iridescence comprised the primary ground color and band pattern elements were formed by reflectance from non-polarizing scales (Fig. 4).

Concentrated changes test

A concentrated changes test was performed on the composite phylogeny in Fig. 5. Eleven gains and four losses of the polarized pattern occurred in the butterflies examined, according to the most recently available published phylogenies.

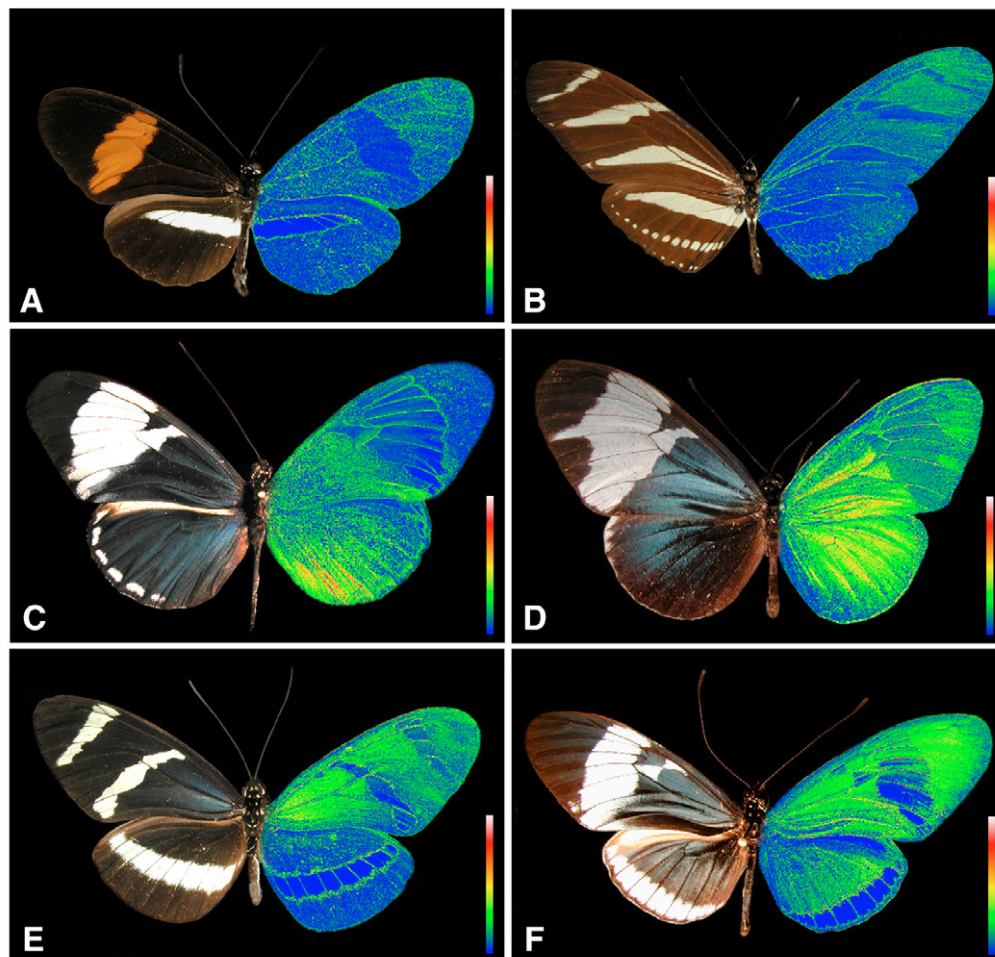


Fig. 4. Composite images of species from the nymphalid subfamily Heliconiinae, genus *Heliconius*. (A) *H. melpomene*, (B) *H. charitonius*, (C) *H. cydno*, (D) *H. sapho*, (E) *H. hewitsoni*, (F) *H. cydno chioneus*. In contrast to the depolarized patterns typical of open areas shown in A and B, C–F show a series of forest living co-mimics, each with polarized blue iridescent scales covering much of the wing surface. Variable white or yellow ‘windows’ of pigmented scales reflect depolarized light. *Heliconius cydno* (C,F) is a close sister species with *H. melpomene* (A), showing the stark contrast that can arise between related butterflies living in dramatically different light environment. False-color portions of the images are coded as in Figs 1 and 3.

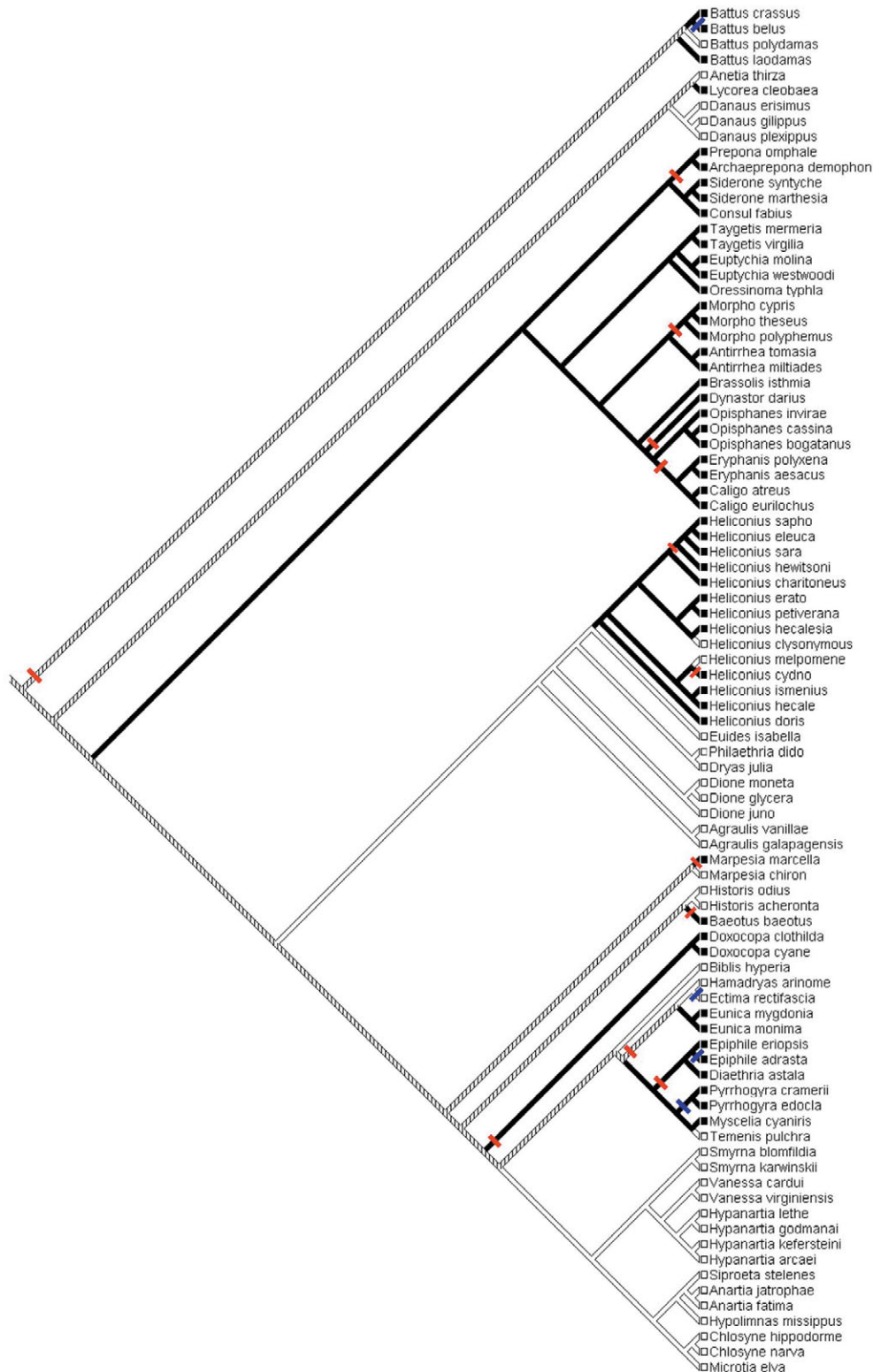


Fig. 5. Phylogenetic tree of the Nymphalidae compiled from published trees (Brower, 1994; Brower and Egan, 1997; Penz, 1999; Wahlberg and Zimmermann, 2000; Willmott et al., 2001; Wahlberg, 2001; Penz and DeVries, 2002; Blum et al., 2003; Wahlberg et al., 2003; Frietas and Brown, Jr, 2004; Murray and Prowell, 2005; Silva-Brandão et al., 2005; Wahlberg et al., 2005a; Wahlberg et al., 2005b) (A. V. Z. Brower, personal communication). Branch lengths are arbitrary. Black branches indicate a forest light environment, while white branches indicate open habitat. Ancestral branch states that could not be resolved by MacClade are hatched. Gains and losses of the polarized reflectance trait are shown as red and blue hatch marks, respectively. A concentrated changes test shows robust support for the correlated evolution of polarized reflectance patterns with life in forest environments ($P \approx 0.008$).

Ten gains and three losses were located on the nymphalid clade; of these, nine gains and three losses were located on branches designated as forest dwelling species. Those butterflies that exhibited polarized reflectance patterns were significantly more likely to exist within a forest light habitat ($P \approx 0.008$). The probability that the arrangement of traits in Fig. 5 is due to chance is negligible (Maddison, 1990). Thus, there is robust support for the hypothesis that the evolution of polarized reflectance patterns is concentrated within those branches containing species that live in a complex forest light environment.

Butterflies of the papilionid genus *Battus* were used as the outgroup in the constructed phylogeny, and some of these species also exhibited polarized light patterns that corresponded to the area of visible iridescence on the hindwings. Butterflies of the subfamily Ithomiinae (clearwing butterflies) exhibit green, red and white polarized reflectance – similar to that of a soap bubble – that appears as a sheen and is likely an artifact of the wing membrane cuticle rather than light reflectance from the scales. The ithomiines were not included in the phylogenetic analysis. However, this does not necessarily imply a lack of ecological significance.

Discussion

Light environment and potential utility of polarized reflectance patterns

Precise light conditions of where these species fly and mate have not been reported for the species in this study, but it is reasonable to assume that they are flying when the sun is not occluded by clouds. Most butterflies only fly when the sun is unobscured for thermoregulatory reasons (Douglas, 1978). Thus, those butterflies that typically fly in the understory are likely to experience ambient light spectra converging on woodland shade, forest shade or small gap light environments, which provide as little as 2.5% of the light intensity of an open light environment (Endler, 1992; Endler, 1997; Shashar et al., 1998). Under these light conditions, it would be advantageous for species specific patterns to be polarized, as this type of signal can be conspicuously independent of ambient light intensity and spectral composition (Shashar et al., 1998; Cronin et al., 2003a; Cronin et al., 2003b).

Conspicuous, polarized reflectance patterns could prove useful in intraspecific communication, including mate selection (Sweeney et al., 2003). Temporal changes in ambient light environment may allow mate-location to be more successful at different times of the day (Endler, 1997; Kemp and Rutowski, 2001). A butterfly using polarized light as a mating signal may be able to circumvent some of the temporal constraint on mating success, as the polarization pattern will be quite independent of temporal variation in light intensity.

Polarized reflectance and iridescence

Signals that would be most efficacious in advertising to conspecifics (and indeed, to other species) in forest light

environments would be composed of those colors that reflect best in woodland shade and forest shade light spectra. The spectra of these light environments appear (to our eyes) greenish-blue and green, respectively (Endler, 1993a). Most of the polarized iridescent patterns in this study are blue, with fewer being greenish-blue or violet. These spectrally pure colors would contrast well with the commonly brown low intensity background (Endler, 1993a).

False colors potentially perceived by butterflies as a result of polarization sensitivity (Wehner and Bernard, 1993; Kelber, 1999; Kelber et al., 2001) may amplify or otherwise augment color content of iridescent signals. Moreover, polarized reflectance patterns of butterflies in flight likely display as flashes, as do the ultraviolet iridescent signals of *Colias* butterflies (Silberglied and Taylor, 1978; Silberglied, 1984). This would provide ample motion contrast against the relatively unchanging polarized pattern in background reflectance of the forest understory (Shashar et al., 1998). The ability to perceive these signals would greatly increase probabilities of finding conspecifics at a distance, which is surely necessary in this visually complex environment.

Concentrated changes test

Within the Nymphalidae, the concentrated changes test provides robust phylogenetic support for the hypothesis that polarized reflectance patterns are evolutionarily correlated with complex light environments. The results of the present study suggest that butterflies inhabiting forests with complex and time-dependent light environments may rely on polarized wing patterns in a manner parallel to that of pigment patterns in other butterflies. Detailed data describing when individual species are flying, foraging, ovipositing, courting and mating will be necessary to understand why polarized iridescence occurs with unusually high incidence in the neotropical forest understory.

Future directions

Polarized light is potentially of great ecological importance in many species and many gaps in our knowledge still remain. Polarization may, for instance, increase perceived signal or organism contrast with the environmental background in forest species. Polarization reflectance also has potential to produce false-color perception, which may alter signal content. Together with the spectral portion of an iridescent signal, polarization may also serve as an indicator of mate quality in butterflies (D. J. Kemp and R. L. Rutowski, manuscript submitted).

In this study we have shown that an evolutionary correlation exists between polarized reflectance patterns in butterflies and specific light environments. Most polarized patterns are found in those species that spend much of their time in forest shade. There seems to be little phylogenetic constraint in these traits, as revealed by the concentrated changes test, which suggests that polarized reflectance patterns have adaptive value as signals for butterflies evolving in complex light environments.

Appendix

Family: Subfamily	Genus	Species	Authority	Polarized reflectance	Light environment
Papilionidae: Papilioninae					
	<i>Battus</i>	<i>crassus</i>	Cramer 1777	1	1
	<i>Battus</i>	<i>belus</i>	Kollar 1850	1	1
	<i>Battus</i>	<i>laodamas</i>	Rothschild and Jordan 1906	1	1
	<i>Battus</i>	<i>polydamas</i>	Linnaeus 1758	1	0
	<i>Papilio</i>	<i>garamas</i>	Godman and Salvin 1878	0	0
	<i>Papilio</i>	<i>polyxenes stabilis</i>	Rothschild and Jordan 1906	0	0
Nymphalidae: Heliconiinae					
	<i>Agraulis</i>	<i>vanillae</i>	Linnaeus 1758	0	0
	<i>Dione</i>	<i>juno</i>	Cramer 1779	0	0
	<i>Dione</i>	<i>moneta</i>	Butler 1873	0	0
	<i>Dryas (Colaenis)</i>	<i>julia</i>	Fabricius 1775	0	0
	<i>Euides</i>	<i>isabella</i>	Cramer 1781	0	0
	<i>Euides</i>	<i>lineata</i>	Salvin 1868	0	0
	<i>Heliconius</i>	<i>charitoneus</i>	Linnaeus 1767	0	0
	<i>Heliconius</i>	<i>clysonymus</i>	Salvin 1871	0	0
	<i>Heliconius</i>	<i>cydno</i>	Bates 1864	1	1
	<i>Heliconius</i>	<i>doris fransiens eratonia amathusia viridis metharmina and aristomache</i>	Linnaeus 1771	0	0
	<i>Heliconius</i>	<i>eleuca primularis</i>	Hewitson 1853	1	1
	<i>Heliconius</i>	<i>erato demophoon phyllis santarem microclea udalrica callista and callicopis</i>	Doubleday 1847	0	1
	<i>Heliconius</i>	<i>hecale zuleika passithoe melicerta</i>	Hewitson 1854	0	1
	<i>Heliconius</i>	<i>hecalesia formosus</i>	Bates 1863	0	1
	<i>Heliconius</i>	<i>hewitsoni</i>	Staudinger 1875	1	1
	<i>Heliconius</i>	<i>ismenius</i>	Doubleday 1847	0	1
	<i>Heliconius</i>	<i>melpomene</i>	Boisduval 1870	0	0
	<i>Heliconius</i>	<i>petiverana</i> (also ' <i>erato petiverana</i> ' DeVries 1987)		0	1
	<i>Heliconius</i>	<i>sapho leuce and sapho</i>	Doubleday 1847	1	1
	<i>Heliconius</i>	<i>sara</i>	Stichel 1906	1	1
	<i>Philaethria</i>	<i>dido</i>	Linnaeus 1763	0	0
Nymphalidae: Nymphalinae					
	<i>Anartia</i>	<i>fatima</i>	Godart 1820	0	0
	<i>Anartia</i>	<i>jatrophae</i>	Linnaeus 1763	0	0
	<i>Baeotus</i>	<i>baeotus</i>	Doubleday 1849	1	1
	<i>Biblis</i>	<i>hyperia</i>	Cramer 1782	0	0
	<i>Chlosyne</i>	<i>hippodrome</i>	Geyer 1837	0	0
	<i>Chlosyne</i>	<i>narva</i>	Fabricius 1893	0	0
	<i>Diaethria</i>	<i>astala</i>	Guérin-Ménéville 1844	1	1
	<i>Ectima</i>	<i>rectifascia</i>	Butler and Druce 1874	0	1
	<i>Epiphile</i>	<i>adrasta</i>	Hewitson 1861	0	1
	<i>Epiphile</i>	<i>eriopsis</i>	Jenkins 1986	1	1
	<i>Epiphile</i>	<i>orea</i>	Godman and Salvin 1883	1	1
	<i>Eunica</i>	<i>alcmena</i>	Druce 1874	1	1
	<i>Eunica</i>	<i>monima</i>	Bates 1864	1	1
	<i>Eunica</i>	<i>mygdonia</i>	Godart 1823	1	1
	<i>Eunica</i>	<i>pomona</i>	Felder 1862	1	1
	<i>Eunica</i>	<i>tatila</i>	Godman and Salvin 1887	1	1
	<i>Hamadryas</i>	<i>amphinome mexicana</i>	Lucas 1853	1	1
	<i>Hamadryas</i>	<i>arinome</i>	Godman and Salvin 1883	1	0
	<i>Hamadryas</i>	<i>feronia</i>	Fruhstorfer 1916	1	1
	<i>Hamadryas</i>	<i>februa ferentina</i>	Godart 1824	1	1
	<i>Hamadryas</i>	<i>fornax</i>	Fruhstorfer 1907	1	1
	<i>Hamadryas</i>	<i>glauconome</i>	Bates 1864	1	1
	<i>Hamadryas</i>	<i>guatemalena</i>	Bates 1864	1	1
	<i>Hamadryas</i>	<i>ipthime</i>	Bates 1864	1	1
	<i>Hamadryas</i>	<i>laodamia</i>	Fruhstorfer 1916	1	1

Appendix continues on following page

Appendix. *Continued*

Family: Subfamily	Genus	Species	Authority	Polarized reflectance	Light environment
	<i>Historis</i>	<i>odius</i>	Fabricius 1775	0	0
	<i>Historis</i>	<i>acheronta</i>	Fabricius 1775	0	1
	<i>Hypanartia</i>	<i>arcaeii</i>	Godman and Salvin 1871	0	1
	<i>Hypanartia</i>	<i>godmanai</i>	Bates 1864	0	0
	<i>Hypanartia</i>	<i>kefersteini</i>	Doubleday 1847	0	0
	<i>Hypanartia</i>	<i>lethe</i>	Fabricius 1793	0	0
	<i>Hypolimnas</i>	<i>missippus</i>	Linnaeus 1764	0	0
	<i>Marpesia</i>	<i>chiron</i>	Fabricius 1775	0	0
	<i>Marpesia</i>	<i>coresia</i>	Godart 1823	0	0
	<i>Marpesia</i>	<i>iole</i>	Drury 1782	1	1
	<i>Marpesia</i>	<i>marcella</i>	Felder 1861	1	1
	<i>Mestra</i>	<i>amymone</i>	Menetries 1857	0	0
	<i>Myscelia</i>	<i>cyaniris</i>	Doubleday 1848	1	1
	<i>Pycina</i>	<i>zamba</i>	Godman and Salvin 1884	0	1
	<i>Panacea</i>	<i>procilla</i>	Godman and Salvin 1883	1	1
	<i>Pyrrhogyra</i>	<i>cramerii</i>	Aurivillius 1882	0	1
	<i>Pyrrhogyra</i>	<i>edocla aenaria</i>	Fruhstorfer 1908	1	1
	<i>Pyrrhogyra</i>	<i>neaerea hypsenor</i>	Godman and Salvin 1884	0	0
	<i>Pyrrhogyra</i>	<i>otolais</i>	Bates 1864	0	1
	<i>Siproeta</i>	<i>epaphus</i>	Latreille 1811	0	0
	<i>Siproeta</i>	<i>stelenes</i>	Fruhstorfer 1907	0	0
	<i>Siproeta</i>	<i>superba</i>	Fox and Forbes 1971	0	0
	<i>Smyrna</i>	<i>blomfieldia</i>	Fruhstorfer 1908	0	1
	<i>Smyrna</i>	<i>karwinskii</i>	Hübner 1816	0	1
	<i>Temenis</i>	<i>pulchra</i>	Hewitson 1816	1	0
	<i>Vanessa</i>	<i>cardui</i>	Linnaeus 1761	0	0
	<i>Vanessa</i>	<i>virginiensis</i>	Drury 1773	0	0
Nymphalidae: Melitaeinae					
	<i>Microtia</i>	<i>elva</i>	Bates 1864	0	0
Nymphalidae: Charaxinae					
	<i>Anaea</i>	<i>aidea</i>	Guerin-Meneville 1844	0	0
	<i>Archaeoprepona</i>	<i>demophon</i>	Fruhstorfer 1905	1	1
	<i>Consul</i>	<i>fabius</i>	Doubleday 1849	0	1
	<i>Hypna</i>	<i>clytemnestra</i>	Cramer 1777	1	1
	<i>Memphis</i>	<i>chaeronea</i>	Salvin 1869	1	1
	<i>Memphis</i>	<i>xenocles</i>	Westwood 1850	1	1
	<i>Prepona</i>	<i>omphale</i>	Fruhstorfer 1904	1	1
	<i>Prepona</i>	<i>gnorima</i>	Bates 1875	1	1
	<i>Siderone</i>	<i>marthesia</i>	Cramer 1777	1	1
	<i>Siderone</i>	<i>syntyche</i>	Hewitson 1853	1	1
Nymphalidae: Apaturinae					
	<i>Doxocopa</i>	<i>clothilda</i>	Felder 1866	1	1
	<i>Doxocopa</i>	<i>cyane</i>	Latreille 1833	1	1
	<i>Doxocopa</i>	<i>laure</i>	Drury 1773	1	1
	<i>Doxocopa</i>	<i>pavon</i>	Latreille 1805	1	1
Nymphalidae: Danainae					
	<i>Anetia</i>	<i>thirza</i>	Salvin 1869	0	0
	<i>Danaus</i>	<i>erisimus</i>	Talbot 1943	0	0
	<i>Danaus</i>	<i>gilippus</i>	Bates 1863	0	0
	<i>Danaus</i>	<i>plexippus</i>	Linnaeus 1758	0	0
	<i>Lycorea</i>	<i>cleobaea</i>	Doubleday 1847	0	1
Nymphalidae: Ithomiinae					
	<i>Aeria</i>	<i>eurimedia</i>	Godman and Salvin 1879	1	1
	<i>Callithomia</i>	<i>hezia</i>	Hewitson 1853	0	0-1
	<i>Dircenna</i>	<i>dero</i>	Felder and Felder 1867	1	1
	<i>Dircenna</i>	<i>klugii</i>	Geyer 1837	1	1
	<i>Dircenna</i>	<i>relata</i>	Butler and Druce 1872	1	1

Appendix continues on following page

Appendix. Continued

Family: Subfamily	Genus	Species	Authority	Polarized reflectance	Light environment
	<i>Episcada</i>	<i>salvinia</i>	Bates 1864	1	1
	<i>Godyris</i>	<i>zavalata</i>	Fox 1968	1	1
	<i>Hyposcada</i>	<i>virginiana</i>	Haensch 1909	1	1
	<i>Ithomia</i>	<i>diasia</i>	Bates 1866	1	1
	<i>Ithomia</i>	<i>heraldica</i>	Bates 1866	0	1
	<i>Ithomia</i>	<i>patilla</i>	Hewitson 1853	1	1
	<i>Ithomia</i>	<i>terra</i>	Haensch 1909	1	1
	<i>Mechanitis</i>	<i>lysimmia dorissus</i>	Bates 1864	0	1
	<i>Mechanitis</i>	<i>menapis</i>	Godman and Salvin 1901	0	1
	<i>Mechanitis</i>	<i>polymnia</i>	Bates 1863	0	1
	<i>Melinaea</i>	<i>ethra lilis</i>	Bates 1864	0	0
	<i>Melinaea</i>	<i>scylax</i>	Salvin 1871	0	0
	<i>Napeogenes</i>	<i>peredia</i>	Schaus 1913	1	1
	<i>Napeogenes</i>	<i>tolosa</i>	Godman 1899	1	1
	<i>Olyras</i>	<i>crathis</i>	Godman and Salvin 1897	1	1
	<i>Pteronymia</i>	<i>artena</i>	Hewitson 1854	1	1
	<i>Pteronymia</i>	<i>cotyto</i>	Guerin 1844	1	1
	<i>Pteronymia</i>	<i>notilla</i>	Butler and Druce 1872	1	1
	<i>Tithorea</i>	<i>harmonia</i>	Godman and Salvin 1879	0	1
	<i>Tithorea</i>	<i>tarricina</i>	Godman and Salvin 1879	0	1
Nymphalidae: Libytheinae					
	<i>Libytheana</i>	<i>carinenta mexicana</i>	Michener 1943	0	0
Nymphalidae: Acraeinae					
	<i>Actinote</i>	<i>anteas</i>	Doubleday 1847	0	0
	<i>Actinote</i>	<i>guatemalena</i>	Bates 1864	0	0
	<i>Actinote</i>	<i>leucomelas</i>	Bates 1864	1	0
Nymphalidae: Satyrinae					
	<i>Cithaeris</i>	<i>menander</i>	Drury 1782	1	1
	<i>Drucina</i>	<i>leonata</i>	Butler 1872	0	1
	<i>Euptychia</i>	<i>mollis</i>	Staudinger 1875	0	1
	<i>Euptychia</i>	<i>westwoodi</i>	Butler 1866	0	1
	<i>Oressinoma</i>	<i>typhla</i>	Westwood 1851	1	1
	<i>Pierella</i>	<i>helvetia incanescens</i>	Godman and Salvin 1877	1	1
	<i>Pronophila</i>	<i>timanthes</i>	Salvin 1871		1
	<i>Taygetis</i>	<i>andromeda</i>	Cramer 1779	0	0-1
	<i>Taygetis</i>	<i>mermeria</i>	Butler 1868	0	1
	<i>Taygetis</i>	<i>virgilia</i>	Staudinger 1888	0	1
Nymphalidae: Morphinae					
	<i>Antirrhea</i>	<i>miltiades</i>	Fabricius 1793	0	1
	<i>Antirrhea</i>	<i>tomasia</i>	Butler 1875	0	1
	<i>Morpho</i>	<i>cypris</i>	Westwood 1851	1	1
	<i>Morpho</i>	<i>polyphemus</i>	Corea and Chacon 1984	1	1
	<i>Morpho</i>	<i>theseus</i>	Butler 1872	1	1
Nymphalidae: Brassolinae					
	<i>Brassolis</i>	<i>isthmia</i>	Bates 1864	0	1
	<i>Caligo</i>	<i>atreus</i>	Fruhstorfer 1912	1	1
	<i>Caligo</i>	<i>eurilochus</i>	Fruhstorfer 1904	1	1
	<i>Caligo</i>	<i>ileoneus</i>	Butler 1870	1	1
	<i>Caligo</i>	<i>memnon</i>	Felder and Felder 1866	1	1
	<i>Caligo</i>	<i>oileus</i>	Boisduval 1870	1	1
	<i>Catoblepia</i>	<i>xanthicles</i>	Godman and Salvin 1881	0	1
	<i>Dynastor</i>	<i>darius</i>	Butler 1872	0	1
	<i>Eryphanis</i>	<i>aesacus</i>	Butler 1872	1	1
	<i>Eryphanis</i>	<i>polyxena</i>	Felder 1862	1	1
	<i>Narope</i>	<i>cyllastros</i>	Godman and Salvin 1878	0	1
	<i>Opisphanes</i>	<i>bogatanus</i>	Distant 1875	0	1
	<i>Opisphanes</i>	<i>cassina</i>	Boisduval 1870	0	1
	<i>Opisphanes</i>	<i>invirae</i>	Stichel 1904	0	1

Polarized reflectance 0=absent 1=present; light environment 0=open 1=forest.

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