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

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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, chalciothea, 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, Symmerton 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 (Heuveson, 1852); P. regina (Bates, 1864); P. divalis (Bates, 1868); P. chalciothea (Bates, 1868); P. lysimache Godman and Salvin, 1883; P. bleuzeni Plantrou and Attal, 1986; and P. bella D’Abera, 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, Ectina, Eunice, Mycalea, 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.
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 Plantinou and Attal (1986), the illustrations in D’Aubrea (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
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 ve­
ation, 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 (Swoford 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-
pandum, 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. chalcodoea, although we did not examine this taxon directly.

Batesia Felder and Felder, 1862


Batesia hypochlolea Felder and Felder, 1862

(Figs. 1, 2, 11, 13)

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


Batesia hypochlolea chrysochantha Fruhstorfer, 1915. Soc. ent. 30(12):66


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-
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‘Abera 1987, Austin & Emmel 1990, Robbins et al. 1996).

**Variation.** Judging by the named subspecies (see synonymic 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 prola (Doubleday, 1848)
(Figs. 3, 11, 13)

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


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


**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.

**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)


**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 Cu₂; faint post-medial ocelli in almost all cells; conspicuous black submarginal line. Females often with a short, white longitudinal stripe in ventral hindwing cell M₂-M₃, 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 Ecuadorean 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).
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)


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 C. Lamas (Fig. 6) may serve as a starting point for identifying this taxon. Here we excerpt correspondence received from C. 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.

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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).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Source of dissected material</th>
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<tbody>
<tr>
<td><strong>Ingroup</strong></td>
<td></td>
</tr>
<tr>
<td><em>Batesia hypochlora</em></td>
<td>2 males: Brazil (GTA)</td>
</tr>
<tr>
<td></td>
<td>8 males: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td></td>
<td>1 female: Brazil (GTA)</td>
</tr>
<tr>
<td></td>
<td>1 female: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td><em>Panacea blezeni</em></td>
<td>1 male: French Guyana (GA)</td>
</tr>
<tr>
<td></td>
<td>1 female: French Guyana (GA)</td>
</tr>
<tr>
<td><em>Panacea divalis</em></td>
<td>5 males: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td></td>
<td>2 males: Brazil, Rondonia (GTA)</td>
</tr>
<tr>
<td></td>
<td>3 females: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td><em>Panacea procilla</em></td>
<td>2 males: Brazil (n = 1) and Colombia (n = 1) (LACM)</td>
</tr>
<tr>
<td></td>
<td>1 male: Colombia (MPM)</td>
</tr>
<tr>
<td></td>
<td>1 female: Colombia (MPM)</td>
</tr>
<tr>
<td><em>Panacea prola</em></td>
<td>5 males: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td><em>Panacea regina</em></td>
<td>5 males: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td></td>
<td>3 females: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td><em>Hamadryas amphinome</em></td>
<td>1 male: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td></td>
<td>1 female: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td><em>Hamadryas arinome</em></td>
<td>1 male: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
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<tr>
<td></td>
<td>1 female: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
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<tr>
<td><em>Hamadryas feronia</em></td>
<td>1 male: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
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<td></td>
<td>1 female: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
<tr>
<td><em>Hamadryas laedaliana</em></td>
<td>1 male: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
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<tr>
<td></td>
<td>1 female: Ecuador, Sucumbios, Garza Cocha (PJD)</td>
</tr>
</tbody>
</table>

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

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


**Species characters.** Dorsal surface with broken iridescent blue-green bands. Forewing ventral sur-
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: M1 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 m1+m2 (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 sacculus 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 + R1
(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 + R1, Rs, M1, M2, M3, Cu1, and Cu2
(15:1) Ventral surface of hindwing with dark line not contiguous and line in cell Cu2 more apical than line in cell Cu1
(18:0) Female: ventral surface of hindwing with white patch of scales in medial area of cell M3

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 M1−M3, 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’Abera 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 M1−M3. In females the white, ventral longitudinal stripe in hindwing cell M1−M3 may be diffuse or faintly expanded into the two cells above.

**Subspecies.** None.

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


**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...
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
$M_5-Cu_1$ 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 Cuianas
(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. ocanar*, from lower Mag-
dalena River, Colombia (Seitz 1916, D’Abrera 1987);
*P. p. salacia*, from Colombia (Seitz 1916, D’Abrera
1987); *P. p. lysimache* from Volcan Chiriqui, Panama,

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

Société Sciences Nat. 50:23.

Neotropical Region, part III: p. 487, new syn-
ynonym

**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 dis-
tally along black medial line from cell Sc + Rs to
Cu$_2$–1A.
**Distribution.** Apparently endemic to the Guianas (Plantrou & Attal 1986). However, its 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
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-

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

**Fig. 12.** Male genitalia: hypandrium, lateral view (inset: uncus in lateral view), ventral view (inset: tip of gnathos in ventral view). *Panacea regina*, *P. proia*, and *Batesia 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. chla\-cothea 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. 13. Female genitalia: ventral view, Panacea procilia, 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.
CARPENTER, C.

HLEIZENI.

AHNQVIST, G.

APOLNAR, and Bud

Freitas improved the clarity of the memory of Sonny providing historical information and comparing type specimens that figures of don), and by loaning specimens. 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. chalciothea 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, Thelonus Sphere Monk, and Bud Powell.

LITERATURE CITED


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 wing: 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. breviuscula was scored using original description, illustration in D’Abera 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. laevis 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); 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 + R1 (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 + R1, Rs, M1, M2, Cu1, and Cu2 (0); devoid of such a pattern (1).
15. Ventral surface of hindwing: dark line in cell Cu1 and cell Cu4 contigious (0); dark line not contiguous and line in cell Cu4 more apical than line in cell Cu1 (1); dark line not contiguous and line in cell Cu4 more basal than cell Cu1 (2); dark line absent from cell Cu4 (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. breviuscula was scored using the illustrations in D’Abera (1987) and photos from the collection of G. Attal.
17. Ventral surface of hindwing with dark line imposed upon cross-vein m2-m3 (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 M4 (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: M1 arched toward anal margin (0); devoid of such a pattern (1).
20. Forewing venation: M1 arched toward anal margin (0); devoid of such a pattern (1).
21. Forewing cross-vein r-m1: joins M1 and Cu1 at or distal to the fork M1 and Cu1 (0); proximally to the fork M1 and Cu1 (1); absent (2).
   Note: M1 + Cu1 denotes the combination of vein M1 and Cu1 proximal to the fork where they split.
22. Forewing cross-vein r-m1, and the base of M1 and M2; 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).
31. Uncus: bifid (0); entire (1).
32. Uncus: elongate (0); short (1).
33. In lateral/dorsolateral 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 hump, not dentate (1).

**Female Genitalia Characters:**
48. Sigina: 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).

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