

PHYLOGENETIC RELATIONSHIPS AMONG THE SPECIES OF *PANTHIADES*  
HÜBNER (LYCAENIDAE: THECLINAE: EUMAEINI)

ROBERT K. ROBBINS

Department of Entomology, P.O. Box 37012, NHB Stop 127, Smithsonian Institution, Washington, DC 20013-7012, U.S.A. (e-mail: RobbinsR@SI.edu)

---

*Abstract.*—A species level phylogenetic analysis of *Panthiades* Hübner was performed using twelve characters of wing pattern, androconia, and male and female genitalia. The purposes were to determine whether *Panthiades* is monophyletic without *Cycnus* Hübner and to provide a cladogram for a project on the evolution of “false head” wing patterns. Parsimony analysis with all characters unordered yielded two trees. One was the strict consensus of the two trees, and the other was the only most parsimonious tree when one of the multi-state characters was ordered. *Panthiades* is characterized by five hypothesized synapomorphies. If *Cycnus* is recognized, *Panthiades* is not monophyletic on either of the most parsimonious cladograms. The “classic” false head wing patterns in *Panthiades* appear to have evolved once.

*Key Words:* hairstreaks, false head hypothesis, *Cycnus*

---

Nicolay's (1976) taxonomic treatment of *Panthiades* Hübner and *Cycnus* Hübner has been stable with minor exceptions. Robbins (2004a, b) changed two specific epithets for nomenclatural reasons and synonymized the monotypic *Cycnus* with *Panthiades*, stating that *Panthiades* was probably not monophyletic without *Cycnus*. Consistent with this synonymy, Nicolay (1976:3) had noted that “the entry of the ductus seminalis on the ventral-lateral side of the corpus bursae” is shared by *Panthiades* and *Cycnus*, but not by other close relatives.

*Panthiades* is of biological interest because it contains two species, *P. bathildis* (Reakirt) and *P. phaleros* (L.), that have wing patterns (Fig. 10) traditionally associated with the “false head” hypothesis of predator avoidance (Robbins 1980). These wing patterns show a significantly greater incidence of unsuccessful predator attacks directed to the “false head” than other Lycaenid wing patterns (Robbins 1981). It is

unclear whether the classic “false head” wing pattern evolved once or twice in the *Panthiades/Cycnus* lineage, especially since Nicolay (1976) placed one in *Cycnus* and one in *Panthiades*.

In this paper, I infer phylogenetic relations among the eight species of *Panthiades* for the purposes of assessing the monophyly of *Panthiades* without *Cycnus* and of providing a cladogram for ongoing studies of the evolution of wing patterns associated with the “false head” hypothesis.

#### MATERIALS AND METHODS

Coded characters were derived from a comparison of adult morphology using 1,009 pinned specimens of *Panthiades* in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA, plus numerous specimens borrowed from other museums. In addition, 41 genitalic dissections of both sexes of the eight *Panthiades* species were examined. *Pan-*

Table 1. Character matrix for *Panthiades*. The outgroups are the type species of *Parrhasius*, *Thepytus*, and *Porthoecla*. Characters and their states are detailed in the text.

Species	Characters											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Panthiades bitias</i>	0	0	1	0	1	1	3	2	1	0	0	0
<i>Panthiades hebraeus</i>	0	0	1	0	1	1	3	2	1	0	0	0
<i>Panthiades aeolus</i>	0	0	0	?	0	1	1	0	1	0	0	0
<i>Panthiades boreas</i>	?	0	1	1	0	0	3	2	1	0	0	0
<i>Panthiades ochus</i>	0	0	1	1	0	0	3	2	1	0	0	0
<i>Panthiades paphlagon</i>	0	0	1	1	0	0	3	2	1	0	0	0
<i>Panthiades bathildis</i>	?	1	1	0	0	1	2	1	1	0	0	0
<i>Panthiades phaleros</i>	?	1	1	0	0	1	2	1	1	1	0	0
<i>Parrhasius polibetes</i>	1	0	0	1	?	1	0	?	0	2	1	1
<i>Thepytus epytus</i>	1	0	0	0	0	1	0	0	1	2	1	1
<i>Porthoecla porthura</i>	1	0	0	0	?	1	0	0	0	2	1	1

*thiades* genitalia have been illustrated (Nicolay 1976) except for the female of *P. boreas* (Felder and Felder), which is figured in this paper. Genitalic terms follow those in Klots (1970), as illustrated in Robbins and Nicolay (2002). Androconial terminology follows Robbins (1991), and wing vein names follow Nicolay (1971, 1977).

The terminal taxa are the eight species that have been placed in *Panthiades* or *Cycenus* (Nicolay 1976, Robbins 2004b). They are: *P. bitias* (Cramer, 1777), *P. hebraeus* (Hewitson, 1867), *P. aeolus* (Fabricius, 1775), *P. boreas* (C. Felder and R. Felder, 1865), *P. ochus* (Godman and Salvin, 1887), *P. paphlagon* (C. Felder and R. Felder, 1865), *P. bathildis* (C. Felder and R. Felder, 1865), and *P. phaleros* (Linnaeus, 1767). These taxa can be identified using the key in Nicolay (1976). The adults were illustrated in D'Abbrera (1995).

One outgroup for the analysis is *Parrhasius polibetes* (Cramer), the type species of *Parrhasius* Hübner, a genus that has been considered to be congeneric with *Panthiades* (Clench 1961) or its closest relative (Nicolay 1976). To test the robustness of the root, I also used as outgroups the type species of *Thepytus* Robbins, *T. epytus* (Godman and Salvin), and of *Porthoecla* Robbins, *P. porthura* (H.H. Druce). Among the genera of the *Panthiades* Section (Robbins 2004a,b), their male genitalia, espe-

cially the valvae, are phenetically most similar to those of *Panthiades*.

The character state for each *Panthiades* and outgroup species is listed in the character matrix (Table 1). I used the implicit enumeration option of Hennig86 software to derive a most parsimonious cladogram. A strict consensus tree was determined. To test the assumption of equally weighted characters, successive weighting was performed (Farris 1969) and a consensus of the resulting trees was determined. All characters were unordered, except for multi-state character 7. Because it forms a morphocline (cf., Pogue and Mickevich 1990), it was analyzed ordered and unordered. Mapping of characters on trees was done with Winclada software (Nixon 2002) with the fast optimization option. Jackknife support was determined in Winclada using Nona (1000 replications with mult\*10, memory 1000 trees).

#### MORPHOLOGY AND CODED CHARACTERS

Ventral wing pattern.—The ventral wing pattern in *Panthiades* is highly variable. However, determining homology among the different wing pattern elements is difficult because these elements are not recognizable in some species. Further, I am interested in using the resulting cladogram to examine wing pattern evolution within *Panthiades*. For these reasons, the only character coded

has one state in *Panthiades* and a second state in all other *Panthiades* Section genera, so it does not affect the inferred phylogenetic relations within the genus.

*Character 1:* Ventral hindwing postmedian line segment in cell Sc+R1-Rs (0) colinear with remainder of postmedian line, (1) basally displaced. In three *Panthiades* species, the postmedian line is not recognizable, so these species were coded with a question mark.

Dorsal wing pattern.—*Character 2:* Dorsal wings of female with (0) shining blue-green iridescence, (1) a varying amount of dull, “chalky” blue scales. The second character state is restricted in *Panthiades* to *P. bathildis* and *P. phaleros*, where it varies within each species from no blue to a dull blue sheen that is distinguishable from the shining iridescent blue-green of the other species.

Androconia.—Androconia in *Panthiades* are restricted to the dorsal forewing and are composed of three parts. The first is a black (rarely gray or tan) scent pad in the discal cell surrounded by a conspicuous ring of scales (Figs. 1–2, also fig. 122 in Eliot 1973), which are usually gray in color. These androconia and the surrounding ring of scales are tightly attached to the wing membrane. They occur in all *Panthiades* except *P. aeolus* (Fig. 3), but nowhere else in the Eumaeini.

The second part is a gray to dark charcoal colored scent pad that is universal in the *Panthiades* Section. It is distal of the ring of scales (Figs. 1–2, 4) and is, in turn, composed of two parts. The first is very roughly oval and usually covers the upper and middle disco-cellular veins and parts of the wings basal and distal of these veins (Fig. 2). There is sometimes a second part at the base of vein M3 (most conspicuous in *P. aeolus*, Fig. 3, arrow C), but its presence is intraspecifically variable in some species, such as *P. bitias*, for which reason it is not coded.

The third part is a patch of black scales, usually on the distal half of the wings (Fig.

4). It is unclear whether these scales form a scent patch, but I tentatively treat them as androconia because they are restricted to males. They occur in three species of *Panthiades*, one *Thepytus*, and two *Parrhasius* (Nicolay 1979). The size and shape of the black scales often varies geographically, at least in *Panthiades* and *Parrhasius* (Nicolay 1976, 1979). There is a patch of dark brown scales in *P. aeolus* between the scent pads on the disco-cellular veins and at the base of vein M3 (Fig. 3, arrow B) that could possibly be homologous with the black scales, for which reason I code the second character below with a question mark for *P. aeolus*.

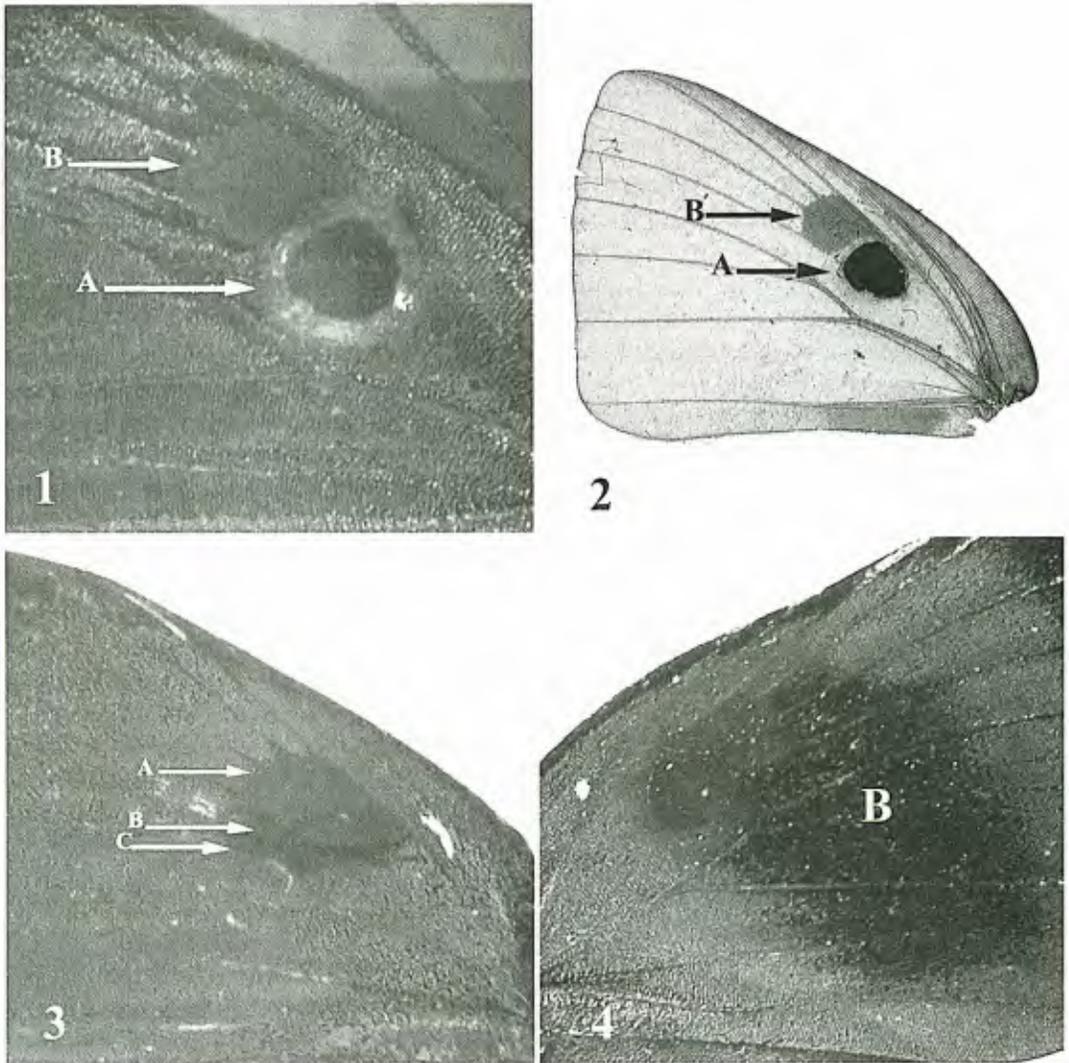
*Character 3:* Scent pad in the discal cell surrounded by a ring of scales that are tightly attached to the wing membrane (0) absent (Fig. 3), (1) present (Fig. 4).

*Character 4:* Black scent patch distal of the discal cell (0) absent, (1) present (Fig. 4, letter B).

Male genitalia.—As noted by Nicolay (1976), the genitalia of *Panthiades* are more interspecifically variable than those of many other eumaeine genera. Five characters are coded.

*Character 5:* Number of cornuti in penis (0) 1, (1) 2. Cornuti are usually easily scored in eumaeines, including *Panthiades*. However, outgroup genera *Parrhasius* and *Porthocla* are problematic in that the folded vesica within the penis has patches of varying sclerotization, making it difficult to determine what is and is not a cornutus. Despite this problem in *Parrhasius* and *Porthocla*, for which reason they are coded with question marks, the two states within *Panthiades* are clear.

*Character 6:* Gnathos tips (0) flared, (1) not flared. Modification of the gnathos is unusual in the *Panthiades* Section, and the first state was illustrated by Nicolay (1976). The gnathos of *P. aeolus* have a laminate carina (*sensu* Field 1967) at the elbow, but it is the only species in the *Panthiades* Section with such a clearly developed carina



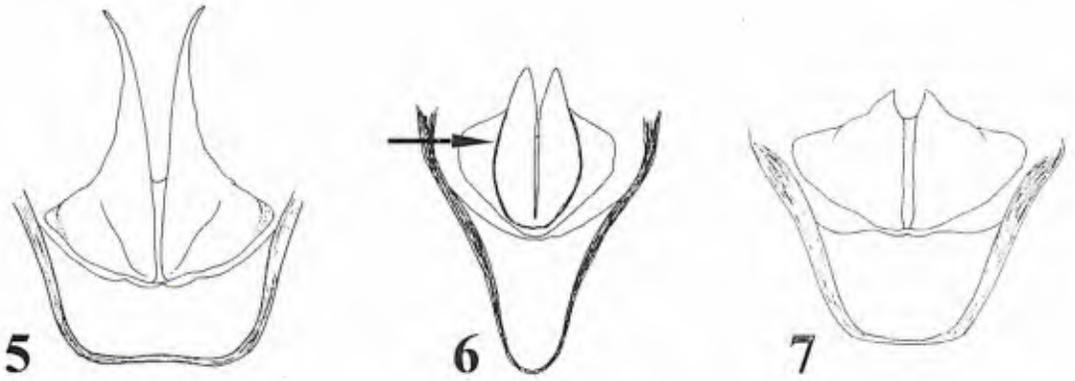
Figs. 1–4. Dorsal forewing androconia. 1, *Panthiades phaleros*, arrow A points to ring of scales around one scent pad (Character 3), arrow B to second scent pad distal of ring of scales. 2, *P. phaleros* wing slide showing scent pads in relation to wing veins, arrows A and B as in previous figure. 3, *P. aeolus*, arrow A points to scent pad covering the upper disco-cellular veins, arrow B points to dark scales that may be androconia, arrow C to scent pad at base of vein M3. 4, *P. ochus*, letter B is in middle of dark scales that may be androconia (Character 4).

on the elbow, for which reason it was not coded.

**Character 7:** Ventral surface of valvae fused anteriorly (0) 0–30% of length, (1) 30–50% of length, (2) 50–70% of length, (3) 70–100% of length. Nicolay (1976) first reported the fused valvae in *Panthiades* (Figs. 5–7).

**Character 8:** Shape of valva in ventral

aspect (0) roughly triangular; but more than twice as long as wide (Fig. 5), (1) duplex with a well-developed internal ridge demarcating the two parts (Fig. 6), (2) roughly an equilateral triangle (Fig. 7). Because the valva of outgroup *P. polibetes* is so different in shape from that in *Panthiades* (cf. fig. 2 in Nicolay 1979), it is coded with a question mark.



Figs. 5-7. Male genitalia saccus and valvae in ventral aspect (anterior is down, digitized from Nicolay 1976). 5, *Panthiades aeolus*, each valva is longer than wide. 6, *P. phaleros*, each valva is duplex, separated by a well-developed internal ridge (arrow). 7, *P. boreas*, each valva is roughly an equilateral triangle.

*Character 9:* Ventral of the notch where the labides meet, the length of the presumed remnant uncus is (0) <0.05mm, (1) ~0.1mm. So far as I am aware, the second character state only occurs in *Panthiades* and *Thepytus*.

*Female genitalia.—Character 10:* Signa (0) skillet-shaped (Fig. 8), (1) rectangular and narrow (fig. 22 in Nicolay 1976), (2) with a single central spine (fig. 3 in Nicolay 1979). The skillet-shaped signa (Fig. 8, terminology from Nicolay 1976) occurs only

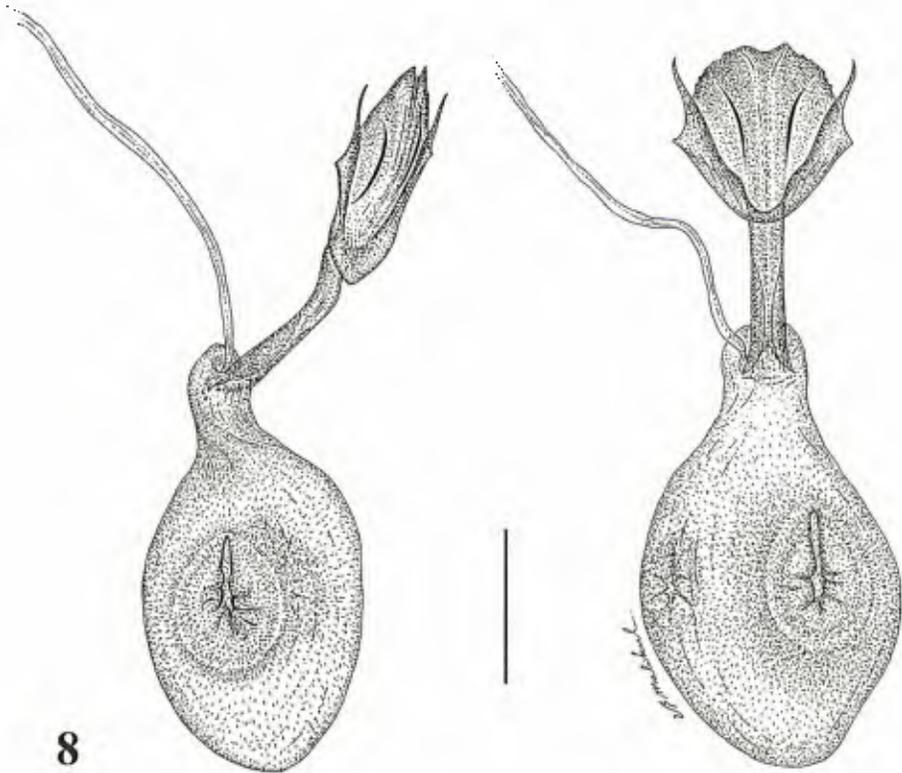
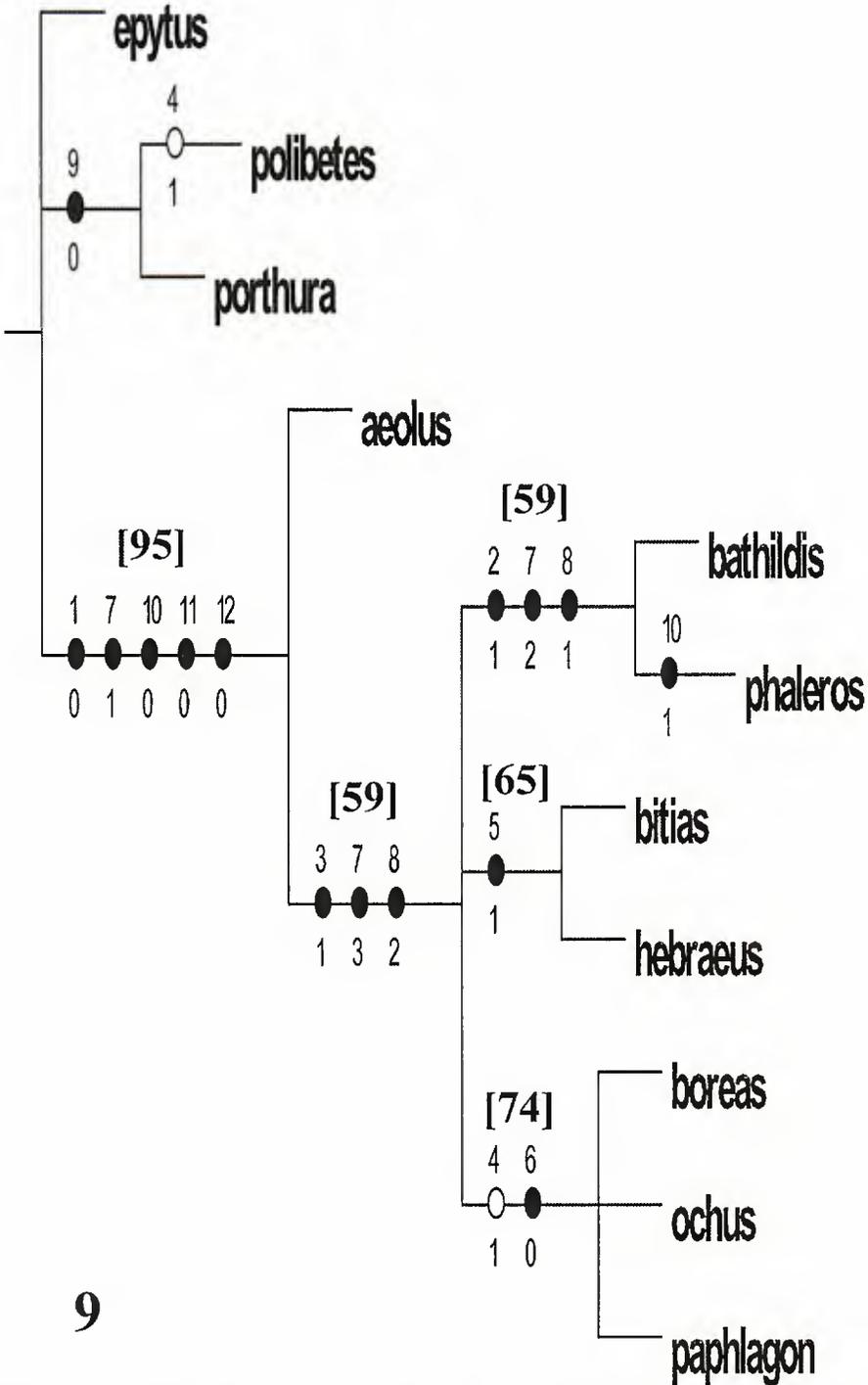
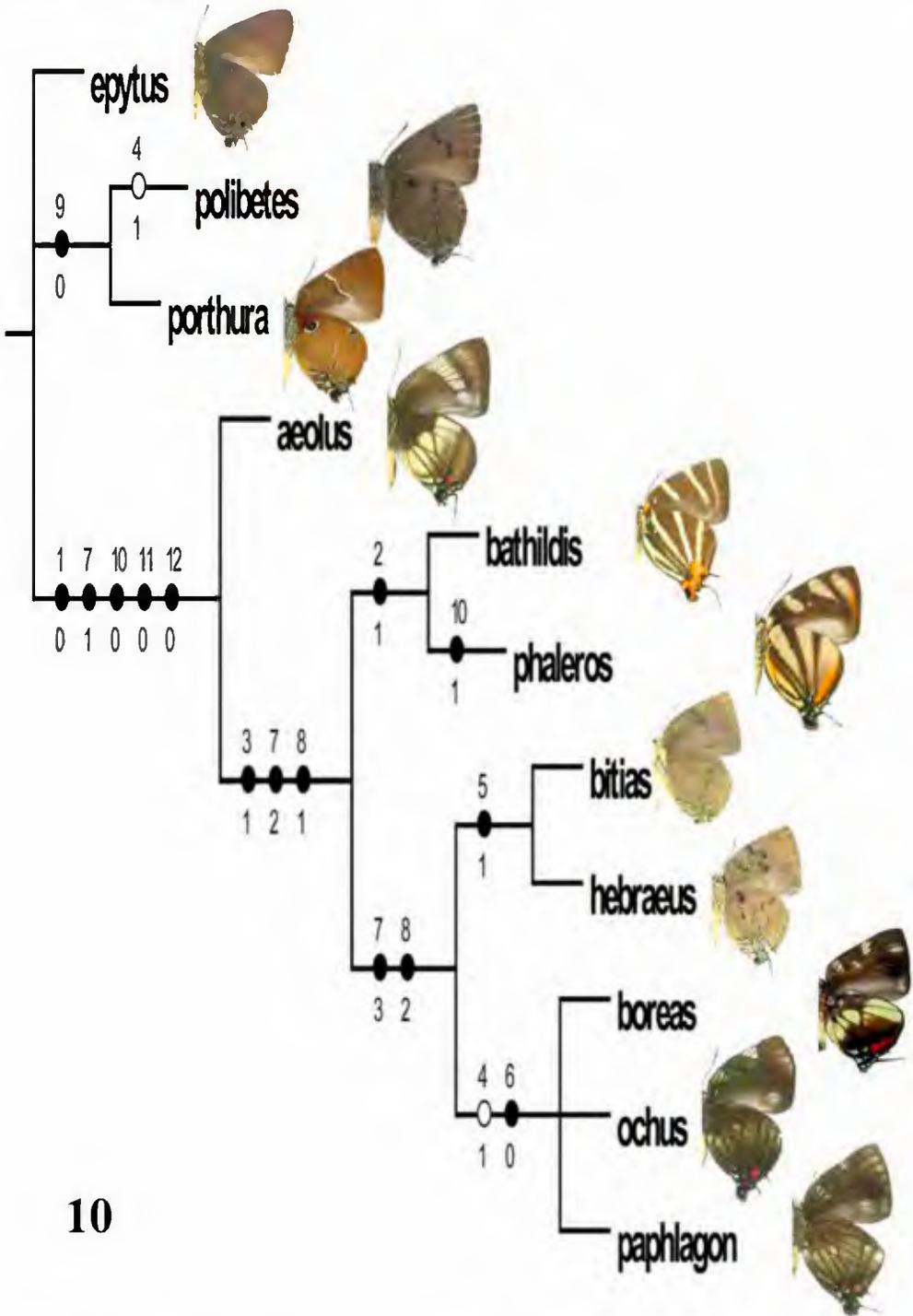


Fig. 8. Female genitalia (bursa copulatrix) of *Panthiades boreas* in lateral (left) and ventral (right) aspects. Scale 1 mm.



9

Fig. 9. One of two most parsimonious cladograms (character 7 unordered, 17 steps, CI = 0.94, RI = 0.96) for *Panthiades* species. *Thepytus epytus*, *Parrhasius polibetes*, and *Porthoclea porthura* are the outgroups. Character numbers are placed above nodes and character state numbers below nodes. Open circles represent reversal or convergence of the character state at that node. Jackknife support is noted in brackets above each node. This cladogram is also the consensus of the two most parsimonious trees.



10

Fig. 10. Most parsimonious cladogram (character 7 ordered, 17 steps, CI = 0.94, RI = 0.96) for *Panthiades* species. *Thepytus epytus*, *Parrhasius polibetes*, and *Porthoclea porthura* are the outgroups. Character numbers are placed above nodes and character state numbers below nodes. Open circles represent reversal or convergence of the character state at that node. This cladogram is also one of the most parsimonious trees when character 7 is unordered. The ventral wing pattern of each species is placed on the cladogram. The classic "false head" wing patterns in *P. bathildis* and *P. phaleros* appear to have evolved once in their immediate common ancestor.

in *Panhiades*, and the rectangular and narrow signa occurs in *P. phaleros* (fig. 23 in Nicolay 1976).

*Character 11:* Lamella postvaginalis in ventral aspect (0) sclerotized and fan-shaped (Fig. 8), (1) not fan-shaped (Fig. 3 in Nicolay 1979). The first state occurs in *Panhiades* and not the other genera of the *Panhiades* Section.

*Character 12:* Origin of ductus seminalis (0) on the left ventral side of the corpus bursae (Fig. 8), (1) on the dorsal side of the corpus bursae. In the *Panhiades* Section, the origin is usually on the left side, but in *Parrhasius*, it is very close to the center.

#### PHYLOGENETIC ANALYSES AND RESULTS

I analyzed the coded data (Table 1) using the Hennig86 "ie\*" option, which searches exhaustively for the most parsimonious cladograms. The analysis with character 7 unordered yielded two equally parsimonious 17-step trees with a consistency index of 0.94 and retention index of 0.96. The first (Fig. 9) is also the strict consensus tree. The second (Fig. 10) is the only most parsimonious tree when character 7 is treated as ordered. Successive weighting did not change the cladogram topology. Jackknife support values are reported for the consensus tree (Fig. 9) and were slightly lower than those for the other most parsimonious tree with character 7 ordered. In both of the most parsimonious trees, *Panhiades* is partitioned into four monophyletic groups; *P. aeolus*, a lineage of *P. phaleros* and *P. bathildis*, a lineage of *P. bitias* and *P. hebraeus*, and a lineage of *P. ochus*, *P. paphlagon*, and *P. boreas*.

#### DISCUSSION

Synapomorphies for *Panhiades* (Figs. 9–10) are (1) ventral hindwing postmedian line segment in cell Sc+R1-Rs co-linear with remainder of postmedian line, (2) ventral surface of valvae fused at their anterior base more than 30% of their length, (3) skillet shaped signa, (4) lamella postvaginalis in ventral aspect sclerotized and fan-

shaped, and (5) ductus seminalis arises on the left ventral side of the corpus bursae. Except for the first, these characters had been explicitly noted by Nicolay (1976). If *P. phaleros* is moved from *Panhiades* to *Cycnus*, then *Panhiades* is not monophyletic on either of the most parsimonious trees (Figs. 9, 10), whether character 7 is ordered or unordered. These results support the classification in Robbins (2004b).

*Panhiades bathildis* and *P. phaleros* have wing patterns that have traditionally been associated with the "false head" hypothesis (Robbins 1980, 1981). The phylogenetic results suggest that this wing pattern evolved in the ancestor of the two species (Fig. 10). In Nicolay's (1976) classification, this result was not evident.

#### ACKNOWLEDGMENTS

I am grateful to Stan Nicolay for more than I can ever reasonably acknowledge, especially sharing for three decades his broad knowledge of the Neotropics and its eumaeine fauna. Specifically for this paper, he allowed me to scan digitally his genitalia drawings. For drawing the female genitalia of *P. boreas*, I thank Vichai Malikul. For making suggestions on the manuscript, I thank Marcelo Duarte, Gerardo Lamas, Tia-go Quental, John Shuey, and Andy Warren.

#### LITERATURE CITED

- Cleneh, H. K. 1961. Tribe Theclini, pp. 177–220. In Ehrlich, P. R. and A. H. Ehrlich, How to Know the Butterflies, Brown Company, Dubuque, Iowa.
- D'Abrera, B.L. 1995. Butterflies of the Neotropical region. Part VII. Lycaenidae. Hill House, Black Rock, pp. 1–xi + 1098–1270.
- Eliot, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): A tentative arrangement. Bulletin of the British Museum (Natural History) Entomology 28: 371–505.
- Farris, J. S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374–385.
- Field, W. D. 1967. Preliminary revision of butterflies of the genus *Calycopis* Scudder (Lycaenidae: Theclinae). Proceedings of the United States National Museum 119 (No. 3552), 48 pp.
- Klots, A.B. 1970. Lepidoptera, pp. 115–130. In Tuxen,

- S. L. ed., Taxonomist's Glossary of Genitalia in Insects. Munksgaard, Copenhagen.
- Nicolay, S. S. 1971. A new genus of hairstreak from Central and South America (Lycaenidae, Theclinae). *Journal of the Lepidopterists' Society* 25, Supplement 1, 39 pp.
- . 1976. A review of the Hübnerian genera *Panathiades* and *Cynus* (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum* 35, 30 pp.
- . 1977. Studies in the genera of American hairstreaks. 4. A new genus of hairstreak from Central and South America (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum* 44, 24 pp.
- . Studies in the genera of American hairstreaks. 5. A review of the Hubnerian genus *Parrhasius* and description of a new genus *Michaelus* (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum* 56, 52 pp.
- Nixon, K. C. 2002. WinClada version 1.00.08. Published by the author, Ithaca, NY.
- Pogue, M. G. and M. F. Mickevich. 1990. Character definitions and character state delineation: the bête noire of phylogenetic inference. *Cladistics* 6: 319–361.
- Robbins, R. K. 1980. The Lycaenid "false head" hypothesis: Historical review and quantitative analysis. *Journal of the Lepidopterists' Society* 34: 194–208.
- . 1981. The "false head" hypothesis: Predation and wing pattern variation of lycaenid butterflies. *American Naturalist* 118: 770–775.
- . 1991. Evolution, comparative morphology, and identification of the eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). *Smithsonian Contributions to Zoology* No. 498, 64 pp.
- . 2004a. Introduction to the checklist of Eumaeini (Lycaenidae), pp. xxiv–xxx. In Lamas, G. ed. Checklist: Part 4A. Hesperioidea—Papilionoidea. In Heppner, J. B. ed. Atlas of Neotropical Lepidoptera, Vol. 5A. Association for Tropical Lepidoptera, Scientific Publishers, Gainesville, xxxvi + 439 pp.
- . 2004b. Lycaenidae. Theclinae. Tribe Eumaeini, pp. 118–137. In Lamas, G. ed. Checklist: Part 4A. Hesperioidea—Papilionoidea. In Heppner, J. B. ed. Atlas of Neotropical Lepidoptera, Vol. 5A. Association for Tropical Lepidoptera, Scientific Publishers, Gainesville, xxxvi + 439 pp.
- Robbins, R. K. and S. S. Nicolay. 2002. An overview of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini). *Journal of the Lepidopterists' Society* 55: 85–100.