Journal of the Lepidopterists' Society
56(4), 2002, 199–215

PHYLOGENETIC ANALYSIS AND REVIEW OF *PANACEA* AND *BATESIA* BUTTERFLIES (NYMPHALIDAE)

RYAN I. HILL

Section of Integrative Biology, University of Texas, Austin, Texas 78712, USA

CARLA M. PENZ[1] AND P. J. DEVRIES

Milwaukee Public Museum, 800 W Wells St., Milwaukee, Wisconsin 53233, USA

ABSTRACT. Phylogenetic analysis of 53 morphological characters for five species of *Panacea* and *Batesia hypochlora* supports the separation of the two genera and showed that the monotypic genus *Batesia* is basal to *Panacea*. Male genitalia were uniform within *Panacea* and characters informative for phylogeny reconstruction were restricted to wing coloration. Illustrations of adults and genitalia, a brief diagnosis, and distributions are provided for each species.

Additional key words: *prola*, *procilla*, *regina*, *divalis*, *bleuzeni*, *chalcothea*, *lysimache*, *bella*, *hypochlora*, *Caryodendron*, Euphorbiaceae.

By possessing distasteful wings or body fluids, brightly colored butterflies are generally avoided by many vertebrate predators in nature. This phenomenon is particularly well known in various genera of Nymphalidae (e.g., *Acraea*, *Heliconius*, many Danainae and Ithomiinae), Papilionidae (e.g., *Battus*, *Parides*) and Pieridae (e.g., *Mylothris*, *Delias*, *Appias*, *Perrhybris*, *Itaballia*) among others (see Poulton 1908, Sywnnerton 1919, Carpenter 1942, Fisher 1958, Chai 1986). Nevertheless, a great many of these same butterflies are eagerly sought after and prized by a different group of predators, human collectors. Although collector value may provide a metric of how garishly colored a particular butterfly might be, it is often a poor measure of how well we understand that species. Therefore, when considering biological or evolutionary understanding of particular butterflies, it is likely that drab ones are equally as well known as those that are brightly colored. Although well represented in museum collections, and available as virtual specimens on the internet, nymphalid butterflies in the genera *Batesia* Felder and Felder, 1862 and *Panacea* Godman and Salvin, 1883 are good examples of this phenomenon.

The Neotropical genus *Batesia* occurs from central Colombia to eastern Ecuador, southeast Peru, western Brazil, and likely into northeast Bolivia; effectively an upper Amazonian distribution. On the other hand, members of *Panacea* are found from Costa Rica south across Venezuela and the Guianas, throughout the Amazon basin, and into Bolivia.

Both *Batesia* and *Panacea* were originally described as monotypic genera, but only *Batesia* with its single species, *hypochlora* Felder and Felder, 1862 has remained so. The history of *Panacea* is somewhat convoluted. *Panacea prola* (Doubleday, 1848) was initially designated the type species of *Pandora* Doubleday, 1848—a name used previously for different insect genera by at least seven different authors, and thus, an invalid homonym (see Hemming 1967). In an attempt to settle this quandary, Kirby (1871) transferred all species of *Pandora* to *Batesia*. Godman and Salvin (1883), however, felt that all species formerly in *Pandora* warranted separation from *Batesia*, and erected the genus *Panacea* to accommodate them—thus providing a panacea to the *Pandora* problem. Eight species have been described in *Panacea*—*P. prola*; *P. procilla* (Hewitson, 1852); *P. regina* (Bates, 1864); *P. divalis* (Bates, 1868); *P. chalcothea* (Bates, 1868); *P. lysimache* Godman and Salvin, 1883; *P. bleuzeni* Plantrou and Attal, 1986; and *P. bella* D'Abrera, 1987, not all that are currently regarded as valid species (see synonymies below).

The vicissitudes of nomenclature aside, nearly all natural history studies suggest that *Batesia* and *Panacea* are distinct, but closely related genera. At present they are classified in the Biblidini along with *Hamadryas*, *Ectima*, *Eunica*, *Myscelia*, *Dynamine*, *Colobura* and other genera (Godman & Salvin 1883, Seitz 1916, Ackery 1984, Harvey 1991).

Recent observations indicate that *Batesia* and *Panacea* share *Caryodendron* spp. (Euphorbiaceae) as host plants, and that their immature stages are very similar (DeVries et al. 1999). The correspondence of immature biology, classification, and the fact that these genera have never been assessed using cladistic methods led us to ask whether *B. hypochlora* was separate from *Panacea*, or if it represented a derived species within *Panacea*. Accordingly, this study tests both hypotheses through phylogenetic analysis of five species of *Panacea* plus *Batesia hypochlora*. Based on adult morphology we show that *Batesia hypochlora* is basal to *Panacea*, and that together they form a monophyletic group. We then present characters to aid in species identification, and provide notes relevant to future work on their taxonomy and natural history.

[1] Adjunct professor at Pontifícia Universidade Católica do Rio Grande do Sul, Av. Ipiranga 6681, Porto Alegre, RS, 90619-900, Brazil.

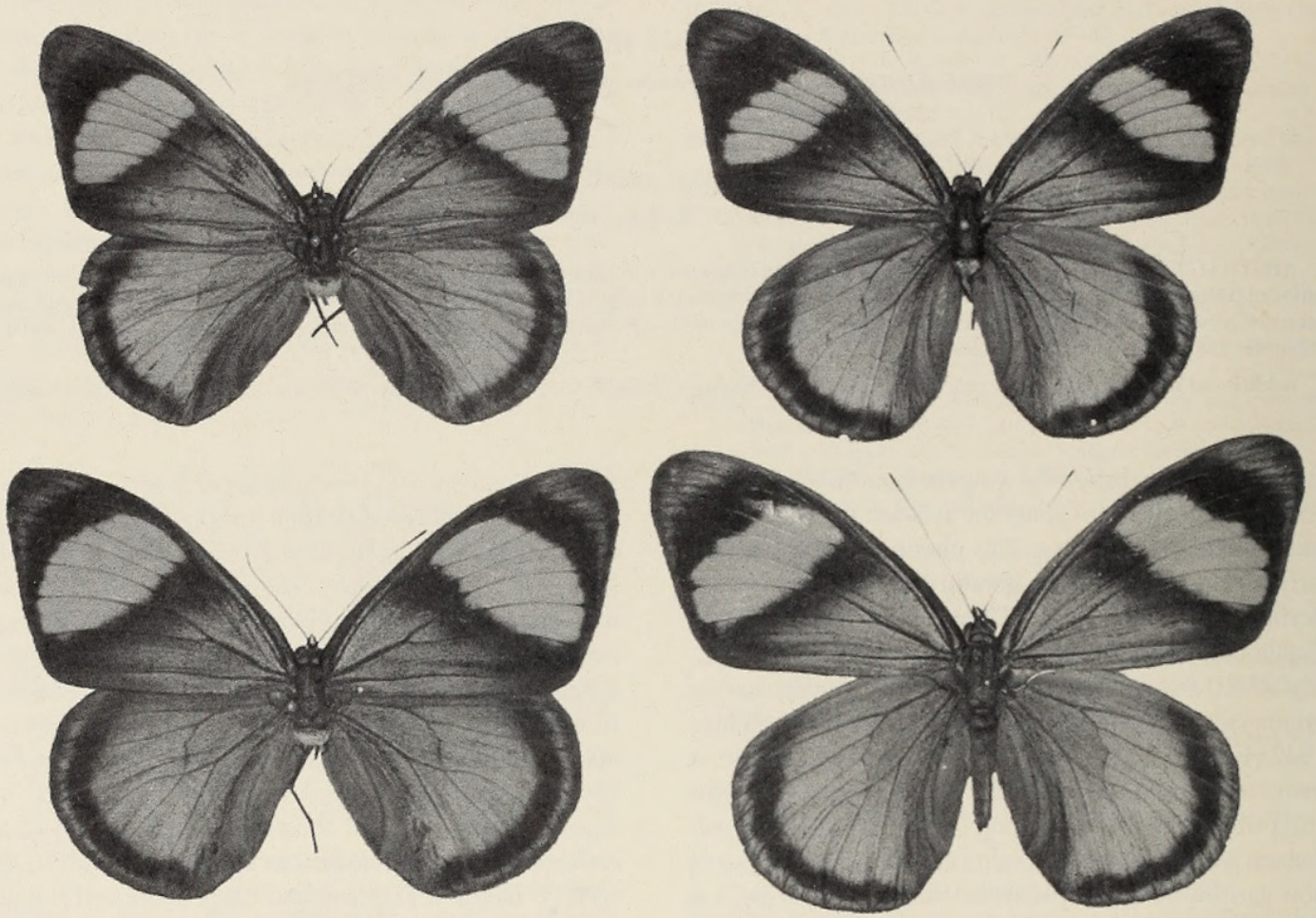

FIG. 1. *Batesia hypochlora*, dorsal. Top row, males; bottom row, females. Left column, Garza Cocha, Ecuador; right column, Rondonia, Brazil.

MATERIALS AND METHODS

Species studied. Excepting *P. chalcothea* (see identification section below), our phylogenetic analysis included all valid species of *Panacea* (*P. prola*, *P. procilla*, *P. regina*, *P. divalis*, and *P. bleuzeni*) and *Batesia hypochlora* (Figs. 1–10).

To assess intra-specific variation in wing pattern and genitalia, we examined specimens from five distinct localities. Abundant material from a single site in eastern Ecuador (*P. prola*, n = 57; *P. divalis*, n = 55; *P. regina*, n = 43; and *B. hypochlora*, n = 24) allowed us to evaluate morphological and phenotypic variation within a single population (see DeVries & Walla 2001 for site description). Whenever possible individuals from different localities were dissected to evaluate morphological variation in the genitalia. Although a small number of specimens were available of *P. procilla* (n = 4) and *P. bleuzeni* (n = 2), these species are phenotypically distinctive from other *Panacea* and characters could be scored with confidence. For *P. bleuzeni*, one specimen of each sex was used to score genitalia characters directly, but wing and body characters were scored using the description of Plantrou and Attal (1986), the illustrations in D'Abrera (1987:487, as *P. bella*) and photographs from the private collection of G. Attal. Characters 22 and 23 were scored as "missing" for *P. bleuzeni* due to lack of material. Table 1 lists the examined taxa, number of dissected individuals, and locality data.

We used *Biblis hyperia* (Cramer, 1780) and *Hamadryas arinome* (Lucas, 1853), *H. amphinome* (Linnaeus, 1767), *H. laodamia* (Cramer, 1777), and *H. feronia* (Linnaeus, 1758) as outgroup taxa for phylogenetic analysis. Based on larval and adult morphology, and host plant use (Euphorbiaceae) these taxa are considered closely related to *Batesia* and *Panacea* (Seitz 1916, Ackery 1984, Harvey 1991).

Preparation of material. Genitalia were prepared with a standard treatment of 10% potassium hydroxide, examined with a stereomicroscope, and subsequently stored in glycerol. Illustrations are given in Figs. 11–13.

Characters and terminology. Our character matrix

FIG. 2. *Batesia hypochlora*, ventral. Left column, Garza Cocha, Ecuador; right column, Rondonia, Brazil.

includes 53 characters (43 binary and 10 multistate), of which 24 were derived from males (23 from genitalia, one from wing coloration), 7 derived from females (6 from genitalia and one from wing coloration), and 22 from both sexes (16 from wing patterns, four from venation, one from forelegs and one from body scales).

Terminology for adult external morphology follows Scoble (1992). Terminology for male and female genitalia follows Klots (1970) except for the use of hypandrium and ramus, which follow the definitions in the glossary of Tuxen (1970) and Jenkins (1986, 1987, 1990). We use hypandrium to mean "a male subgenital plate," and ramus as "lateral or ventro-lateral process of male eighth sternite, directed posteriorly" (see glossary in Tuxen 1970; Jenkins 1983, 1986). In character 10 we follow D'Abrera (1987) where a "complete ocellus" consists of a spot surrounded by a round ring (e.g., *P. procilla*, Fig. 6), and an "incomplete ocellus" is a spot without a round outer ring (e.g., *P. bleuzeni*, Fig. 7).

Phylogenetic analysis. We used a heuristic search in PAUP 3.1 (Swofford 1993) with all characters given equal weight, multi-state characters unordered, polymorphic characters treated as exhibiting both states, and the search used a TBR branch swapping routine. Following analysis, *Biblis hyperia* was used to root the tree. Branch support was estimated by 500 bootstrap replicates, and we used MacClade 3.01 (Maddison & Maddison 1992) to identify character changes along the branches of the tree. The character list and data matrix are in Appendix 1 and 2.

RESULTS

Phylogeny

Our analysis indicates that *Panacea* and *Batesia* are monophyletic, sister taxa. The single most parsimonious tree (tree length = 79, CI = 0.82, RI = 0.88) suggests that *Batesia hypochlora* is a sister species to *Panacea*, a relationship supported by four characters (Fig. 14; Table 2, clade 1). We found 11 autapomorphies for *B. hypochlora* (Table 2, clade 2), and nine characters that justify the monophyly of *Panacea* (Table 2, clade 3). Our analysis also showed that all members of *Panacea* are morphologically similar, but they differ strongly from *Batesia hypochlora*.

Among *Panacea* the genital morphology was notably conservative, and characters providing the basis for inferring species relationships were derived mostly from wing morphology. Only one male genital character (hy-

FIG. 3. *Panacea prola*, dorsal and ventral. Top row, left, male; right, female. Bottom row, left male; right, female. All from Garza Cocha, Ecuador.

pandrium, character 28) could be used to distinguish among *Panacea* species. However, as it represents an autapomorphy for *P. divalis*, character 28 was uninformative for establishing phylogenetic relationships within *Panacea*. The grouping of *P. regina*, *P. divalis*, *P. bleuzeni* and *P. procilla* was supported by seven characters, all derived from wing pattern morphology (Table 2, clade 4). One character justified grouping *P. divalis*, *P. bleuzeni* and *P. procilla* (Table 2, clade 5) and a single character grouped *P. bleuzeni* and *P. procilla* (Table 2, clade 6).

Identification and Taxonomy

Here we provide synonymies, characters for identification of the study taxa, approximate geographical distributions, and comments on phenotypic variation of the species included in our analysis. For completeness, we also provide taxonomic notes on *P. chalcothea*, although we did not examine this taxon directly.

Batesia Felder and Felder, 1862

Batesia Felder and Felder, 1862. Wien. ent. Monats. 6:112.

Batesia hypochlora Felder and Felder, 1862 (Figs. 1, 2, 11, 13)

Batesia hypochlora Felder and Felder, 1862. Wien. ent. Monats. 6:113

Batesia hypochlora hypoxantha Salvin and Godman, 1868. Ann. Mag. Nat. Hist. (4)2:147

Batesia hypochlora hemichrysa Salvin and Godman, 1868. Ann. Mag. Nat. Hist. (4)2:147

Batesia hypochlora chrysocantha Fruhstorfer, 1915. Soc. ent. 30(12):66

Batesia hypochlora f. *intermedia* Michael, 1931. Ent. Zeit. 44(20):309–312

Species characters. Forewing dorsal surface dark iridescent blue from basal to submedial areas, a prominent postmedial red band surrounded by black, apex iridescent blue. Hindwing dorsal surface mostly iridescent blue, with a postmedial black band and an iridescent blue marginal band from apex to tornus. Forewing ventral surface dark brown from basal to submedial areas and tornus, postmedial red band surrounded by brown, subapex yellow. Hind-

FIG. 4. *Panacea regina*, dorsal. Top row, male; bottom row, female. All from Garza Cocha, Ecuador.

wing ventral surface chalky yellow with a distinct black postmedial band and yellow marginal band from apex to tornus.

Distribution. Western Amazonas, Brazil; Ecuador, Peru (Seitz 1916, D'Abrera 1987, Austin & Emmel 1990, Robbins et al. 1996).

Variation. Judging by the named subspecies (see synonomic list) the intensity of yellow on the ventral surface of the HW may vary. However, whether these names are biologically meaningful remains uncertain. We found little variation in our samples from Garza Cocha, Ecuador, although we note that Ecuadorian and Brazilian material differ in the respective width of the forewing subapical band (Fig. 1).

Panacea Godman and Salvin, 1883

Pandora Doubleday, 1848. Gen. Diurnal Lep. p. 300 Pl. 3 fig 5

Panacea Godman and Salvin, 1883. Biol. Centr. Am. pp. 274–275

Panacea prola (Doubleday, 1848) (Figs. 3, 11, 13)

Pandora prola Doubleday, 1848. Gen. Diurnal Lep. p. 300 Pl. 3 fig. 5

Panacea prola female f. *dubia* Kretzschmar 1894. Deutsche ent. Zeit. "Iris" 6(2):158–160

P. prola zaraja Fruhstorfer, 1912. Ent. Rundschau 29(6):46

P. prola amazonica Fruhstorfer, 1915. Soc. ent. 30(12):66

P. prola prolifica Fruhstorfer, 1915. Soc. ent. 30(12):66

P. prola amazonica f. *bronzina* Bryk, 1953. Arkiv. Fur Zool. 5(1):1–268

Species characters. Dorsal surface with broken blue-green iridescent bands. Forewing dorsal surface without a subapical line in both sexes, but some females with a faint greenish-white subapical band. Hindwing dorsal surface without ocelli or blue submarginal line. Hindwing ventral surface bright red, generally without black markings, but sometimes with a faint black submarginal line.

FIG. 5. *Panacea regina*, ventral. Top row, male; bottom row female. All from Garza Cocha, Ecuador.

Distribution. Panama, Colombia, Venezuela, Guianas and upper Amazon basin (Seitz 1916, D'Abrera 1987, Emmel & Austin 1990, Otero & Romero 1992, Lamas 1994, Robbins et al. 1996, Neild 1996).

Variation. We found wide variation in wing length, but little variation in color pattern in large samples from Garza Cocha, Ecuador. Small individuals appear to be the result of caterpillars feeding on poor quality *Caryodendron* leaves, or those that were semi-starved (pers. obs.).

Subspecies. *Panacea prola zaraja*, from Venezuela, Merida; *P. p. amazonica*, from the upper Amazon; *P. p. prolifica*, from Ecuador.

Panacea regina (Bates, 1864)
(Figs. 4, 5, 11, 13)

Pandora regina Bates, 1864. J. Entom. 2(10):213.
Panacea regina victrix Fruhstorfer, 1915. Soc. ent. 30(12):66.

Species characters. Dorsal surface with broken blue-green iridescent bands. Forewing ventral surface with reddish apex and white subapical band but without the distinct red spots outlined by black in discal cell (see *P. divalis*). Hindwing dorsal surface with a blue medial band adorned with incomplete black ocelli that vary in size, and may reach the distal margin of the band; submarginal wavy line sometimes faint. Hindwing ventral surface red with broken submedial to medial transverse black lines, the most distal starting at Sc + Rs and ending at Cu_2; faint post-medial ocelli in almost all cells; conspicuous black submarginal line. Females often with a short, white longitudinal stripe in ventral hindwing cell M_2–M_3, nearly at the center of wing.

Distribution. Western and upper Amazon (Ecuador, Peru, Brazil) (Seitz 1916, D'Abrera 1987, Lamas 1994, Robbins et al., 1996).

Variation. In Ecuadorian and Brazilian samples we found that the medial ocelli on the dorsal hindwing vary considerably within populations. In females we found the ventral hindwing ocelli were sometimes incomplete.

Subspecies. *Panacea regina victrix*, from Ecuador; see also *P. chalcothea* (below).

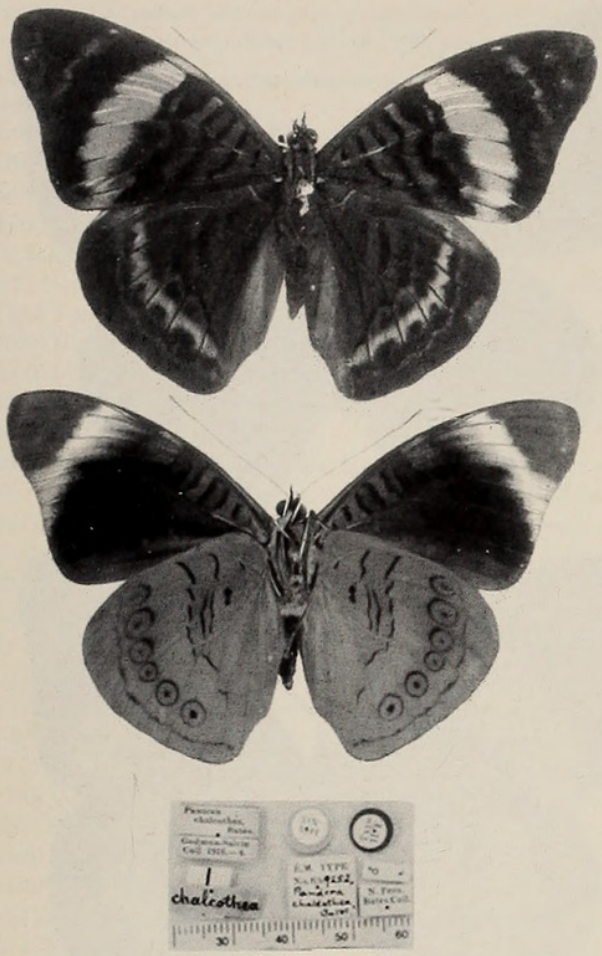

FIG. 6. *Panacea chalcothea*, male, dorsal and ventral, plus label. This specimen is an apparent syntype (see Identification and Taxonomy). Note: whether *chalcothea* is a subspecies of *P. regina* or a valid species remains to be resolved.

Panacea chalcothea (Bates, 1868) (Fig. 6)

Pandora divalis Bates, 1868. Ent. mon. Mag. 4(44):170.

This somewhat obscure taxon figures importantly in the history of *Panacea*, and its taxonomic status is unresolved. Although we were unable to examine material of *chalcothea* directly, the photo provided by G. Lamas (Fig. 6) may serve as a starting point for identifying this taxon. Here we excerpt correspondence received from G. Lamas that bears directly on the taxonomic interpretation of *Panacea chalcothea*:

"Bates (1868:170) described *chalcothea* based on at least 2 specimens, one female (?) illustrated by Hewitson ([1854], Ill. exot. Butts 1: pl. [42], fig. 4), and thought by the latter to be the female of *procilla*; and one male from "southern Equador". Hewitson's "female" belonged to the collection of the Entomological Society of London, and that specimen is almost certainly lost, while Bates' male would have been in his collection, and should have gone to the BMNH through Godman and Salvin. There seems to be no Bates specimen of *chalcothea* from southern Ecuador at the BMNH. However, there is a male specimen from Bates' collection, labeled *chalcothea* by Bates himself, but from "N Peru", and I interpret this as a possible syntype of *chalcothea*, agreeing very well with the written description of the male given by Bates in his original paper. Bates may well have confused "S Ecuador" with "N Peru". Anyway, that specimen from "N Peru" most probably came from Amazonas department in Peru. . . . Now, [it] seems to me that *chalcothea* (based on Bates' o.d. and the syntype referred to above) is . . . very probably a subspecies of *regina*, or could even be a full species. For the time being, I'm calling those 2 specimens as *Panacea regina chalcothea*, though I wouldn't be too surprised if they were to represent a high altitude species distributed from Colombia to N Peru (if Hewitson's "New Granada" locality for his specimen is correct, which is quite doubtful)."

TABLE 1. Number of dissected individuals and locality data. Abbreviations for source collections are: P. J. DeVries (PJD); G. Austin (GTA); G. Attal (GA); Los Angeles County Museum (LACM); Milwaukee Public Museum (MPM).

Taxa	Source of dissected material
Ingroup	
Batesia hypochlora	2 males: Brazil (GTA)
	8 males: Ecuador, Sucumbios, Garza Cocha (PJD)
	1 female: Brazil (GTA)
	1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
Panacea bleuzeni	1 male: French Guyana (GA)
	1 female: French Guyana (GA)
Panacea divalis	5 males: Ecuador, Sucumbios, Garza Cocha (PJD)
	2 males: Brazil, Rondonia (GTA)
	3 females: Ecuador, Sucumbios, Garza Cocha (PJD)
Panacea procilla	2 males: Brazil (n = 1) and Colombia (n = 1) (LACM)
	1 male: Colombia (MPM)
	1 female: Colombia (MPM)
Panacea prola	5 males: Ecuador, Sucumbios, Garza Cocha (PJD)
	3 females: Ecuador, Sucumbios, Garza Cocha (PJD)
Panacea regina	5 males: Ecuador, Sucumbios, Garza Cocha (PJD)
	3 females: Ecuador, Sucumbios, Garza Cocha (PJD)
Outgroups	
Biblis hyperia	1 male: Ecuador, Sucumbios, Garza Cocha (PJD)
	1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
Hamadryas amphinome	1 male: Ecuador, Sucumbios, Garza Cocha (PJD)
	1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
Hamadryas arinome	1 male: Ecuador, Sucumbios, Garza Cocha (PJD)
	1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
Hamadryas feronia	1 male: Ecuador, Sucumbios, Garza Cocha (PJD)
	1 female: Ecuador, Sucumbios, Garza Cocha (PJD)
Hamadryas laodamia	1 male: Ecuador, Sucumbios, Garza Cocha (PJD)
	1 female: Ecuador, Sucumbios, Garza Cocha (PJD)

FIG. 7. *Panacea divalis*, dorsal. Left column, males; right column, females. Top row, Rondonia, Brazil; middle and bottom rows, Garza Cocha, Ecuador. Note variation in medial bands and submarginal ocelli.

Distribution. Apparently Western Amazonas (Ecuador, Peru) and Colombia (?).

Panacea divalis (Bates, 1868)
(Figs. 7, 8, 12, 13)

Pandora divalis Bates, 1868. Ent. mon. Mag. 4(44):171.
Panacea procilla divalis Seitz, 1916. Die Gross Schmetterlinge der Erde p. 537.

Species characters. Dorsal surface with broken iridescent blue-green bands. Forewing ventral sur-

TABLE 2. Characters justifying the groupings of species and genera. MacClade 3.01 was used to map character changes on the most parsimonious tree. Characters indicated in bold type were unique to the group they support (independent of reversals).

Clade 1. *Panacea* and *Batesia*
(2:0) Fringe of scales in forewing and hindwing outer margin solid dark color
(16:0) Ventral surface of hindwing with black submarginal line that is discrete in anal area and more diffuse toward costal area
(24:0) Thorax: ventral portion completely covered with red-orange scales
(27:1) In lateral view: Hypandrium without anterior rod-like projections
Clade 2. *Batesia hypochlora*
(8:2) Males: Ventral surface of forewing apex dark, with a yellow band
(19:0) Forewing venation: M_1 arched toward anal margin
(25:0) Hypandrium: narrow, plate like, with obvious constriction near the middle of its long axis
(29:0) In lateral view, anterior portion of tegumen extremely projected
(30:1) Uncus tip in lateral view sharply hooked
(32:1) Uncus short
(33:0) In lateral/ dorso-lateral view, base of uncus with obvious large dorsal ridges
(34:1) In lateral view, tip of uncus not reaching or extending beyond tip of valva
(37:0) Distal portion of gnathos small and projected ventrally
(38:0) In ventral view, distal portion of gnathos with a rounded invagination
(43:1) Distal portion of valva with small bare chitinous tip
(53:0) Antrum mostly membranous
Clade 3. *Panacea*
(4:1) Forewing postmedial band expressed dorsally only
(5:1) In dorsal view, forewing subapical white band reduced
(7:0) Ventral surface of forewing with white subapical band
(10:0) Ventral surface of hindwing largely colored red-orange, with or without purplish sheen
(17:0) Ventral surface of hindwing with dark line imposed upon cross-vein m_2–m_3 (at distal edge of discal cell)
(23:0) Foreleg with white scales laterally
(42:0) Distal portion of valva curving ventrally
(44:0) In lateral view, basal portion of valva with large conspicuous ventrally produced rounded projection
(46:1) In lateral view, distal portion of saccus straight to slightly projected upward
Clade 4. *Panacea procilla*, *Panacea bleuzeni*, *Panacea divalis* and *Panacea regina*
(8:0) Males: Ventral surface of forewing apex uniformly dirty red-orange
(11:0) Ventral surface of hindwing with prominent dark line across basal half of cell Sc + R_1
(12:0) Ventral surface of hindwing with prominent dark line across discal cell
(13:0) Ventral surface of hindwing discal cell with two black dots in basal half
(14:0) Ventral surface of hindwing with nearly continuous line through medial area that crosses cells Sc + R_1, Rs, M_1, M_2, M_3, Cu_1 and Cu_2
(15:1) Ventral surface of hindwing with dark line not contiguous and line in cell Cu_2 more apical than line in cell Cu_1
(18:0) Female: ventral surface of hindwing with white patch of scales in medial area of cell M_2
Clade 5. *Panacea procilla*, *Panacea bleuzeni* and *Panacea divalis*
(5:0) In dorsal view, forewing subapical white band well developed
(6:0) In ventral view, forewing discal cell with two red-orange spots, one at base and one at mid-length
Clade 6. *Panacea procilla* and *Panacea bleuzeni*
(3: 0) In dorsal view, male forewing with oblique, diffuse black band encroaching on postmedial blue/green band.

face with reddish apex, white subapical band and distinct red spots outlined by black in discal cell (see *P. regina*). Hindwing ventral surface brownish red with a faint purple sheen; broken transversal black medial lines, the most distal starting at Sc + Rs and ending at 1A; postmedial ocelli (black "rings") on almost all cells; conspicuous black submarginal line. Females with a short, white longitudinal stripe in ventral hindwing cell M_2–M_3, nearly at the center of wing. Incomplete ocelli on dorsal surface of hindwing vary in size, and may be absent in some specimens.

Distribution. Upper Amazon (Seitz 1916), Colombia to Peru (D'Abrera 1987) and western Brazil (Emmel & Austin 1990).

Variation. In males the dorsal hindwing marginal band varies among samples from Brazil and Ecuador; the dorsal hindwing ocelli vary from diffuse to sharp; a short, ventral longitudinal stripe may occur in ventral hindwing cell M_2–M_3. In females the white, ventral longitudinal stripe in hindwing cell M_2–M_3 may be diffuse or faintly expanded into the two cells above.

Subspecies. None.

Panacea procilla (Hewitson, 1852)
(Figs. 9, 12, 13)

Pandora procilla Hewitson, 1852. Exot. Butt. 1.
Panacea lysimache Godman and Salvin 1883. Biol. Centr. Americana p. 275.
P. procilla ocana Fruhstorfer, 1912. Ent. Rundschau 29(6):46.

FIG. 8. *Panacea divalis*, ventral. Left column, males; right column, females. Top row, Rondonia, Brazil; middle and bottom rows, Garza Cocha, Ecuador. Note variation in white stripe centered in cell M_2–M_3.

P. procilla salacia Fruhstorfer, 1915. Soc. Ent. 30(12):66.
P. procilla lysimache Seitz, 1916. Die Gross Schmetterlinge der Erde p. 537.
P. procilla var. *marmorensis* Hall, 1917. Entomologist 50(651):171–174.

Species characters. Dorsal surface with broken blue-green iridescent bands. Forewing ventral surface with distinct red outlined by black in discal cell, reddish apex and white subapical band. Hindwing ventral surface brownish red with a faint purple

FIG. 9. *Panacea procilla*, dorsal and ventral. Left column, male; right column, female. Specimens from Cali, Colombia.

sheen; broken transverse medial black lines, the most distal starting at Sc + Rs and ending at 1A; complete postmedial ocelli on almost all cells, those on cells M_3–Cu_1 and Cu_1–Cu_2 with iridescent pupil; conspicuous black submarginal line. Dorsal surface of hindwing with a medial blue band adorned with black ocelli; conspicuous submarginal wavy line. Females with white medial band on ventral forewing, and also with a white band on ventral hindwing from cell Sc + R_1–Rs to M_2–M_3, sometimes interrupted on M_1–M_2.

Distribution. Costa Rica south to Colombia and throughout the upper Amazon basin and the Guianas (Kretzschmar 1894, Apolinar 1926).

Variation. We observed some males that have a short, white longitudinal stripe in ventral hindwing cell M_2–M_3, nearly at the center of wing—a pattern similar to females of *P. regina* and *P. divalis*.

Subspecies. *Panacea procilla procilla,* western Venezuela (Neild 1996), *P. p. ocana*, from lower Magdalena River, Colombia (Seitz 1916, D'Abrera 1987); *P. p. salacia*, from Colombia (Seitz 1916, D'Abrera 1987); *P. p. lysimache* from Volcan Chiriqui, Panama, Finca la Selva, Costa Rica (DeVries 1987, 1989).

Panacea bleuzeni Plantrou and Attal, 1986 (Figs. 10, 12, 13)

Panacea bleuzeni Plantrou and Attal, 1986. Bull. Société Sciences Nat. 50:23.

Panacea bella D'Abrera, 1987. Butterflies of the Neotropical Region, part III: p. 487, **new synonoym**

Species characters. Dorsal surface distinctively blue or blue-green. Dorsal surface of hindwing with a blue medial band adorned with large black ocelli; wavy iridescent submarginal line conspicuous. Ventral forewing with distinct red outlined by black in discal cell, reddish apex and white subapical band (similar to *procilla*). Ventral hindwing with transverse medial black line continuous from cell Sc + Rs to vein 1A; ocelli faint. Females with white marking extending distally along black medial line from cell Sc + Rs to Cu_2–1A.

FIG. 10. *Panacea bleuzeni*, female, dorsal and ventral. This figure is reproduced through the kind permission of B. d'Abrera [Butterflies of the Neotropical Region, part III:487]. It is the type of *Panacea bella* D'Abrera, 1987.

Distribution. Apparently endemic to the Guianas (Plantrou & Attal 1986). However, it's overlapping range with *procilla* and close relationship to it (Table 2, clade 6) suggest the possibility that this taxon may be a subspecies of *procilla*. This point needs critical evaluation.

Synonymic notes. Examination of the collection of the BMNH by A. Neild (pers. com.) revealed that the single female holotype of *P. bella* is also a paratype of *P. bleuzeni*. This, therefore, indicates that *P. bella* and *P. bleuzeni* represent a single species with *bella* as a junior synonym of *bleuzeni*. Comparing the illustration of the type specimen of *bella* (in D'Abrera 1987) with photographs of male and female *P. bleuzeni* provided by G. Attal confirms this assessment.

DISCUSSION

Our analysis showed that *Batesia* and *Panacea* form a monophyletic group, with *B. hypochlora* basal to *Panacea*. Therefore, despite similarities in early stage morphology and host plant use, we reject the hypothesis that *B. hypochlora* is a derived species from within *Panacea*. Our study confirms the maintenance of *Batesia* and *Panacea* as separate taxa (e.g., Godman & Salvin 1883, Seitz 1916), and serves as a framework for future systematic work on both genera. We note that, without examining material firsthand, *P. chalcothea* is presumed to be the sister taxon of *P. regina*. However, the phylogenetic position of *chalcothea* requires confirmation, including its taxonomic rank.

Insect genitalia are widely used for phylogenetic

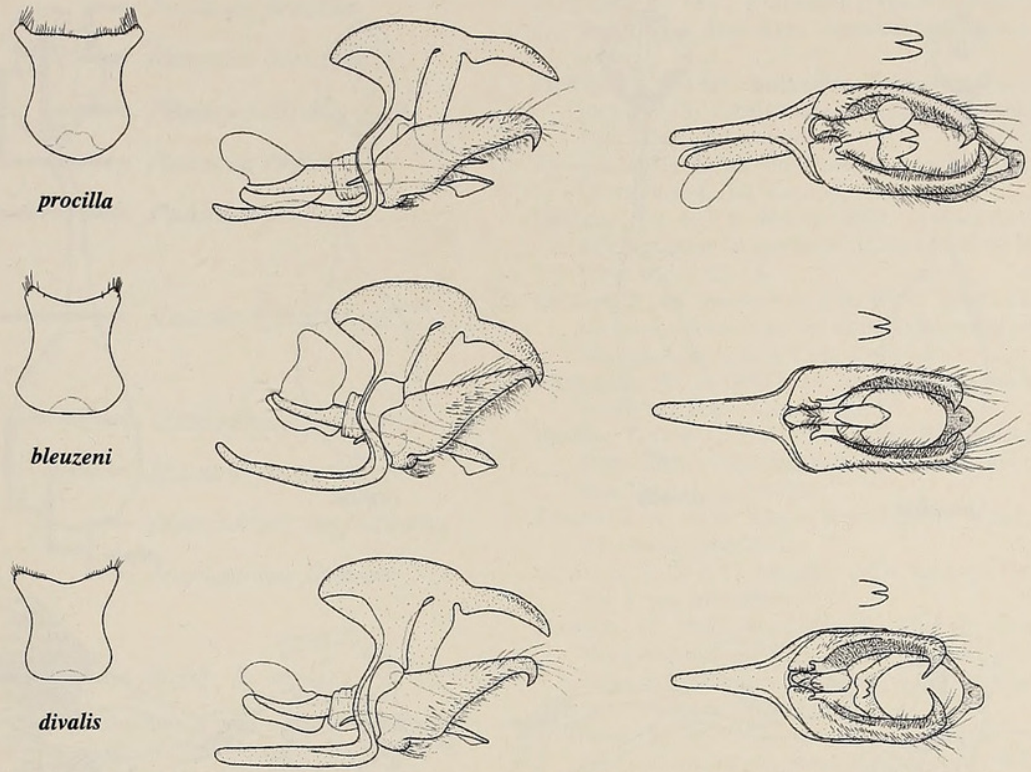

FIG. 11. Male genitalia: hypandrium, lateral view, ventral view (inset: tip of gnathos in ventral view). *Panacea procila*, *P. bleuzeni*, and *P. divalis*.

reconstruction and delimiting species boundaries because their morphology may diverge rapidly, and therefore provide informative characters (Eberhard 1985, Porter & Shapiro 1990, Arnqvist 1998). In *Panacea*, however, we found that the genitalia were highly conserved and provided no informative characters for phylogeny reconstruction, or discrimination among species. Rather, the species-level rela-

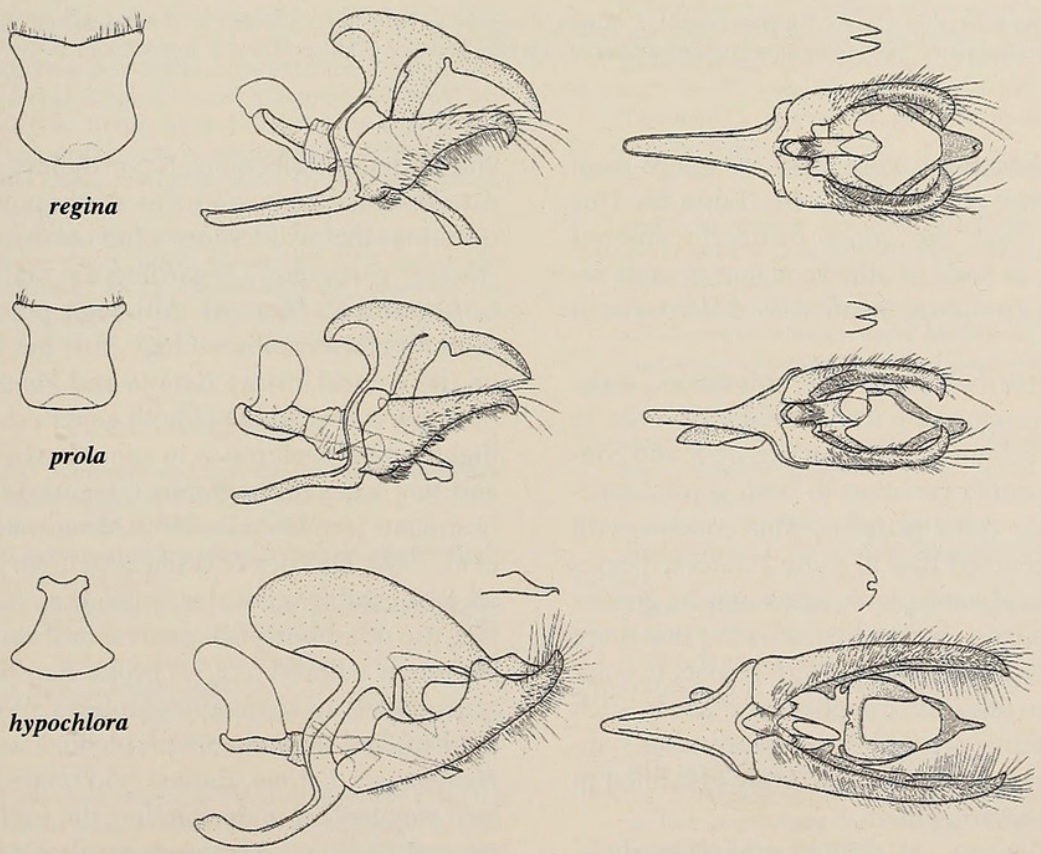

FIG. 12. Male genitalia: hypandrium, lateral view (inset: uncus in lateral view), ventral view (inset: tip of gnathos in ventral view). *Panacea regina*, *P. prola*, and *Batesia hypochlora*.

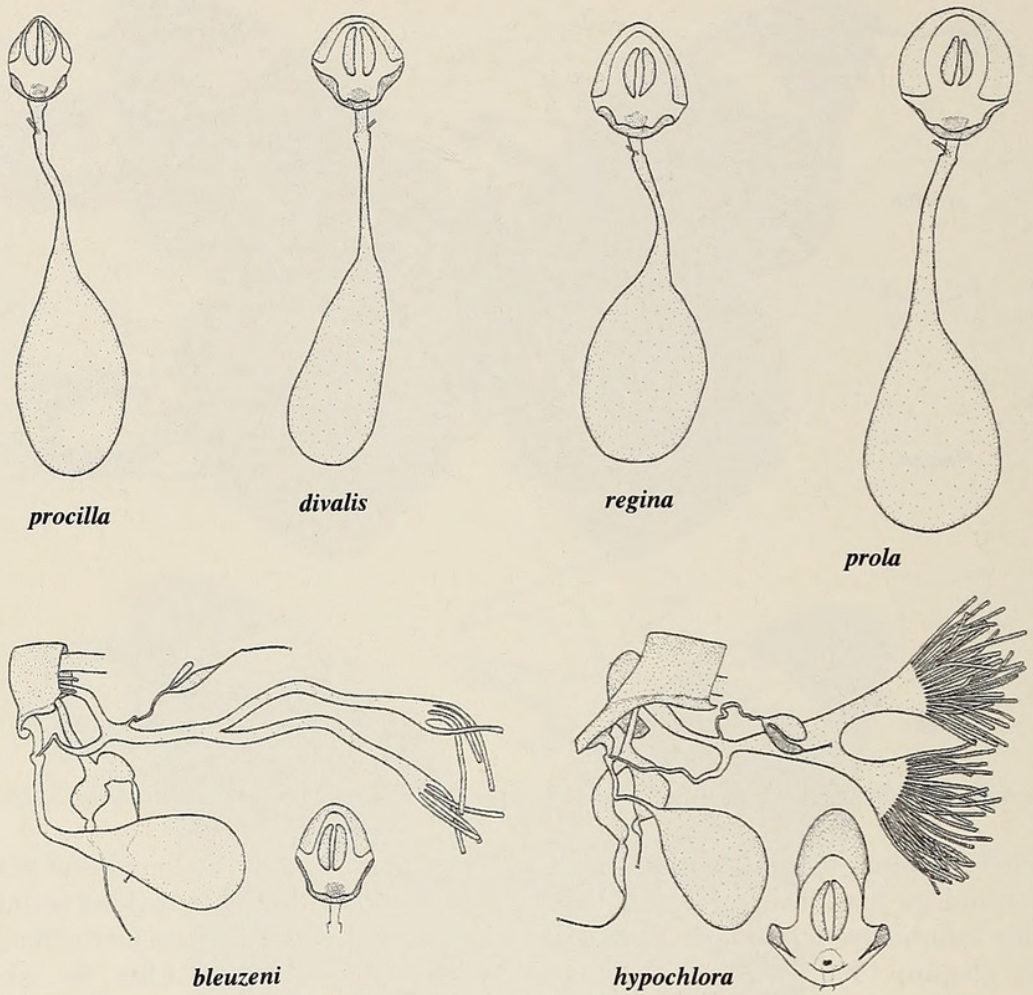

FIG. 13. Female genitalia: ventral view, *Panacea procila*, *P. divalis*, *P. regina*, and *P. prola*. Lateral view: *P. bleuzeni*, and *Batesia hypochlora* (insets: genitalia in ventral view). Note differences in the number of ovarioles between *P. bleuzeni* and *B. hypochlora*.

tionships proposed here were derived solely from characters of wing pattern (Fig. 14, Table 2). Our study suggests that the most distinctly colored species, *P. prola*, is basal to other congeners, with remaining species groupings justified by differences in wing patterns.

The distinctive behavior and coloration make *Panacea* easily recognizable in the field. However, in large samples from one Ecuadorian site we found considerable intraspecific variation in both genital morphology and wing color patterns. This concurs with Seitz (1916) who noted that in some *Panacea* species within population phenotypic variation may be greater than among population variation, indicating that there may be transitions among species with respect to color pattern. With the possible exception of *P. prola*, such phenotypic variation precludes the notion that sympatric *Panacea* species can be positively identified in nature without capturing them.

Batesia and *Panacea* are obvious and often abundant elements of many Neotropical butterfly faunas and museum collections. Nevertheless, some taxa are rare in collections, and this study points to several questions that will require a full taxonomic revision to resolve, particularly regarding the status of *P. chlacothea* and *P. bleuzeni*. Although potentially useful tools for conservation ecology, little has been reported on the natural history *Batesia* and *Panacea*. What we do know is that adults of both genera show significant flight height preference in some lowland rainforests, and that trees in the genus *Caryodendron* are larval hostplants (see DeVries 1989, Montoya 1991, DeVries et al. 1999, DeVries & Walla 2001). We do not know if all taxa exhibit vertical stratification, if these butterflies use other hostplant genera, or if some species are warningly colored (e.g., *P. prola, Batesia*) that represent models in mimicry complexes. We believe that field studies, in concert with phylogenetic analyses of *Hamadryas*, *Ectima*, *Eunica*, and related genera is the next step toward understanding the evolution of *Batesia* and *Panacea*, and the diversification of the Biblidini.

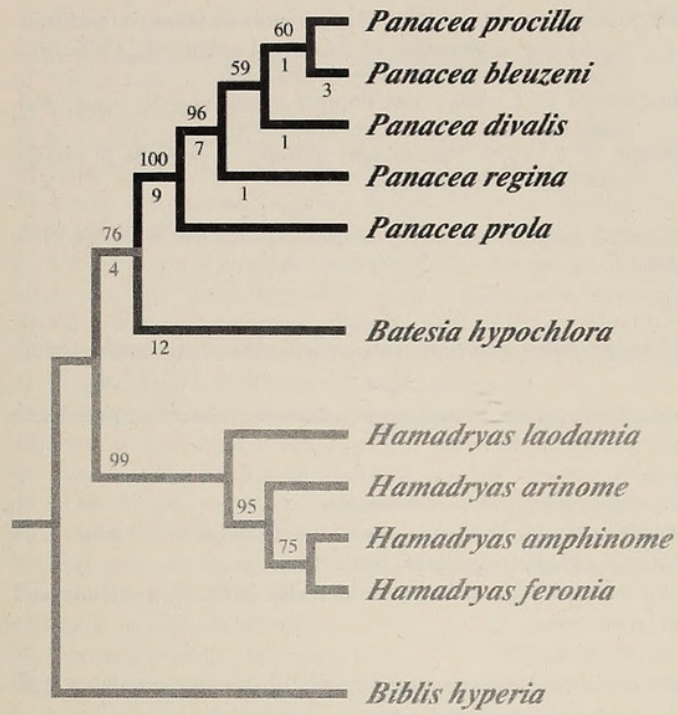

FIG. 14. Single most parsimonious tree obtained from the analysis of 53 characters for 11 species (tree length = 79, CI = 0.82, RI = 0.88). Numbers above and below tree branches represent bootstrap values and the number of unambiguous changes respectively.

ACKNOWLEDGMENTS

We thank Eric Schwartz and the staff of La Selva Jungle Lodge for supporting this and other aspects of our research. G. Attal (France), G. Austin (Nevada State Museum), and B. Brown (Natural History Museum of Los Angeles County) kindly facilitated our work by loaning specimens. We are sincerely grateful to P. Ackery (The British Natural History Museum), G. Lamas (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Peru), G. McGavin (Oxford University Natural History Museum), A. Neild (London), and C. Smith (The British Natural History Museum) for providing historical information and comparing type specimens that helped unravel the taxonomic mysteries of *P. chalcothea* and *P. bleuzeni*. We thank B. d'Abrera for permission to reproduce his figures of *Panacea bella*. Comments by G. T. Austin and André Freitas improved the clarity of this manuscript. RIH thanks Lee Robertson for inspiration. This study was supported in part by the National Science Foundation (DEB 00-96241) and is dedicated to the memory of Sonny Clark, Bill Evans, Thelonius Sphere Monk, and Bud Powell.

LITERATURE CITED

ACKERY, P. R. 1984. Systematic and faunistic studies on butterflies, pp. 9–21. *In* Vane-Wright, R. I. & P. R. Ackery (eds.), The biology of butterflies. Academic Press, London.

APOLINAR, H. 1927. [Notes] Boletin de la Sociadad Colombiana de Ciencias Naturales. 16:34–35.

ARNQVIST, G. 1998. Comparative evidence for the evolution of genitalia by sexual selection. Nature 393:784–786.

BATES, H. W. 1868. Note on the genus *Pandora* (Diurnal Lepidoptera). Ent. Month. Mag. 4:169–171.

CARPENTER, G. D. H. 1942. The relative frequency of beak-mark on butterflies of different edibility to birds. Proc. Zool. Soc. London 111:223–231.

CHAI, P. 1986. Field observations and feeding experiments on the response of rufous tailed jacamars (*Galbula ruficauda*) to free-flying butterflies in a tropical rainforest. Biol. J. Linn. Soc. 29:166–189.

D'ABRERA, B. 1987. Butterflies of the Neotropical Region. Part III. Brassolidae, Acraeidae, Nymphalidae (partim). Hill House, Victoria.

DEVRIES, P. J. 1987. Butterflies of Costa Rica: and their natural history. Vol. 1: Papilionidae, Pieridae, Nymphalidae. Princeton Univ. Press, Princeton.

———. 1989. Notes on *Panacea procilla* (Nymphalidae) from Costa Rica. J. Res. Lep. 27:141–142.

DEVRIES, P. J. & T. R. WALLA. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. Biol. J. Linn. Soc. 74:1–15.

DeVries, P. J., C. M. Penz & T. R. Walla. 1999. The biology of *Batesia hypochlora* from an Ecuadorian rainforest (Lepidoptera, Nymphalidae). Trop. Lep. 10:43–46.

EBERHARD, W. G. 1985. Sexual selection and animal genitalia. Harvard Univ. Press, Cambridge.

EMMEL, T. C. & G. T. AUSTIN. 1990. The tropical rain forest butterfly fauna of Rondonia, Brazil: species diversity and conservation. Trop. Lep. 1:1–12.

FISHER, R. A. 1958. The genetical theory of natural selection. 2nd ed. Dover, New York.

GODMAN, F. D. & O. SALVIN. 1883. Biologia Centrali-Americana. Vol. 1. pp. 265–288.

HARVEY, D. 1991. Appendix B: Higher classification of the Nymphalidae, pp. 255–273. *In* Nijhout, H. F., The development and evolution of butterfly wing patterns. Smithsonian Institution Press, Washington.

HEMMING, F. 1967. The generic names of the butterflies and their type species (Lepidoptera: Rhopalocera). Bull. Brit. Mus. (Nat. Hist.) Ent. supplement 9:1–509.

HEWITSON, W. C. 1854. Illustrations of new exotic butterflies. London, John Van Voorst.

JENKINS, D. W. 1983. Neotropical Nymphalidae I. Revision of *Hamadryas*. Bulletin of the Allyn Museum 81:1–146.

———. 1986. Neotropical Nymphalidae V. Revision of *Epiphile*. Bulletin of the Allyn Museum 101:1–70.

———. 1987. Neotropical Nymphalidae VI. Revision of *Asterope* (=*Callithea* Auct.). Bulletin of the Allyn Museum 114:1–66.

———. 1990. Neotropical Nymphalidae VIII. Revision of *Eunica*. Bulletin of the Allyn Museum 131:1–177.

KLOTS, A. B. 1970. Lepidoptera, pp. 115–130. *In* Tuxen, S. L. (ed.), Taxonomist's glossary of genitalia in insects. Munksgaard, Copenhagen.

KRETZSCHMAR, E. 1894. Eine neue *Perisama* von Columbia, das female von *Panacea prola* Doubl. Hew. Und ein Zwitter. Deutsche entomol. Zeitschrift "Iris" 6:158–160.

LAMAS, G. 1994. List of butterflies from Tambopata (Explorer's Inn Reserve), pp. 162–177. *In* Foster, R. B., J. L. Carr & A. B. Forsyth (eds.), The Tambopata reserve zone of soueastern Peru: a biological assessment. Rapid Assessment Program, RAP working papers 6. Washingtin, D.C., Conservation International.

MADDISON, W. P. & D. R. MADDISON. 1992. MacClade: version 3.01. Sinauer, Sunderland.

MONTOYA, D. C. 1991. Aspectos biologicos del gusano cachón del inchi (*Panacea* sp. possible *prola*) Revista Colomb. Ent. (Bogota) 17:41–45.

NEILD, A. F. E. 1996. The butterflies of Venezuela Part I. Nymphalidae 1. Meridian Publications, Greenwich, London.

OTERO, L. D. & F. ROMERO. 1992. Nota sobre la presences de Panacea prola Dbldy & Hew. (Lepidoptera: Nymphalidae) en el sector central de Cordillera de la costa Venezulana. Boletin de Entomologia Venezulana (N.S.) 7:171–172.

PLANTROU, J. & S. ATTAL. 1986. Description D'une Nouvelle Espece Du Genre *Panacea* Decouverte En Guyane Française: *Panacea bleuzeni* nov. sp. (Lepidoptera Nymphalidae). Bulletin de la Société Sciences Nat. 50:23–24.

PORTER, A. H. & A. M. SHAPIRO. 1990. The lock-and-key hypothesis: lack of mechanical isolation in a butterfly hybrid zone. Entomol. Soc. Amer. 83:107–114.

POULTON, E. B. 1908. Essays on evolution. Clarendon Press, Oxford.

ROBBINS, R. K., G. LAMAS, O. H. H. MIELKE, D. J. HARVEY & M. M. CASAGRANDE. 1996. Taxonomic composition and ecological structure of the species-rich butterfly community at Pakitza, Parque Nacional de Manu, Peru, pp. 217–252. *In* Wilson, D. E. & A. Sandoval (eds.), Manu, the biodiversity of southeastern Peru. Washington, D.C., Smithsonian.

SCOBLE, M. J. 1992. The Lepidoptera: form, function and diversity. British Museum (Natural History), London.

SEITZ, A. 1916. 52. Genus *Panacea*. 53. Genus *Batesia*, pp. 536–537. *In* Seitz, A. (ed.), Macrolepidoptera of the World. Vol. 5. Alfred Kernen, Stuttgart.

SWYNNERTON, C. M. F. 1919. Experiments and observations bearing on the explanation of form and colouring, 1908–1913, Africa. J. Linn. Soc. (Zoology) 33:203–385.

SWOFFORD, D. L. 1993. PAUP: phylogenetic analysis using parsimony, version 3.1.1. Sinauer, Sunderland.

TUXEN, S. L. 1970. Taxonomist's glossary of genitalia in insects. Munksgaard, Copenhagen.

Received for publication 19 June 2002; revised and accepted 3 July 2002.

APPENDIX 1. Character list used in the phylogenetic analysis. Relevant figures are noted, and comments are included when needed. Definitions are in the Characters and Terminology section.

Wing Characters:

1. Forewing outer margin: concave (0), straight (1), convex (2).
2. Fringe of scales in the outer margin of wings: solid dark color (0), dark interspersed with white sections (1).
3. In dorsal view, male forewing with oblique, diffuse black band encroaching on postmedial blue-green band (0); devoid of such a pattern (1). Note: *P. bleuzeni* was scored using original description, illustration in D'Abrera and photos provided by G. Attal.
4. Forewing postmedial band expressed dorsally and ventrally (0); expressed dorsally only (1); absent or reduced (2). Note: *H. laodamia* and *P. procilla* were polymorphic for this character because of differences between the sexes.
5. In dorsal view, forewing subapical white band well developed (0); reduced (1); absent (2).
6. In ventral view, red-orange spots on forewing discal cell: two spots present, one at base and one at mid-length (0), one spot present, at mid-length (1), absent (2).
7. Ventral surface of forewing with white subapical band (0); devoid of such pattern (1).
8. Males, ventral surface of forewing apex: uniformly dirty red-orange (0); dark, same color as medial area (1); dark, with a yellow band (2).
9. Dorsal and ventral sides of hindwing consistently with four complete ocelli (0); dorsal side of hindwing with five incomplete ocelli (lacking outer ring) and clearly separated from any black lines (1); ventral side of hindwing with four to six complete ocelli (2); devoid of such patterns (3). Note: To understand the variation in this character a large number of specimens were examined, and we found no exceptions to the patterns described here (see Methods, Species studied).
10. Ventral surface of hindwing largely colored red-orange, with or without purplish sheen (0); devoid of such a pattern (1). Note: although the presence of a purplish sheen has been used to separate *P. procilla* and *P. divalis*, we found this character to be present in both these species and variable within each of them.
11. Ventral surface of hindwing with prominent dark line across basal half of cell Sc + R_1 (0); devoid of such a pattern (1).
12. Ventral surface of hindwing with prominent dark line across discal cell (0); devoid of such a pattern (1).
13. Ventral surface of hindwing: discal cell with two black dots in basal half (0); devoid of such a pattern (1). Note: of the 57 *P. prola* specimens examined, three had two dots, 22 had one dot, and 32 lacked dots; in *P. divalis*, four of the 53 specimens had dots merged into a single marking.
14. Ventral surface of hindwing with: nearly continuous line through medial area that crosses cells Sc + R_1, Rs, M_1, M_2, M_3, Cu_1 and Cu_2 (0); devoid of such a pattern (1).
15. Ventral surface of hindwing with: dark line in cell Cu_2 and cell Cu_1 contiguous (0); dark line not contiguous and line in cell Cu_2 more apical than line in cell Cu_1 (1); dark line not contiguous and line in cell Cu_2 more basal than cell Cu_1 (2); dark line absent from cell Cu_2 (3).
16. Ventral surface of hindwing with black submarginal line which is discrete in anal area and becomes more diffuse toward costal area (0); devoid of such a pattern (1). Note: *P. bleuzeni* was scored using the illustrations in D'Abrera (1987) and photos from the collection of G. Attal.
17. Ventral surface of hindwing with dark line imposed upon cross-vein m_2–m_3 (at distal edge of discal cell) (0), devoid of such a dark line (1). Note: in *P. prola*, three of 53 specimens lacked the dark line.
18. Female, ventral surface of hindwing with white patch of scales in medial area of cell M_2 (0); devoid of white patch (1). Note: two males of *P. procilla* had similar white patch. In *P. divalis* one of 12 lacked the patch, and in *P. regina* two of 14 lacked the patch.
19. Forewing venation: M_1 arched toward anal margin (0); devoid of such a pattern (1).
20. Forewing venation: M_2 arched toward anal margin (0); devoid of such a pattern (1).
21. Forewing cross-vein m_2–m_3 + cu_1: joins M_3 + Cu_1 at or distal to the fork M_3 and Cu_1 (0); proximally to the fork M_3 and Cu_1 (1); absent (2). Note: M_3 + Cu_1 denotes the combination of vein M_3 and Cu_1 proximal to the fork where they split.
22. Forewing cross-vein r–m_1, and the base of M_1 and M_2: inflated (0); not inflated (1).

Body Characters:

23. Foreleg with white scales laterally (0); devoid of white scales (1).
24. Thorax: ventral portion completely covered with red-orange scales (0); devoid of such a pattern (1).

Male Genitalia Characters:

25. Hypandrium: narrow, plate like, with obvious constriction near the middle of its long axis (0); broad, curling laterally, without a constriction (1).
26. In lateral view, hypandrium with long ramus projecting posteriorly (0); devoid of projections (1).
27. In lateral view, hypandrium with anterior rod-like projections (0); devoid of such a pattern (1).
28. In lateral view, posterior corner of hypandrium extended into an obvious lobe-like process that projects dorsally (0); less lobe-like and not as projected dorsally (1).
29. In lateral view, anterior portion of tegumen extremely projected (0); devoid of such a pattern (1).
30. In lateral view, uncus tip: pointed (0); sharply hooked (1).

APPENDIX 1. Continued.

31. Uncus: bifid (0); entire (1).
32. Uncus: elongate (0); short (1).
33. In lateral/ dorso-lateral view, base of uncus with obvious large dorsal ridges (0); with small ridges (1); devoid of such a pattern (2).
34. In lateral view, tip of uncus reaching or extending beyond tip of valva (0); devoid of such a pattern (1).
35. Uncus with obvious, long setae dorsally (0); devoid of setae (1).
36. Distal portion of gnathos: completely fused (0); bifid (1).
37. Distal portion of gnathos: small and projected ventrally (0); large and projected posteriorly (1).
38. In ventral view, distal portion of gnathos: with a rounded invagination (0); invaginated in a perfect "V" (1).
39. Valva: with dentate process approximately 2/3 from its base (0); without such a process (1).
40. Process of valva: projecting dorsally (0); projecting medially (1).
41. Process of valva: with setae (0); without setae (1).
42. Distal portion of valva: curving ventrally (0); curving dorsally or straight (1).
43. Distal portion of valva with large bare chitinous tip (0); with small bare chitinous tip (1); devoid of such patterns (2).
44. In lateral view, basal portion of valva: with large conspicuous ventrally produced rounded projection (0); devoid of such a pattern (1).
45. In lateral view, rod-like projections of juxta: large (0); small (1).
46. In lateral view, distal portion of saccus: strongly projected upward (0); straight to slightly projected upward (1).
47. In lateral view, vinculum with obvious dentate process along anterior margin (0); process shaped as a bump, not dentate (1).

Female Genitalia Characters:

48. Signa: present (0); absent (1).
49. Sterigma: present (0); absent (1).
50. Lamella antevaginalis: continuous across ventral surface (0); split (1).
51. Lamella antevaginalis: fused to edge of eighth sternite (0); not fused (1).
52. Ductus seminalis connecting to ductus bursa: very near corpus bursa (0); far from corpus bursa, and near ostium bursa (1).
53. Antrum: heavily sclerotized (0); mostly membranous (1).

APPENDIX 2. Character Matrix.

Ingroup						
Batesia hypochlora	1010221231	1111301101	0110011?01	1101110000	1111001111	111
Panacea prola	0011100130	1111300111	0100111010	101011111?	?000011110	110
Panacea procilla	000(0,1)000000	0000100011	0100111010	101011111?	?000011110	110
Panacea divalis	0011000030	0000100011	0100111110	101011111?	?000011110	110
Panacea regina	0011120020	0000100011	0100111010	101011111?	?000011110	110
Panacea bleuzeni	0002000010	0010000011	??00111010	101011111?	?000011110	110
Outgroups						
Biblis hyperia	2112221131	1111311111	2111110?10	0020101?1?	?101001100	110
Hamadryas laodamia	211(0,2)221131	1111311111	1011100?10	1010011?01	0121100011	000
Hamadryas arinome	1110221131	1111311110	1001100?10	1011011101	0121100011	000
Hamadryas amphinome	11102?1130	1111310110	1001100?10	10?1011101	0121100011	000
Hamadryas feronia	111?211?01	0110210?10	1001100?10	1011011101	0121110011	000