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Exoskeleton Morphology of Three Species of Preponini, with Discussion of Morphological Similarities Among Neotropical Charaxinae (Lepidoptera: Nymphalidae)—I. Head, Cephalic Appendages, and Cervix

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The present study compares the morphology of the head, appendages, and cervical region of three species of the butterflies *Archaeoprepona demophon demophon* (Linnaeus, 1758), *Archaeoprepona licomedes licomedes* (Cramer, 1777), and *Prepona pylene pylene* Hewitson, [1854], through descriptions, illustrations, and scanning electron micrographs. The results are compared with *Prepona claudina annetta* (Gray, 1832), *Memphis moruus stheno* Hübner, [1819], and *Zaretis itys itylus* (Westwood, 1850), showing unique characteristics for each species and/or genus, or characteristics shared among the species analyzed. The detailed morphology of these three species was previously unknown.

Key words: adults, *Archaeoprepona*, comparative morphology, *Prepona*

INTRODUCTION

Charaxinae, one of the many subfamilies of Nymphalidae, contains approximately 400 species of butterflies in 28 genera and five tribes distributed worldwide, although they occur mostly in the tropics (Peña and Wahlberg, 2008; Aduse-Poku et al., 2009; Wahlberg et al., 2009). In the Neotropical region are three tribes: Anaeini, Anaeomorphini, and Preponini, with 109 species in 15 genera (Salazar and Constantino, 2001; Lamas, 2004; Salazar, 2008; Ortiz-Acevedo and Willmott, 2013). This group of butterflies includes some of the largest and most beautiful species, always among the favorites of collectors and curators (Miller and Miller, 1976). Specimens are customarily treated with great care, and any procedure that may damage the samples is generally avoided. Nonetheless, the detailed morphology of members of *Archaeoprepona* Fruhstorfer, 1915, a genus with quite common species, is completely unknown to date. Due to marked differences in the morphology of immatures and adults, and also in habitats, this subfamily has been placed at different levels of classification, including as a separate family (Rydon, 1971). Ehrlich (1958a) considered the morphological pattern of Charaxinae as anomalous compared to other nymphalids, although the current classification as a subfamily of Nymphalidae is widely accepted (Harvey, 1991; Freitas and Brown, 2004; Wahlberg et al., 2005; Heikkilä et al., 2011). This subfamily is supported by several synapomorphies, such as: sclerotized parapatagia; hindwing discal cell closed by a nontubular vein; veins R₄ and R₅ larger than their common branch; and R₄ curved

downward (Ehrlich, 1958b; Ackery, 1984; Mielke et al., 2004a, b, c).

Although the taxonomy of Preponini has been the focus of many studies (Rydon, 1971; Descimon, 1977; Llorente-Bousquets et al., 1992; Salazar, 1999), few have examined the morphology of these butterflies in detail. One of the most conclusive studies was the recent phylogenetic analysis based on DNA sequences, by Ortiz-Acevedo and Willmott (2013), which resulted in some important taxonomic changes. In order to complement existing information for understanding the morphological differentiation of the tribe, we illustrated, described, and compared the detailed morphology of three species. This is the first of three contributions; the next (second) will treat the thorax, and the third the abdomen and genitalia. The general aim was to complement recent studies that are based only on DNA sequences, and to help to fill the lacuna of basic studies that can expand our knowledge of the systematics of this group of butterflies.

MATERIALS AND METHODS

For the morphological studies we used specimens of both sexes of *Archaeoprepona demophon demophon* (Linnaeus, 1758) (Fig. 1), from Santa Isabel do Pará, state of Pará, Brazil (01°18'12"S, 48°09'04"W); *Archaeoprepona licomedes licomedes* (Cramer, 1777) (Fig. 2) from the Reserva Experimental Catuaba, Senador Guimard, state of Acre, Brazil (10°04'41"S, 67°37'25"W); and *Prepona pylene pylene* Hewitson, [1854] (Fig. 3) from Britador, Turvo, state of Paraná, Brazil (25°02'11"S, 51°32'17"W). The vouchers are deposited in the Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil. These species were chosen because of the adequate amount of material available in this collection, and for this reason, different numbers of males and females were analyzed.

Head and appendages were boiled in a 10% potassium hydroxide (KOH) solution to soften the structures and facilitate removal of

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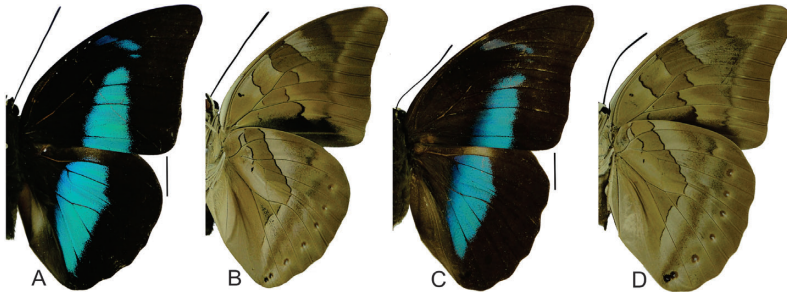


Fig. 1. *Archaeoprepona demophon demophon* (Linnaeus, 1758). (A) Male, dorsal view; (B) male, ventral view; (C) female, dorsal view; (D) female, ventral view. Scale bar: 1 cm.



Fig. 2. *Archaeoprepona licomedes licomedes* (Cramer, 1777). (A) Male, dorsal view; (B) male, ventral view; (C) female, dorsal view; (D) female, ventral view. Scale bar: 1 cm.

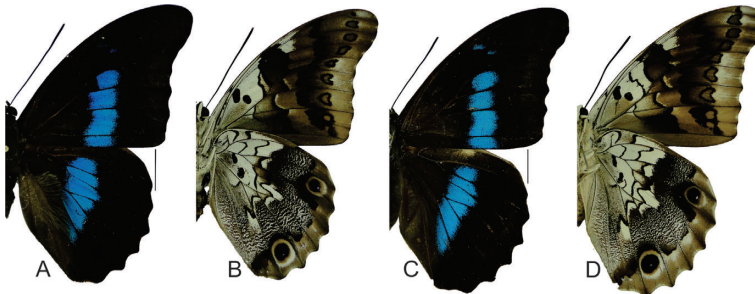


Fig. 3. *Prepona pylene pylene* Hewitson, [1854]. (A) Male, dorsal view; (B) male, ventral view; (C) female, dorsal view; (D) female, ventral view. Scale bar: 1 cm.

the scales. Illustrations were made with a stereoscopic microscope coupled to a camera lucida. Further details of some structures were obtained using scanning electron micrographs, following the standard procedures of Kaminski et al. (2008) and Leite et al. (2010). The terminology used follows Ehrlich (1958a, b), Casagrande (1979), Mielke et al. (2004a), and Kawahara et al. (2012).

The results are compared with those of other studies of the same nature performed for the Preponini and Anaeni (Table 1), using the morphological drawings and descriptions in those articles. The species compared were: *Prepona claudina annetta* (Gray, 1832) (Mielke et al., 2004a), as a species of Preponini; and *Memphis moruus sthenos* Hübner, [1819] (Dias et al., 2010) and *Zaretis itys itylus* (Westwood, 1850) (Mielke et al., 2004a), as representatives of Anaeni.

RESULTS

Archaeoprepona demophon demophon (Linnaeus, 1758) (Fig. 1)

In anterior view (Fig. 4A), head with compound eyes gla-

brous and anterolaterally prominent, higher than wide, ocelli absent. Paraocular area narrow between ocular margin and laterofacial suture separating this area from frontoclypeal region. Frontoclypeus quadrangular; transfrontal sulcus with slight dorsal projection; anterior tentorial pit opening approximately at ventral fourth of this sclerite, contiguous with an invagination of integument; transclypeal suture absent. Labrum broad, twice as wide as high, transverse, delimited by clypeolabral boundary. Pilifers triangular, with setae directed toward base of galeae. Epipharynx located internally between galeae.

In dorsal view (Fig. 4B), antennal sclerite occupying about 1/3 of antennal alveolus space; chaetosemata inconspicuous.

In posterior view (Fig. 4C), postgena occupying most of posterior area of head, covered with short translucent setae. Occiput triangular, four times wider than high. Postocciput separated from occiput by postoccipital sulcus, this sulcus surrounding dorsal occipital foramen, forming small median flap. Dorsal occipital foramen medially divided by tentorial bridge into two parts: dorsal foramen, ellipsoidal, dorsally dentate; and ventral foramen, ellipsoidal and with dorsal projection.

In lateral view (Fig. 6A), compound eye prominent, frontoclypeus projected; occipital area slightly projected.

Antenna (Figs. 7A, 9A) clubbed, tricarinate, without sexual dimorphism, and with 60 flagellomeres. Scape dilated and with antennal organ, other flagellomere slightly conical and wider at apex. Club formed from 49th flagellomere on; three carinae arising from 5th and extending to last flagellomere.

Hypostomal bridge (Fig. 4D) triangular, little sclerotized, posteriorly larger and narrowing between stipes. Galeae (Fig. 6A) four times longer than height of head; basiconic sensilla in apical region. Stipes (Fig. 4D) elongated, with

different degrees of sclerotization, and with median folds. Cardio (Fig. 4D) subcircular.

Labial palp (Figs. 8A, B, 9D, G) trisegmented, basal segment robust, with sensory Reuter's organ on its inner face, middle segment slightly sinuous and long, four times longer than basal segment, distal segment 1/5 size of middle segment and with sensory vom Rath organ, as an invagination of its apex.

Cervical sclerite (Fig. 8G) possibly of mixed origin, mostly membranous, articulating anteriorly with head and posteriorly with prothorax, having flat "T"-shape, with vertical and horizontal portions of similar size and smooth angles. Cervical organ on ventral face of sclerite covered with setae.

Archaeoprepona licomedes licomedes (Cramer, 1777) (Fig. 2)

Head in anterior view with morphological pattern similar to *A. d. demophon* (Fig. 5A), with the following differences:

Table 1. Morphological differences among species of neotropical Charaxinae.

Characters	<i>Archaeoprepona d. demophon</i>	<i>Archaeoprepona l. licomedes</i>	<i>Prepona p. pylene</i>	<i>Prepona claudina annetta</i>	<i>Memphis moruus sthenos</i>	<i>Zaretis itys itylus</i>
Frontoclypeus	Quadrangular	Quadrangular	Rectangular	Rectangular	Trapezoidal, wider dorsally	Quadrangular
Transfrontal suture	Slight dorsal projection	Slight dorsal projection	Slight dorsal projection	Truncated	Lightly depressed	Lightly depressed
Transclypeal suture	Absent	Absent	Present	Present	Present	Present
Labrum	Broad, twice as wide as high	Narrow, four times as wide as high	Narrow and tiny, three times as wide as high	Narrow, four times as wide as high	Narrow, four times as wide as high	Narrow, four times as wide as high
Pilifers	Triangular	Discoidal	Triangular	Rectangular	Semioval	Straight
Size of antennal sclerite relative to antennal alveolus	1/3	1/4	1/5	1/4	1/3	1/3
Postgenal setae	Present	Present	Present	Absent	Absent	Absent
Dorsal occipital foramen	Ellipsoidal, dorsally dentate	Ellipsoidal, internal dorsal projection	Triangular	Ellipsoidal	Trapezoidal, wider ventrally	Pentagonal
Ventral occipital foramen	Ellipsoidal	Semicircular	Semicircular	Ellipsoidal	Trapezoidal, wider ventrally	Pentagonal
Basiconic sensillae on the galea	Present	Present	Present	Present	Present	Present
Number of flagellomeres (average)	60	59	54	60	46	46
Antennal organ on the scape	Present	Present	Present	Present	Present	Present
Flagellomere where the antennal carinae begin	5	5	1	5	5	6
Cervical sclerite	Flat T-shape, with vertical and horizontal portions of similar size and smooth angles	Flat T-shaped, with sub-triangular base	Flat T-shaped, with membranous median portion	Flat T-shaped, with dorsal and ventral portion of the same size	Flat T-shaped	Flat "T" shaped, with smaller base

frontoclypeus quadrangular, labrum narrow, four times as wide as high, and pilifers with discoidal appearance. In dorsal view (Fig. 5B), antennal sclerite occupying about 1/4 of antennal alveolus. In posterior view (Fig. 5C), occiput triangular, three times wider than high. Dorsal occipital foramen ellipsoidal and with dorsal projection, ventral occipital foramen semicircular. In lateral (Fig. 6B) and ventral view (Fig. 5D), head with pattern similar to *Archaeoprepona d. demophon*.

Antenna (Figs. 7B, 9B) similar to *A. d. demophon*, but with 59 flagellomeres and club formed from 43rd flagellomere on.

Labial palp (Figs. 8C, D, 9E, H) with middle segment five times longer than basal segment.

Galeae (Fig. 6B) similar to *A. d. demophon*, four times longer than height of head, with basiconic sensilla in apical region.

Cervical sclerite (Fig. 8H) shaped as flat "T", with subtriangular base. Cervical organ similar to *A. d. demophon*.

***Prepona pylene pylene* Hewitson, [1854] (Fig. 3)**

Head in anterior view with morphological pattern similar to *A. d. demophon* and *A. l. licomedes* (Fig. 5E), with the following differences: frontoclypeus rectangular, transclypeal suture present; labrum narrow and tiny, three times as wide

as high, and pilifers triangular. In dorsal view (Fig. 5F), antennal sclerite occupying about 1/5 of antennal alveolus space. In posterior view (Fig. 5G), occiput triangular, three times wider than high; dorsal foramen triangular and ventral foramen semicircular. In lateral (Fig. 6C) and ventral view (Fig. 5H), head with a pattern similar to *A. d. demophon* and *A. l. licomedes*. Galeae (Fig. 6C) three times longer than height of head.

Antenna (Figs. 7C, 9C) similar to that of *A. l. licomedes* and *A. d. demophon*, with 54 flagellomeres; club formed from 41st flagellomere on, with three carinae arising from 1st and extending until last flagellomere.

Labial palp (Figs. 8E, F, 9F, I), middle segment three times longer than basal segment, and apical segment 1/6 length of middle segment.

Galeae (Fig. 6C) similar to *A. d. demophon*.

Cervical sclerite (Fig. 8I) with flat "T" shape, right angles, membranous median portion, and triangular base articulating with thorax. Cervical organ similar of *A. l. licomedes* and *A. d. demophon*.

Intraspecific variation

Males and females showed very few differences, consisting of variations in the size of the specimen, and in consequence, the tagma. Naturally, all females were larger than the

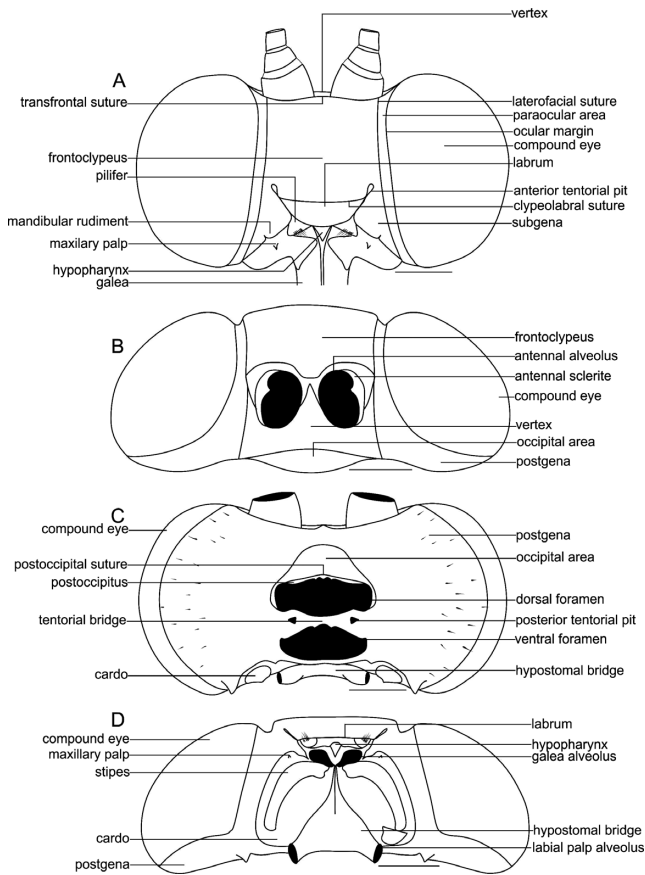


Fig. 4. Head of *Archaeoprepona demophon demophon* (Linnaeus, 1758). (A) Anterior view; (B) dorsal view; (C) posterior view; (D) ventral view. Scale bars: 1 mm.

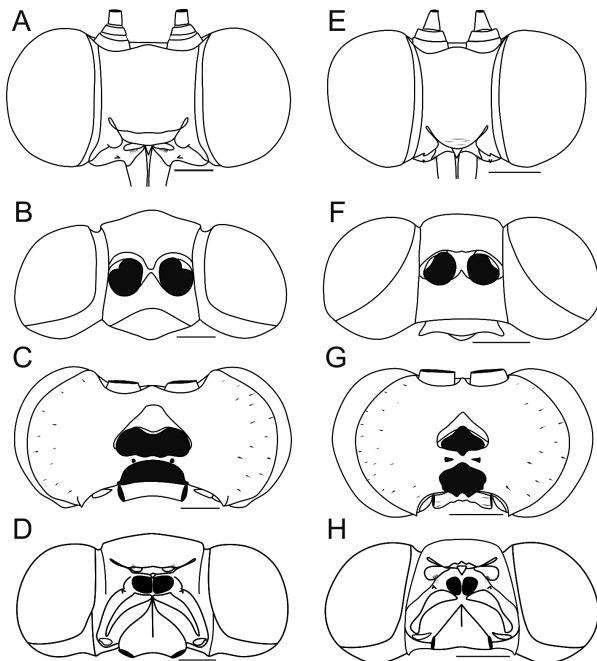


Fig. 5. Head; (A–D) *Archaeoprepona licomedes licomedes* (Cramer, 1777); (E–H) *Prepona pylene pylene* Hewitson, [1854]; (A), (E) anterior view; (B), (F) dorsal view; (C), (G) posterior view; (D), (H) ventral view. Scale bars: 1 mm.

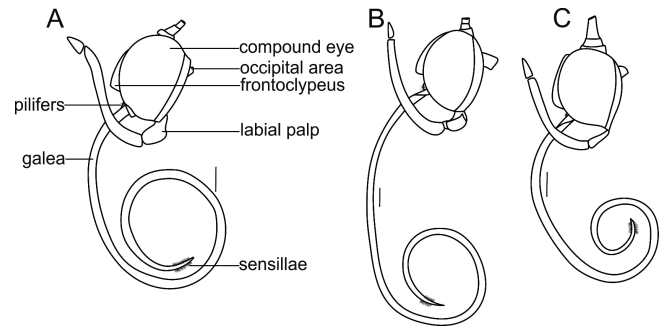


Fig. 6. Lateral view of head; (A) *Archaeoprepona demophon demophon* (Linnaeus, 1758); (B) *Archaeoprepona licomedes licomedes* (Cramer, 1777); (C) *Prepona pylene pylene* Hewitson, [1854]. Scale bar: 1 mm.

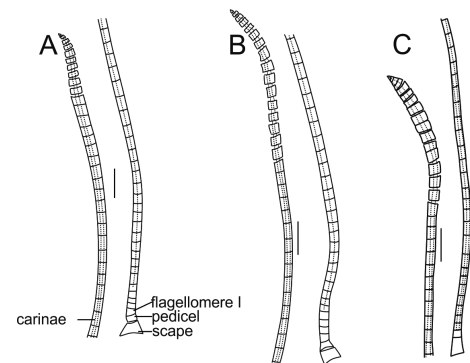


Fig. 7. Antenna; (A) *Archaeoprepona demophon demophon* (Linnaeus, 1758); (B) *Archaeoprepona licomedes licomedes* (Cramer, 1777); (C) *Prepona pylene pylene* Hewitson, [1854]. Scale bar: 1 mm.

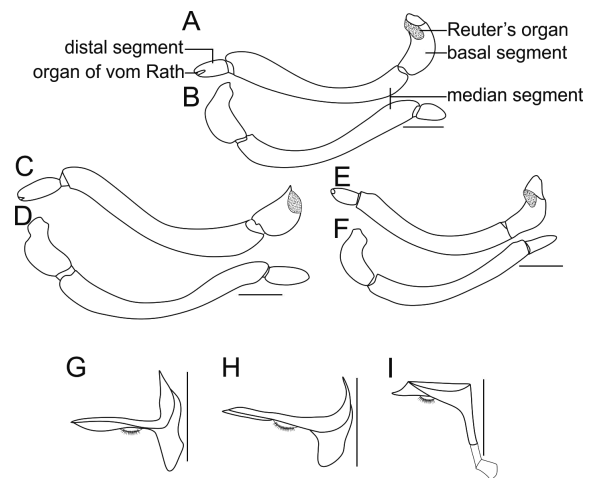


Fig. 8. (A–F) Labial palp; (A), (C), (E) internal view; (B), (D), (F) external view; (G–I) cervical sclerite; (A), (B), (G) *Archaeoprepona demophon demophon* (Linnaeus, 1758); (C), (D), (H) *Archaeoprepona licomedes licomedes* (Cramer, 1777); (E), (F), (I) *Prepona pylene pylene* Hewitson, [1854]. Scale bar: 1 mm.

males. Fifteen males and seven females of *Archaeoprepona d. demophon*, 13 males and five females of *Archaeoprepona l. licomedes*, and 15 males and five females of *Prepona p.*

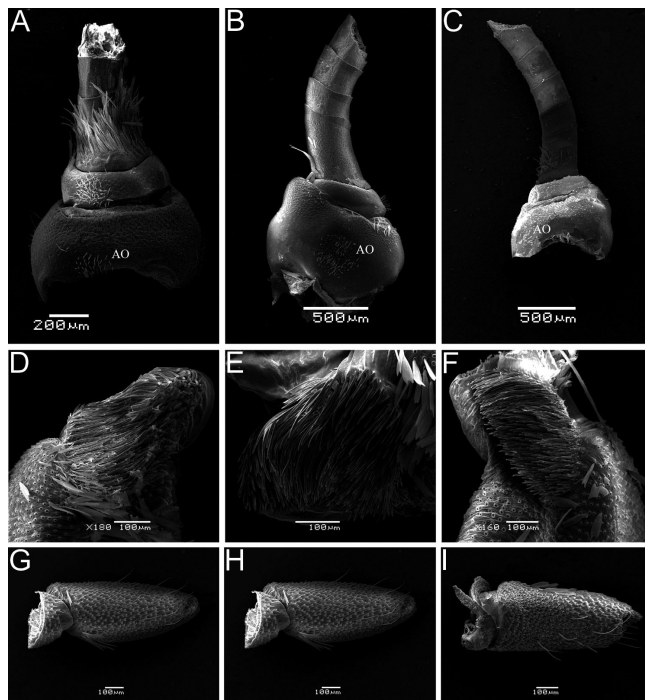


Fig. 9. (A–C) Antennal organ on the scape (AO); (D–F) Reuter's organ; (G–I) distal segment and organ of vom Rath. (A), (D), (G) *Archaeoprepona demophon demophon* (Linnaeus, 1758); (B), (E), (H) *Archaeoprepona licomedes licomedes* (Cramer, 1777); (C), (F), (I) *Prepona pylene pylene* Hewitson, [1854].

pylene were examined.

DISCUSSION

The head and cephalic appendages showed a morphological pattern with minor differences among the species. These observations demonstrate that the use of this tagma by itself may be inappropriate for diagnoses of species, and furthermore for a detailed analysis such as in this study, because it requires extensive dissections that cause irreversible damage to the specimen.

The most characteristic morphological pattern among the neotropical Charaxinae was found in *Prepona p. pylene*, involving the antennal carinae originating from the basal flagellomere and the shape of the cervical sclerite. These characters also distinguish *P. p. pylene* from *Prepona claudina annetta*.

However, some characters are shared among species, suggesting that these characters can be used to diagnose genera. In the case of *Archaeoprepona*, these are the quadrangular shape of the frontoclypeus and the absence of the transclypeal suture. Similarly, in *Prepona* the rectangular shape of the frontoclypeus is shared by *P. p. pylene* and *P. claudina annetta*.

The species of Preponini examined here bear translucent setae on the postgena. However, *P. claudina annetta* does not have these setae, or perhaps because of their diminutive size these setae were not illustrated or included in the original descriptions. Even so, the shape of the labial palps easily distinguishes between species of Anaeini and Preponini, as described by Rydon (1971); straight palps are

common among the species of Preponini and “S”-shaped palps are common among the species of Anaeini. All species of Preponini analyzed herein showed the characteristic palp of the tribe. However, Mielke et al. (2004a) illustrated a straight palp for *Zaretis itys itylus*, even describing it as S-shaped. Therefore, an S-shaped palp cannot be assumed for all species of Anaeini, and therefore the shape of the palps is not a reliable character to distinguish these two tribes.

Based on the present results, Anaeini and Preponini have few characteristics in common, although the synapomorphies of the subfamily are very clear and well supported. Within Anaeini, the species analyzed often show the same morphological pattern, for example, 46 flagellomeres in the antenna, which in Preponini is a widely varying character. However, only two species were analyzed, and thus we cannot assert whether this is a case of simple coincidence or if Anaeini has a very stable morphological pattern of the head with only minor variations, leaving this question as a suggestion for future studies.

The presence of basiconic sensilla on the apical portion of the galea and the antennal organ on the scape are common characters among the species of neotropical Charaxinae analyzed herein. These morphological differences can be compared with other Nymphalidae, such as Biblidinae, Morphinae, Danainae, Heliconiinae, and Ithomiinae, which do not exhibit any of these characteristics (Leite et al., 2013). Unfortunately, comparisons with the third tribe of neotropical Charaxinae, Anaeomorphini, cannot be made, because the morphology of members of this tribe has not been studied.

The other two tagmata, the thorax and abdomen of Charaxinae and Preponini, are better studied, because they concentrate the most important characters for taxonomy. The importance of this is indicated by the number of characters or character sets that are synapomorphies of Charaxinae (Ehrlich, 1958b; Ackery, 1984), or the character set that diagnoses species of this subfamily (Mielke et al., 2004a, b, c; Dias et al., 2012; Bonfanti et al., 2013). In any event, this is the first study focused on analyzing a poorly known part of the body, and also indicated some potentially useful characteristics for taxonomy, phylogeny or meriting further exploration in other kinds of studies. The two subsequent contributions on the morphology of the thorax and abdomen of Preponini will define more efficient or more easily observed characters for use in the diagnosis of the species, and will complement these results and extend our knowledge of the unique morphology of these spectacular butterflies.

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