THE EARLY STAGES AND NATURAL HISTORY OF *CORADES MEDEBA* HEWITSON, 1850 IN EASTERN ECUADOR (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE: PRONOPHILINA)

Harold F. Greeney[1,3], Tomasz W. Pyrcz[2], Lee A. Dyer[3], Miguel Sánchez Z.[4] and Thomas R. Walla[5]

[1]Yanayacu Biological Station & Center for Creative Studies, Cosanga, Ecuador, c/o 721 Foch y Amazonas, Quito, Ecuador, [2]Zoological Museum of the Jagiellonian University, Ingardena 6, 30-060 Kraków, Poland, [3]Biology 0314, University of Nevada, Reno, 1664 N. Virginia St., Reno, Nevada 89557, USA, [4]Escuela de Biologia y Química de la Universidad Central del Ecuador, Quito, Ecuador, [5]Department of Biology, Mesa State College, 1100 North Avenue, Grand Junction, Colorado 81501, USA.

Abstract- The early stages are not described for any species of *Corades* Doubleday 1849. We describe the immature stages of *Corades medeba* Hewitson 1850 from northeastern Ecuador. *Chusquea* cf. *scandens* (Poaceae, Bambusoidea) is the larval food plant. Eggs are laid singly or in clusters of up to 11 on the bottom side of mature host plant leaves. The life cycle from egg to adult lasts 95-106 days. Adults are encountered most frequently on sunny days, flying rapidly over areas dominated by their food plant or feeding on the ground at mammal feces. Males guard perches near areas of food plant, usually in sunny areas or forest edges.

Resumen- No existen hasta este momento descripciones de los inmaduros para ninguna especie del género *Corades* Doubleday 1849. En este trabajo describimos los estados inmaduros de *Corades medeba* Hewitson 1850 en el noreste de Ecuador. *Chusquea* cf. *scandens* (Poaceae, Bambusoidea) es la planta hospedera. La hembra pone huevos uno por uno o en grupos de hasta 11 unidades en el envés de las hojas maduras. El ciclo de vida dura de 95 a 106 días. Los adultos pueden ser encontrados más fácilmente en días soleados sobrevolando áreas dominadas por sus plantas hospederas, o cuando se alimentan de los excrementos de mamíferos en el suelo. Los machos establecen territorios generalmente situados cerca de las plantas hospederas, en zonas limítrofes a los claros del bosque.

Key words: Andes, bamboo, *Chusquea*, cloud forest, egg, larva, Poaceae, pupa.

The genus *Corades* Doubleday 1849 encompasses 22 species (Lamas *et al.* 2004; Pyrcz unpubl.) confined to the Andes of South America (Pyrcz 2004). *Corades* spp. are immediately identifiable in the field by the short to mid-length tail-like extension on the hind wing at the Cu2 vein. This is apparently the only known synapomorphy uniting the genus (Pyrcz 2004). While the shape of some sclerites of the male genitalia suggests that *Corades* is related to *Pronophila* Doubleday 1949, *Lasiophila* C. & R. Felder 1859, *Arhuaco* Adams & Bernard 1977, and *Pseudomaniola* Röber 1889, there are no characters which eleucidate the sister relationships of *Corades* (Pyrcz 2004).

Corades medeba Hewitson 1850 is one of the most widely distributed species within the genus and includes three subspecies (Lamas *et al.* 2004). It occurs from Venezuela to Bolivia, flying generally at elevations from 2000 to 2400 m, often aggregating in large numbers at water seeps or dung (Pyrcz & Wojtusiak 2002). Subspecies *C. m. columbina* Staudinger occurs from the Venezuelan Cordillera de Mérida, throughout Colombia and Ecuador to northernmost Peru (Pyrcz 2004). While Pyrcz (2004) observed ovipositions of two *Corades* species on *Chusquea* bamboo, there are no published life histories for any member of the genus. Here we describe the early stages of *C. medeba columbina* from northeastern Ecuador, providing the first larval description for any member of *Corades*.

MATERIALS AND METHODS

We reared larvae of *C. medeba columbina* at the Yanayacu Biological Station & Center for Creative Studies (00°35.949 S, 77°53.403 W, 2150 m), located in the Napo Province of northeastern Ecuador. Yanayacu is five kilometers west of the town of Cosanga and, with the private reserves of Cabañas San Isidro and the Napo Andean Forest Foundation, encompasses around 2000 hectares of primary cloud forest bordered by cattle pasture and other disturbed habitats. Landslides are common in the steep terrain surrounding Yanayacu, most of which are subsequently colonized by *Chusquea* bamboo. Large patches of bamboo also occur in flatter areas, especially along streams. For a more complete site description, see Valencia (1995). We collected larvae and eggs at elevations ranging from 2000 to 2200 m, and reared them in glass jars at the ambient research lab, located at 2150 m. Voucher specimens of shed head capsules and pupal exuviae are retained in the private collections of the senior author.

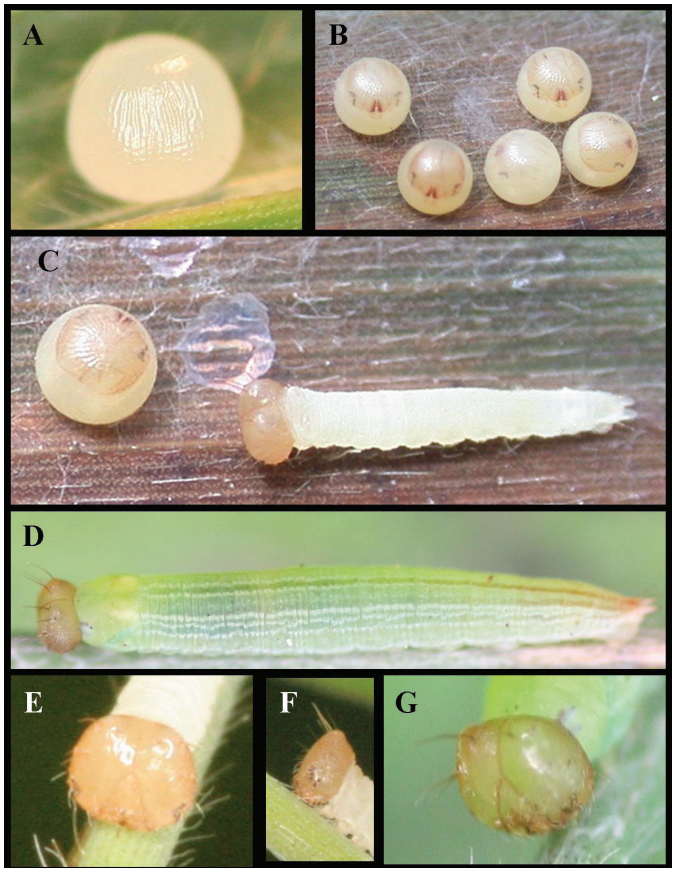
RESULTS

Larval behavior: *Chusquea* cf. *scandens* (Poaceae, Bambusoidea) is the larval food plant of *C. medeba columbina* at our study site. First and second instars rest on the skeletonized mid-vein at the apical portion of the leaf. Their coloration makes them extremely cryptic as it matches well the natural coloration of the tips of *Chusquea* leaves. Later instars rest on the dorsal surface of mature leaves with their head scoli flattened against the surface. Green individuals of the fifth instar (see below) generally rest on living leaves while brown individuals tend to be found on dead leaves. When disturbed, larvae rear back and try to bite the offending object, usually dropping from the plant if disturbed further.

Immature stages

Egg (Figures 1a-c) n = 22; 1.2 mm diameter; 13 days. Egg round, white to yellowish-white, appearing smooth but with minute, irregular, vertically oriented striations visible under

Fig. 1. Immature stages of *Corades medeba columbina* at Yanayacu Biological Station, Napo Province, 2150 m, Ecuador: **a)** freshly laid egg; **b)** pre-hatch clutch of eggs; **c)** recently hatched larva after consuming egg shell; **d)** pre-molt larva; **e-g)** detail of first instar head.



dissecting scope (Fig. 1a). Eggs are laid singly (n = 2) or in groups of 4 (n = 1), 5 (n = 2), or 8 (n = 2) to 11 (n = 1) on the lower surface of mature leaves. 24-48 hours prior to hatching the larval head capsule is clearly visible through the chorion (Figs. 1b-c). Upon emergence, larvae consume the entire egg shell (Fig. 1c).

First instar (Figures 1c-g) n = 16; 3-7.5 mm; 12 days. Head nearly round with slight epicranial crease, pale brown, smooth with sparse pale setae, darker and longer near epicranium and laterally (Figs. 1e-g); at hatching body white (Fig. 1c), nearly bare but with minute pale setae, round in cross-section, widest at T1, tapering gradually to two small, slightly separated caudal tails; becomes greenish after feeding commences; later in stadium larvae develop thin, indistinct whitish lines subdorsally, laterally, and ventrolaterally (Fig. 1d); a thin, greenish, mid-dorsal line runs the length of body gradually becoming reddish posteriorly beginning on A6, caudal tails and dorsum of A10 distinctly reddish.

Second instar (Figure 2) n = 15; to 11.5 mm; 8-10 days. Head green to greenish brown, rounded with two well developed, conical, epicranial scoli projecting slightly foreward, slightly browner than rest of head (Figs. 2d-g); posterior surface of scoli and back of head with indistinct pale stripes (Figs. 2f-g); head appearing smooth but with minute pale setae and reticulations visible under dissecting scope; after molting body widest at T1, tapering gradually to well-developed caudal tails held tightly appressed (Fig. 2b); body coloration similar to that described for late-stadium first instar; later in stadium caudal tails more distinctly red-brown, with pale stripes laterally and no longer held tightly appressed (Figs. 2a, c); prior to molting new head capsule visible below skin as two bright yellow triangles on dorsum of T1 (Fig. 2c), dorsum with faint reddish tinge.

Third instar (Figure 3) n = 19; to 19 mm; 10-11 days. Head green with red-brown, well-developed scoli, posteriorly darker with distinct pale, vertical stripes extending onto scoli (Figs. 3a-c); head appearing smooth but with minute granulations and pale setae (Fig. 3c); body more dorso-ventally flattened, roughly trapezoidal in cross-section, coloration similar to older second instars with fine pale and reddish striping on a bright green background, ventrolaterally with prominent but thin white stripe (Fig. 3b); well developed caudal tails are held tightly appressed through stadium (Fig. 3e), spiracles appear as small yellow spots.

Fourth instar (Figure 4) n = 27; to 32 mm; 11-14 days. Overall very similar to third instar, especially early in stadium (Fig. 4a); head scoli well developed forming a ≥45º angle (Figs. 4a, g-h); later in stadium head and body coloration becoming clearer and brighter (Figs. 4c-e, h); colors fading again just prior to molt, head capsule becoming uniformly brown, pronotum

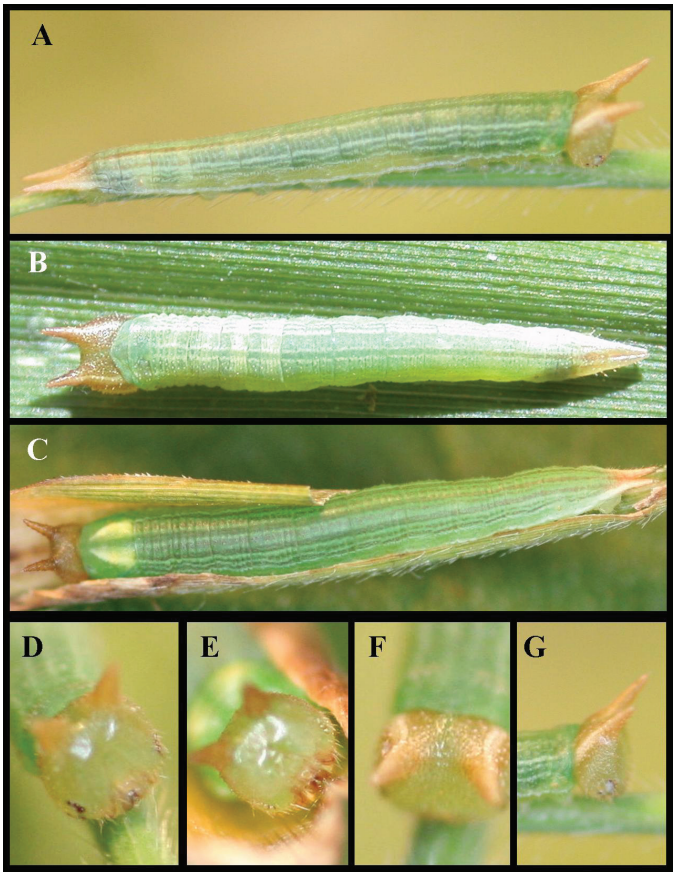


Fig. 2. Second instar larvae of *Corades medeba columbina* at Yanayacu Biological Station, Napo Province, 2150 m, Ecuador: **a)** mid-stadium larva; **b)** recently molted larva; **c)** pre-molt larva; **d-g)** detail of larval head.

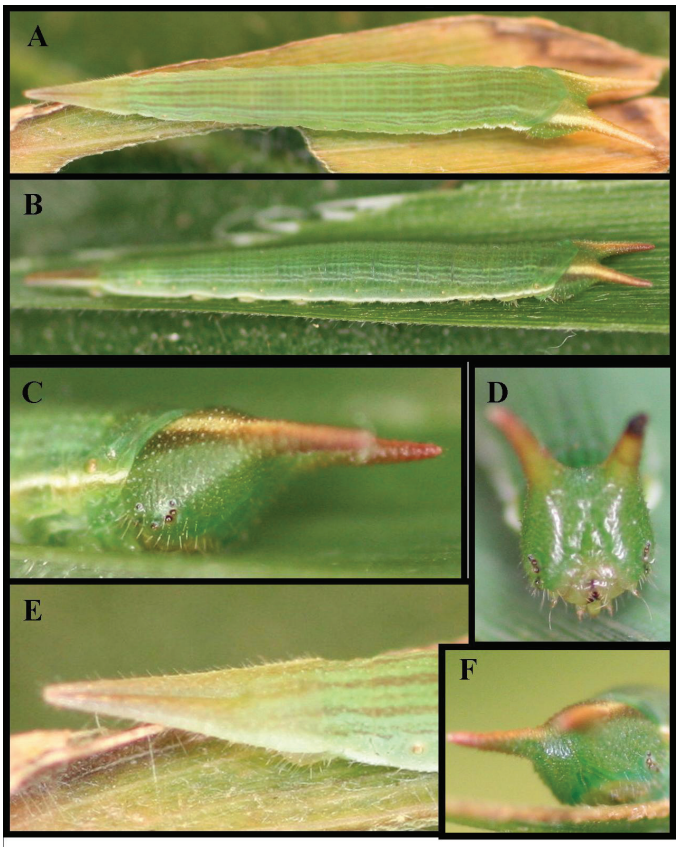


Fig. 3. Third instar larvae of *Corades medeba columbina* at Yanayacu Biological Station, Napo Province, 2150 m, Ecuador: **a)** recently molted larva; **b)** mid-stadium larva; **c-d)** detail of larval head; **e)** detail of caudal tails; **f)** detail of larval head.

with yellow triangles (Figs. 4b, g); later in stadium body shape becomes markedly flattened and trapezoidal in cross-section, widest around A1 (Fig. 4h); caudal tails long and held tightly appressed (Fig. 4f).

Fifth instar (Figures 5-6) n = 33; to 49 mm; 17-21 days including pre-pupa. Overall similar in shape to late fourth instar, more distinctly trapezoidal in cross-section; larvae somewhat variable in coloration between individuals, changing slowly with development (Fig. 5a-d) from greenish to pale brown; head similarly variable and showing same ontogenetic changes (Figs. 5e-h); early in stadia (Figs. 5a-c) larvae with complex counter-shading patterns, sometimes nearly absent by late in stadium (Figs. 5d, 6d), sometimes present to varying degrees (Figs. 6a-c); some individuals with dark lateral spot on A4 and indistinct dark chevron dorsolaterally on A8 (Fig. 5c); note that Figures 4b and 4c are from the same clutch; ground color of late stadium larvae varies from pale brown to red-brown to green (Fig. 6).

Pre-pupa (Figure 7a) n = 26; 2-3 days. Pre-pupal larvae similar in variation of coloration to fifth instars, overall patterns faded.

Pupa (Figures 7b, 8, 9a-c) n = 14; *ca*. 24 mm; 24-25 days. Pupae hang downward, shape angular with slightly keeled thorax and lateral keel running from head projections along dorsal edge of wing pads and onto abdomen; head with well-developed, forward oriented, conical projections; pupal ground color varies from green (Figs. 7b, 8b) to brown (Fig. 8a) according to larval coloration; regardless of ground color, patterning similar in all pupae; abdomen with pairs of dark spots subdorsally (Fig. 9a), lateral keel highlighted with dark and light markings, wing pads and venter with pale leaf-like markings, head projections dark at tips, yellowish basally (only in green specimens); cremaster similar to ground color of pupae, those of green specimens often yellowish, all with dark stripe dorsally (Fig. 9a).

Adult behavior: *Corades medeba* is one of the most abundant pronophiline butterflies at our study site. Adults are most frequently found along roads and open trails feeding on urine-enriched sand or dung (Fig. 9d). Males guard perches on or near large patches of *Chusquea* bamboo. They fly out and chase all passing butterflies, and even dragonflies and other large insects. When searching for ovipostion sites the flight of females is fast and erratic. They drop suddenly onto the host plant and oviposit by curling their abdomen under a leaf. They rarely or never appear to "test" host leaves by rapping their forelegs as seen in other nymphalids (DeVries 1987). Adults fly on most days, even in light rain, but are most common on sunny days.

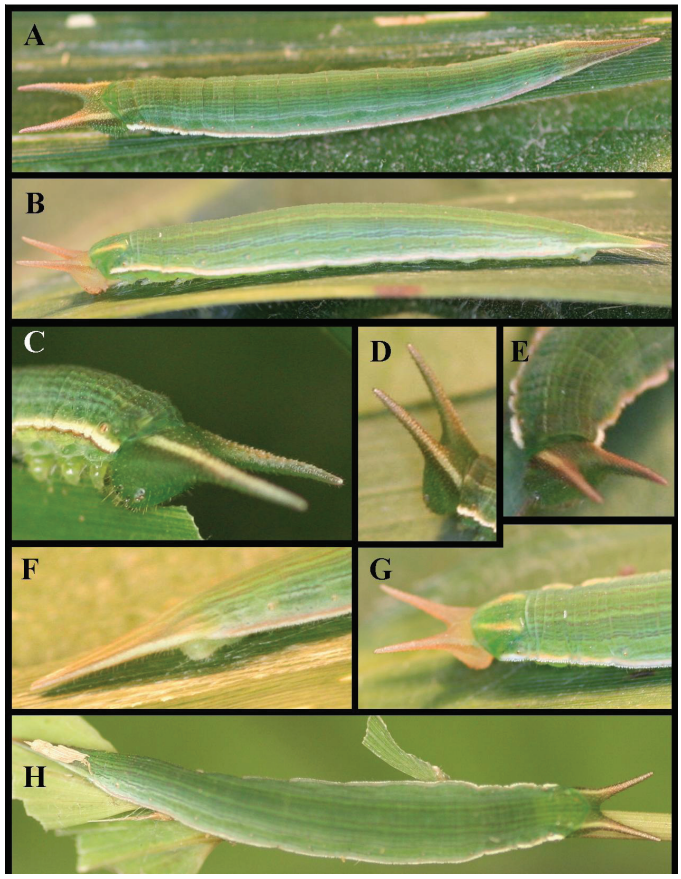


Fig. 4. Fourth instar larvae of *Corades medeba columbina* at Yanayacu Biological Station, Napo Province, 2150 m, Ecuador: **a)** mid-stadium larva; **b)** pre-molt larva; **c-e)** detail of larval head; **f)** detail of caudal tails; **g)** detail of pre-molt larval head and thorax; **h)** mature fourth instar.

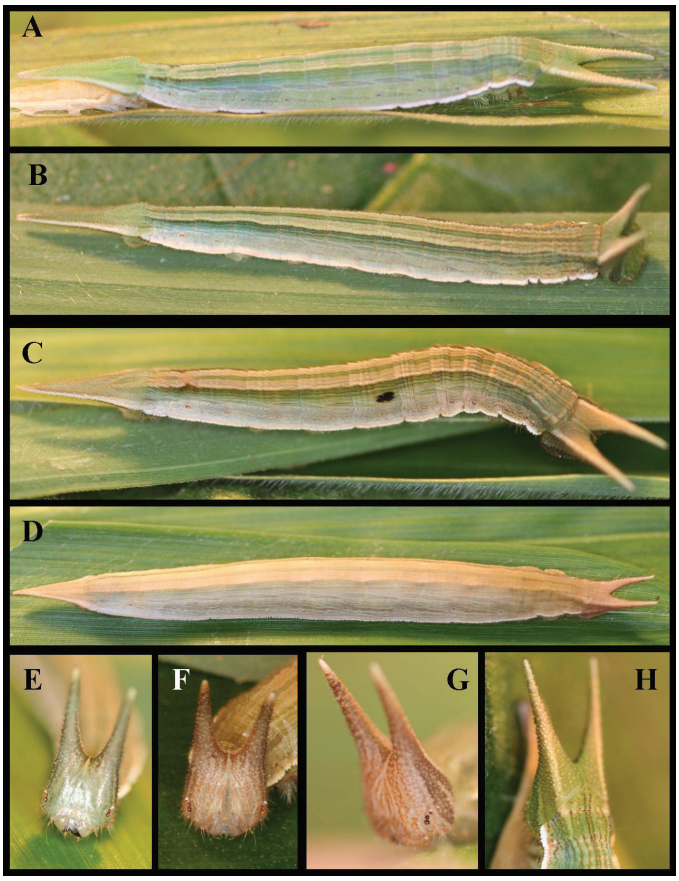


Fig. 5. Fifth instar larvae of *Corades medeba columbina* at Yanayacu Biological Station, Napo Province, 2150 m, Ecuador: **a)** recently molted larva; **b-c)** mid-stadium larvae; **d)** late-stadium larva; **f)** detail of larval head.

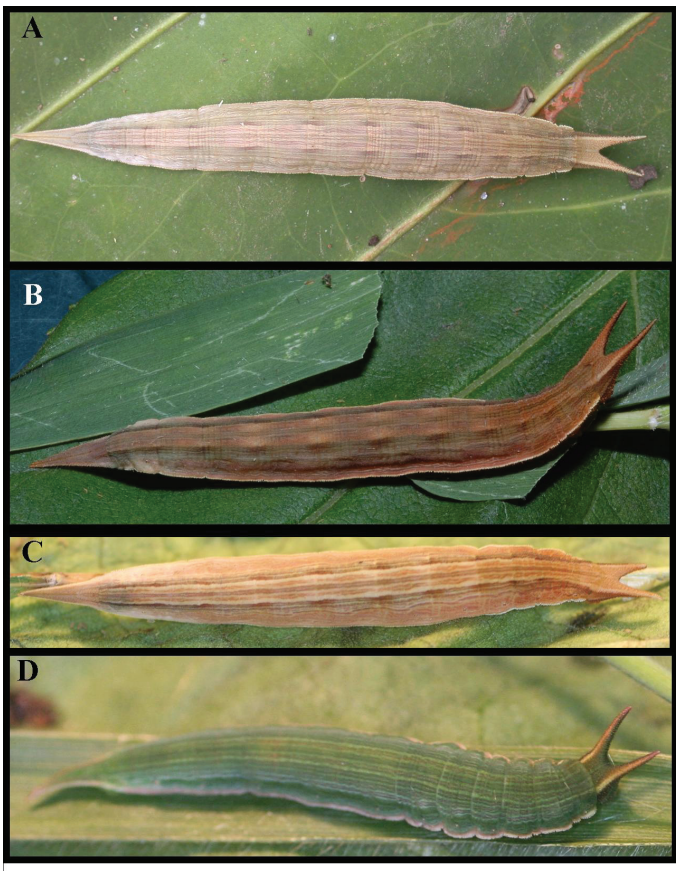


Fig. 6. Fifth instar larvae of *Corades medeba columbina* at Yanayacu Biological Station, Napo Province, 2150 m, Ecuador: **a-d)** mature larvae illustrating variation in coloration.

DISCUSSION

Few data are available on the early stages of any genus of Pronophilina and this is the first report of larval morphology for the genus *Corades*. Most genera of this subtribe use bamboos as larval food plants (Schultze 1929, DeVries 1987, Heredia & Viloria 2004; Beccaloni *et al.* 2008), and *C. medeba* is no exception. Schultze (1929), Pelz (1997), Heredia & Viloria (2004), and Greeney *et al.* (2009) describe the early stages of a few species of *Pedaliodes* Butler 1867. Larvae of *C. medeba* are distinct in having longer caudal tails which are held together rather than separated and head scoli which are much more produced and pointed than those of *Pedaliodes*. *Corades* larvae differ in similar ways from the larvae of *Daedalma* Hewitson 1858 described and illustrated by Pyrcz *et al.* (2010). Schultze (1929) also illustrates the last instar of *Lymanopoda samius* Westwood 1851, which has similarly well-developed head scoli and caudal tails which are held together. *Corades medeba*, however, lacks the long hairs and granulations present on the head of *Lymanopoda*. *Corades* also shares long caudal tails held together and long head scoli with the *Junea doraete* Hewitson 1858 larvae illustrated by Schultze (1929), but differs in having the head scoli separated rather than together.

The pupa of *C. medeba* is unique among described pronophiline pupae. It shares, with *Daedalma*, long projections on the head (Pyrcz *et al.* 2010). These projections are lacking in *Pedaliodes* and *Lymanopoda* (e.g. Schultze 1929, Greeney *et al.* 2009) and are tightly appressed into a single projection in *Junea* (Schultze 1929). While not as sculptured as pupae of *Daedalma*, those of *C. medeba* are more angular and robust than those described for other Pronophilina. The strong variation in coloration between individuals (final instars and pupae) of *C. medeba* is also a trait which has not been described in other Pronophilina. Sample sizes for most species, however, are limited, and it remains to be seen how coloration varies intra-specifically in other genera.

The phylogeny of the subfamily Satyrinae based on molecular data place *Corades* in a clade alongside *Junea, Pronophila,* and *Pseudomaniola* (Peña *et al.* 2006). *Mygona* and *Daedalma* were not included in this study; however their adult morphology indicates a close relationship with the genera belonging in the *Corades* clade (Pyrcz 2004; Pyrcz *et al.* 2010). The genus *Pedaliodes* (and related genera of the *Pedaliodes* complex) forms its sister clade, whereas *Lymanopoda* is shown to be rather distantly related to both groups. A preliminary comparison of the early stages supports a close relationship between *Corades, Junea,* and *Mygona,* all of which are united by the presence of fairly well-developed head scoli and dorso-ventrally flattened bodies (Schultze 1929; this study; unpubl. data), rather than to *Pedaliodes* or *Lymanopoda*. Both of these latter genera have bodies more rounded or square in cross-section, and though *Lymanopoda* possesses well developed head scoli, they are unique in their sculpturing and covering of

Fig. 7. Early stages of *Corades medeba columbina* at Yanayacu Biological Station, Napo Province, 2150 m, Ecuador: **a)** pre-pupal larva; **b)** pupa, ventral view.

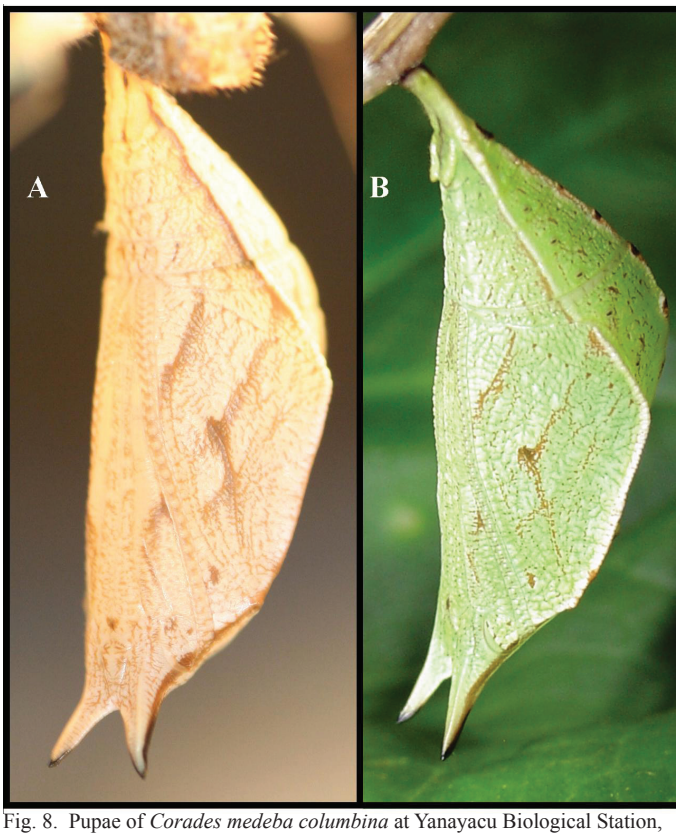


Fig. 8. Pupae of *Corades medeba columbina* at Yanayacu Biological Station, Napo Province, 2150 m, Ecuador: **a)** brown morph pupa; **b)** green morph pupa.

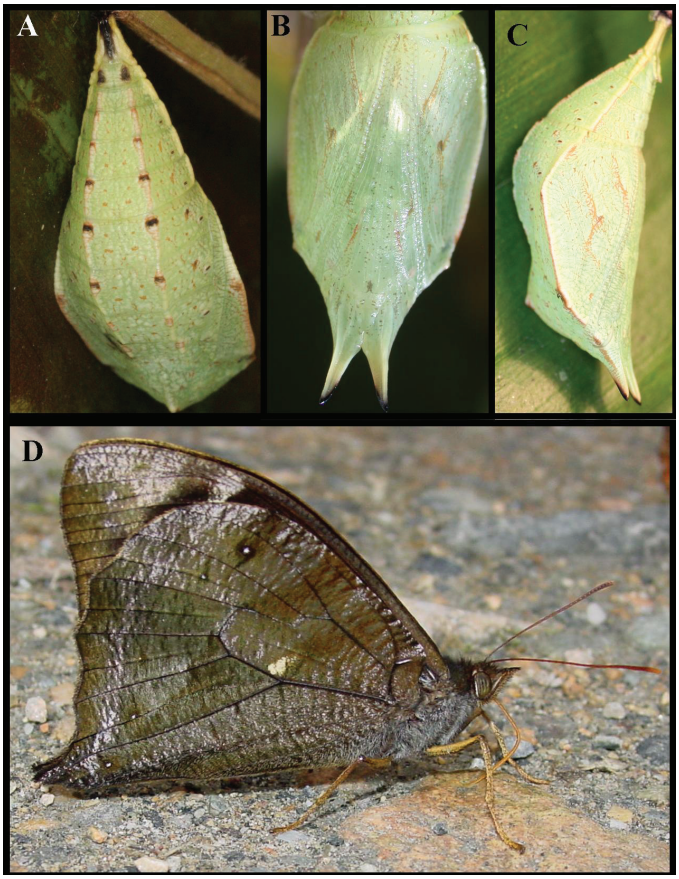


Fig. 9. Pupae and adult of *Corades medeba columbina* at Yanayacu Biological Station, Napo Province, 2150 m, Ecuador: **a-c)** green morph pupae; **d)** adult feeding at urine-enriched sand.

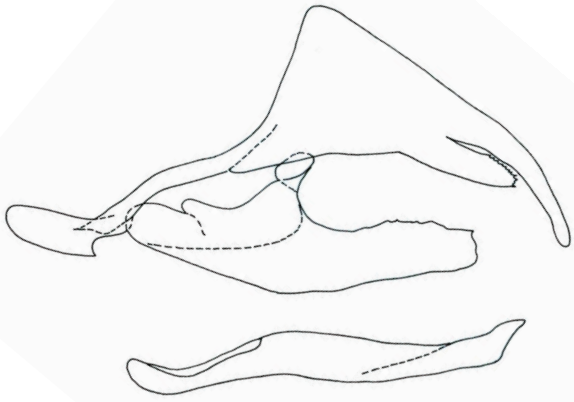


Fig. 10. Male genitalia of *Corades medeba*

long, stiff setae (Schultze 1929; unpubl. data).

As stated in the introduction, the monophyly of *Corades* is questionable in light of the lack of salient synapomorphies in adult morphology, with the exception of the "tailed hindwing." On the other hand, the male genitalia are much more heterogeneousin *Corades* than within other genera of Pronophilina such as *Daedalma* (Pyrcz *et al.* 2010), *Pronophila* (Pyrcz 1999) or *Lasiophila* (Pyrcz 1999). Based on male genitalia, *Corades* can be divided into two morphological groups. One is very cohesive and composed of *C. enyo* Hewitson*, C. iduna* Hewitson*, C. chelonis* Hewitson and *C. pax* Watkins, all recognized by short valves and massive uncus, and all sharing a roughly similar color pattern characterised by the presence of orange or reddish patches on the forewing. In contrast, the second group presents a wide array of color patterns and highly diverse male genitalia. The male genitalia of *Corades medeba* are unlike other congeners in various ways (Fig. 10), in particular the gnathos is extremely stout and has a serrate dorsal surface, and the valves are rectangular with a slightly irregular dorsal surface and a wide, blunt apex, while other *Corades* have elongated, in some cases very elongated, with acute apical endings. Both of these features are unique within the genus *Corades*. Thus, any additional data on the early stages of other species of *Corades,* particularly the *C. enyo* group, would be particularly useful in further testing the robustness of the two *Corades* clades suggested by genitalic differences.

Unfortunately, however, we lack larval descriptions for most genera of Pronophilina, and only when our knowledge is more complete will we be able to derive informative characters for testing phylogenetic hypotheses in this poorly known and hyper-diverse group. As larval morphology and behavior have helped eleucidate phylogenetic relationships in other groups (e.g., Brown & Freitas 1994; Freitas *et al.* 2002, Devries *et al.* 2004, Penz *et al.* 2006), we encourage others to publish information on the life histories of further Pronophilina.

ACKNOWLEDGMENTS

For assistance in the field, we thank Lucia Salazar, Wilmer Simbaña, and José Simbaña. HFG thanks John V. Moore, Matt Kaplan, and the Population Biology Foundation for financial support. This study was funded by grant # NSF DEB-0346729 and writing of the manuscript was funded in part by National Geographic Grant #W38-08. For continued support of our Neotropical natural history studies we thank the PBNHS. This is publication number 205 of the Yanayacu Natural History Research Group.

REFERENCES CITED

Beccaloni, G., A. L. Viloria, S. K. Hall & G. S. Robinson
2008. *Catalogue of the hostplants of the Neotropical butterflies*. The Natural History Museum, London 536 pp.

Brown, K. S., Jr. & A. V. L. Freitas
1994. Juvenile stages of Ithomiinae: overview and systematics (Lepidoptera: Nymphalidae). *Tropical Lepidoptera*, 5: 9-20.

DeVries, P. J.
1987. *The butterflies of Costa Rica and their natural history.* Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Princeton, New Jersey.

DeVries, P. J., B. Cabral & C. M. Penz
2004. The early stages of *Apodemia paucipuncta* (Riodinidae): myrmecophily, a new caterpillar ant-organ and consequences for classification. *Milwaukee Public Musem Contributions to Biology and Geology*, 102: 1-13.

Freitas, A. V. L., D. Murray & K. S. Brown Jr.
2002. Immatures, natural history and the systematic position of *Bia actorion* (Nymphalidae). *Journal of the Lepidopterists' Society*, 56: 117-122.

Greeney, H. F., T. W. Pyrcz, P. J. DeVries & L. A. Dyer
2009. The early stages of *Pedaliodes poesia* in eastern Ecuador (Lepidoptera, Nymphalidae, Satyrinae, Pronophilina). *Journal of Insect Science***,** 9: 34.

Heredia, M. D. & A. L. Viloria
2004. Description and life history of *Pedaliodes zingara*, a new satyrine species from Colombia (Nymphalidae). *Journal of the Lepidopterists' Society,* 58: 80-87.

Lamas, G., A. L.Viloria & T. W. Pyrcz
2004. Subtribe Pronophilina. Pp. 206-215 In: Lamas G. (ed.), *Atlas of Neotropical Lepidoptera, Checklist: Part 4A, Hesperoidea – Papilionoidea.* Association for Tropical Lepidoptera/Scientific Publishers, Gainesville, Florida.

Pelz, V.
1997. Life history of *Pedaliodes parepa* from Ecuador (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera*, 8: 41-45.

Peña, C., N. Wahlberg, E. Weingartner, U. Kodandaramaiah, S. Nylin, A. V. L. Freitas & A. V. Z. Brower
2006. Higher level phylogeny of Satyrinae butterflies (Lepidoptera: Nymphalidae) based on DNA sequence data. *Molecular Phylogenetics and Evolution*, 40: 29-49.

Penz, C. M., P. J. DeVries & L. Kirton
2006. Early stages of *Xanthotaenia busiris* (Lepidoptera, Nymphalidae), and the first report of a larval anal comb in the Nymphalidae. *Malayan Nature Journal*, 59: 51-61.

Pyrcz, T. W.
1999. Contributions to the knowledge of Ecuadorian Pronophilini, Part 2, The genus *Lasiophila*. *Genus*, 10(3): 479-495.

Pyrcz, T. W.
2004. Pronophiline butterflies of the highlands of Chachapoyas in northern Peru: faunal survey, diversity and distribution patterns (Lepidoptera, Nymphalidae, Satyrinae). *Genus*, 15: 455-622.

Pyrcz, T. W., H. F. Greeney, J. Wojtusiak & K. R. Willmott
2010. A survey of the genus *Daedalma* Hewitson with descriptions of new taxa and immature stages (Lepidoptera: Nymphalidae: Satyrinae). *Systematics and Biodiversity,* 8 (in press).

Pyrcz, T. W. & J. Wojtusiak
2002. The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along a elevational transect in Monte Zerpa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. *Global Ecology & Biogeography*, 11: 211-221.

Schulzte, A.
1929. Die erste Stande von drei kolumbischen hochandinen Satyriden. *Deutsche entomologische Zeitschrift Iris*, 43: 157-165.

Valencia, R. R.
1995. *Composition and structure of an Andean forest fragment in eastern Ecuador.* pp. 239-249. In: Churchill, S., H. Balslev, E. Forero, & J. L. Luteyn, (eds). *Biodiversity and conservation of Neotropical montane forests.* The New York Botanical Garden, New York.