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Exoskeleton Morphology of Three Species of Preponini, with Discussion of Morphological Similarities Among Neotropical Charaxinae (Lepidoptera: Nymphalidae)—II. Thorax and Thoracic Appendages

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The present report, the second part of a study of the external morphology of Preponini, compares the thorax and thoracic appendages of *Archaeoprepona demophon demophon* (Linnaeus, 1758), *Archaeoprepona licomedes licomedes* (Cramer, 1777) and *Prepona pylene pylene* Hewitson, [1854], through descriptions and illustrations. The results are compared with three other species, *Prepona claudina annetta* (Gray, 1832), *Memphis moruus sthenos* Hübner, [1819] and *Zaretis itys itylus* (Westwood, 1850), revealing previously unrecognized similarities among species of Charaxinae.

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

INTRODUCTION

This is the second contribution to a series of detailed studies on the exoskeletons of *Archaeoprepona demophon demophon* (Linnaeus, 1758), *Archaeoprepona licomedes licomedes* (Cramer, 1777), and *Prepona pylene pylene* Hewitson [1854]. The first part consisted of the comparative morphology and analysis of the head, cephalic appendages and cervical sclerite (Bonfantti et al., 2015).

MATERIALS AND METHODS

The material analyzed in this study was the same as that used in the first contribution, as well as for the preparation of body structures and illustrations (Bonfantti et al., 2015). However, the methodology for preparing the wings differs. These were removed and cleared by immersion first in 70% ethanol, then in a sodium hypochlorite (NaOCl) solution until completely cleared, and then again in 70% ethanol to neutralize the action of the sodium hypochlorite, after which they were dried on absorbent paper.

The characters compared are presented in Table 1, together with characters of the other three species: *Prepona claudina annetta* (Gray, 1832) (Mielke et al., 2004) as a representative of Preponini; and *Memphis moruus sthenos* Hübner, [1819] (Dias et al., 2010) and *Zaretis itys itylus* (Westwood, 1850) (Mielke et al., 2004), as representatives of Anaeni.

The terminology used follows other morphological studies, such as those of Ehrlich (1958), Casagrande (1979), Mielke et al. (2004), Dias et al. (2010), and Kawahara et al. (2012).

RESULTS

Archaeoprepona demophon demophon (Linnaeus, 1758)
Prothorax. In dorsal view (Fig. 1A), subtriangular pronotum

visible. Patagia globular, internally articulated with pronotum; parapatagium sclerotized, elongated, about four times as long as wide, and inserted between membranes.

In lateral view (Fig. 2A), episternum reduced; proepisternum with slight anterior projection. Coxa occupying most of space in lateroventral part of prothorax.

In ventral view (Fig. 3A), proepisternum bilobate. Episternum laterally delimited by patagium between proepisternum and coxal alveolus. Furca originating at base of prothoracic coxae, articulating with spinasternum forming inverted “Y” shape.

Mesothorax. In dorsal view (Fig. 1A), prescutum wide, triangular, occupying whole anterior margin of scutum; latter being subrectangular, medially divided by mesoscutal line. Externally, suralare triangular with apical projection. Scutellum projected, lozenge-shaped with median and anterolateral projections, situated posterior to scutum and separated by mesoscutoscutellar sulcus. In lateral view (Fig. 2A), prealar process elongated and anteroventral to subtegula. Ventrally, basalare subtriangular. Adnotal projecting as long ventral lobe of postalar plate, situated posterior to suralare, and fused to scutum. Subalare narrow and irregularly shaped. Posteriorly, axillary cord originating from postnotum, and projecting over laterophragma. Anepisternum situated ventral to subalare, articulating ventrally to proepisternum; latter being completely separated from katepisternum by preepisternal suture. Epimeron divided into three different parts by dorsal and ventral sutures; anterior sclerite called proepimeron. Basisternum located ventral to proepimeron, articulating with eucoxa and meron.

In ventral view (Fig. 3A), proepisternum narrow. Spinasternum I articulating with basisternum; the latter in turn articulating with proepimeron. In ventral view, meron being the largest of mesothoracic sclerites, separated from eucoxa by

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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>
Shape of parapatagium	Elongated, four times as long as wide	Elongated, three times as long as wide	Narrow, seven times as long as wide	Elongated, three times as long as wide	Narrow, nine times as long as wide	Narrow, nine times as long as wide
Shape of spinasternum I	Inverted "Y"	Subtriangular	Subtriangular	Inverted "Y"	Subtriangular	Subtriangular
Size and shape of prescutum II	Large and triangular	Large and lozenged	Small and triangular	Small and triangular	Small and triangular	Small and lozenged
Prescutum II in relation to scutum II	Occupying the entire anterior margin	Occupying the median portion of the anterior margin	Occupying the median portion of the anterior margin	Narrow, four times as wide as high	Occupying the median portion of the anterior margin	Occupying the median portion of the anterior margin
Shape of scutum II	Subrectangular	Hourglass	Subrectangular with bulged outer margin	Subrectangular	Subrectangular with bulged outer margin	Ellipsoidal
Shape of scutellum II	Lozenged with median and anterolateral projections	Lozenged with median and anterolateral projections	Semicircular with antero-median salience	Lozenged with median and anterolateral projections	Half moon	Lozenged with median and anterolateral projections
Shape of basalare II	Subtriangular	Subquadrangular	Elongated	Subquadrangular	Subquadrangular	Irregular
Preepisternal suture	Complete	Incomplete	Complete	Incomplete	Incomplete	Incomplete
Divisions of epimeron II	Three parts	Three parts	Three parts	Three parts	Two parts	Two parts
Epimeral lobe II	Absent	Absent	Present	Absent	Absent	Absent
Extension of mesothoracic discrimen	To the basisternum II	To the furcal pit	To the furcal pit	To the furcal pit	To the furcal pit	To the furcal pit
Median conformation of scutum III	Divided	Divided	Narrowed	Divided	Divided	Divided
Shape of scutellum III	Subtriangular	Trapezoidal	Elongated	Trapezoidal	Trapezoidal	Trapezoidal
Shape of scutum III	Cordate	Cordate	Subtriangular	Triangular	Triangular	Quadrangular
Shape of katepisternum III	Four times as long as wide	Five times as long as wide	Two times as long as wide	Four times as long as wide	Three times as long as wide	Four times as long as wide
Divisions of epimeron III	Two parts	Two parts	Undivided	Three parts	Undivided	Three parts
Inclination of coxal suture III	Oblique	Oblique	Transverse	Transverse	Transverse	Oblique
External margin of forewing	Straight and concave along the median third	Straight and concave along the median third	Straight and concave along the median third	Convex along superior and inferior thirds and concave along the middle third	Concave along the anterior and convex along the posterior halves, after M ₃	Concave along the superior three-fourths and convex along the inferior fourth
Bifurcation of R ₁ and R _s , in the forewing	Distal third of discal cell	Distal third of discal cell	Middle third of discal cell	Distal third of discal cell	Anastomosis of R ₁ and R ₂ + R ₃	Distal third of discal cell
Bifurcation of R ₂ and R ₃ , R ₄ + R ₅	Apex of discal cell	Distal third of discal cell	Distal third of discal cell	Distal third of discal cell	Anastomosis of R ₂ and R ₃	Distal third of discal cell
dcu vein in forewing	Nontubular	Nontubular	Nontubular	Tubular	Tubular	Tubular
Odoriferous scales	Present	Present	Present	Present	Absent	Absent
Conformation of odoriferous scales	Scales long and parallel to venation	Scales long and parallel to venation	Scales short and perpendicular to venation	Scales short and perpendicular to venation	—	—

coxal suture, delimiting alveolus of trochanter. Discrimen extending longitudinally to basisternum.

Metathorax. In dorsal view (Fig. 1A), metathorax divided

into scutum and scutellum, separated by scutoscuteellar suture. Scutum medially divided by scutellum, forming two subtriangular areas. Scutellum subtriangular.

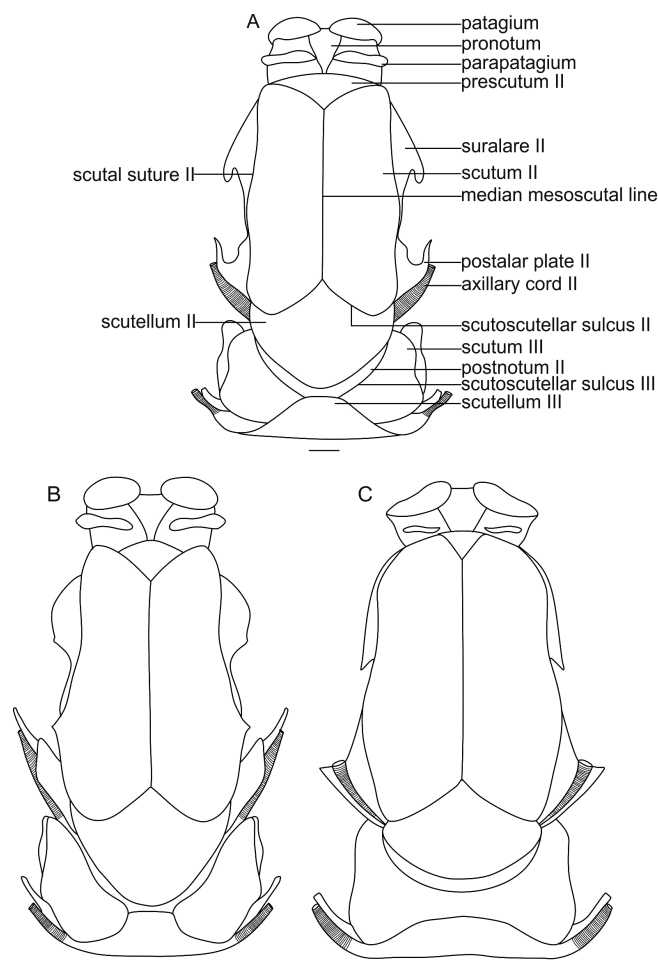


Fig. 1. Thorax, dorsal view; **(A)** *Archaeoprepona demophon demophon* (Linnaeus, 1758); **(B)** *Archaeoprepona licomedes licomedes* (Cramer, 1777); **(C)** *Prepona pylene pylene* Hewitson, [1854]. Scale bars: 1 mm.

In lateral view (Fig. 2A), cordate scutum completely separated from suralare by scutal suture; scutellum extending ventrolaterally to form axillary cord, which extends out over notal process of hindwing. Postnotum projected posteroventrally to scutellum. Subalare narrow, located in center of pleural membrane. Sternopleura divided by pleural suture into episternum and epimeron. Episternum divided into three regions, anepisternum, katepisternum, and basisternum. Anepisternum subcircular, lightly sclerotized, and having long setae. Katepisternum elongate, approximately four times as long as wide, and being separated from epimeron by pleural suture. Epimeron divided by dorsal suture.

In ventral view (Fig. 3A), basisternum appearing as subtriangular plate, anterior to metathoracic coxae. Meron separated from eucoxa by coxal suture.

Thoracic appendages. Tegula (Fig. 4A), being protruded, mobile projection of mesothorax, projected at height of subtegula; latter being subtriangular in shape, having laterodorsal projections covering suralare II.

Axillary sclerites (Fig. 5A) articulating wings with thorax through three sclerites. In mesothorax, first axillary II articulating distally with sclerites of second axillary II; latter in turn articulating distally with basal process of subcostal II; third

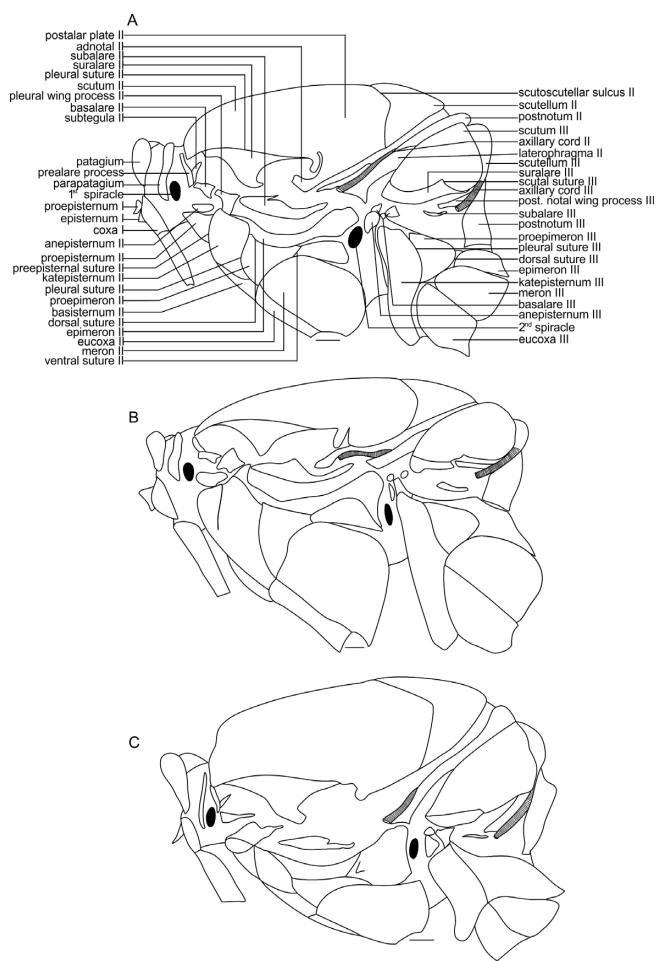


Fig. 2. Thorax, lateral view; **(A)** *Archaeoprepona demophon demophon* (Linnaeus, 1758); **(B)** *Archaeoprepona licomedes licomedes* (Cramer, 1777); **(C)** *Prepona pylene pylene* Hewitson, [1854]. Scale bars: 1 mm.

axillary II being in contact with base of anal veins. In metathorax, first axillary III articulating distally with second axillary III; latter in turn articulating with basal process of subcostal vein; third axillary III being in contact with anal veins.

Forewing (Fig. 6A) subtriangular in both sexes. Outer margin straight, but concave along median third; costal margin convex throughout its length, and inner margin straight; subcostal (Sc) initiating in axillary region, thicker at base, ending along distal third of costal margin; narrow radial (R) appearing along and parallel to Sc; upon reaching end of distal third of discal cell, R forking into R_1 and R_5 (R_2 , R_3 , R_4 and R_5); R_2 , R_3 , and branch of $R_4 + R_5$ bifurcating at apex of discal cell soon after this, R_3 bifurcating from branch of $R_4 + R_5$; R_2 ending on costal margin of wing, R_3 at apex, and R_4 and R_5 on outer margin. Final third of R_4 curving downward. Veins dcs and dcm tiny, while dci appearing as non-tubular vein. M_1 and M_2 running separately from upper region of discal cell; M_3 separated from M_1 and M_2 by inferior region of discal cell, together with inferior end of dci. CuA_1 and CuA_2 being parallel to outer margin, CuA_1 originating near base of M_3 , and CuA_2 originating from median third of cubital vein; 2A, only anal vein, being parallel to

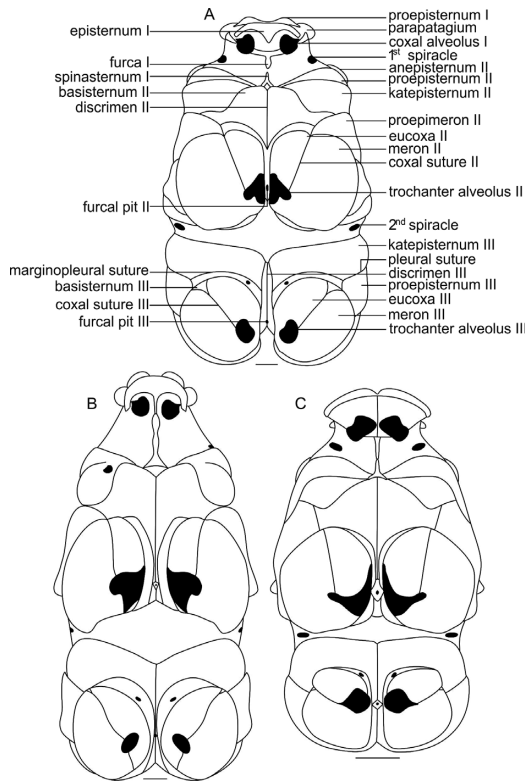


Fig. 3. Thorax, in ventral view; **(A)** *Archaeoprepona demophon demophon* (Linnaeus, 1758); **(B)** *Archaeoprepona licomedes licomedes* (Cramer, 1777); **(C)** *Prepona pylene pylene* Hewitson, [1854]. Scale bars: 1 mm.

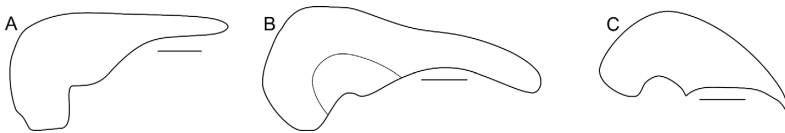


Fig. 4. Tegula; **(A)** *Archaeoprepona demophon demophon* (Linnaeus, 1758); **(B)** *Archaeoprepona licomedes licomedes* (Cramer, 1777); **(C)** *Prepona pylene pylene* Hewitson, [1854]. Scale bars: 1 mm.

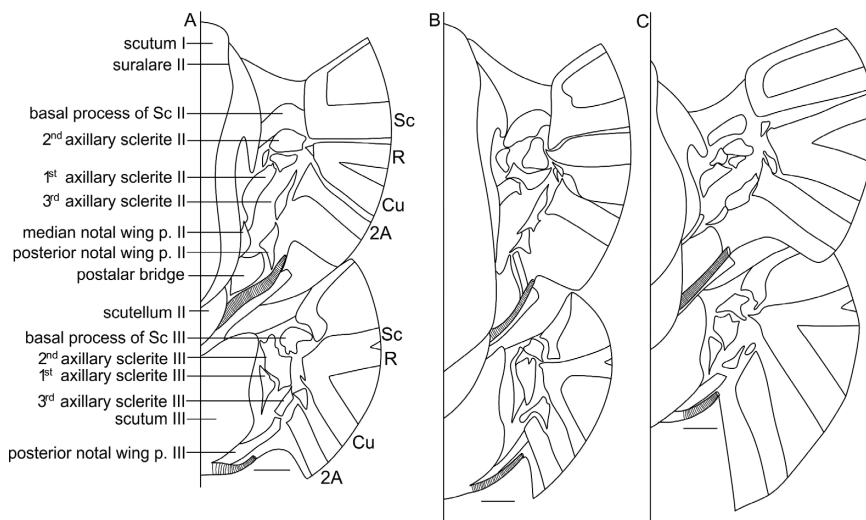


Fig. 5. Wing sclerites; **(A)** *Archaeoprepona demophon demophon* (Linnaeus, 1758); **(B)** *Archaeoprepona licomedes licomedes* (Cramer, 1777); **(C)** *Prepona pylene pylene* Hewitson, [1854]. Scale bars: 1 mm.

inner margin, having slight curve at base, leaving axillary region, running separately from discal cell, and reaching anal angle of wing.

In both sexes, hindwing (Fig. 6B) having convex costal margin and straight outer margin; latter having prominent convexity along its median third. Sc + R₁ extending from axillary region to apex of wing. Humeral vein (h) curving toward proximal region of costal margin, arising close to separation of Sc + R₁ and R₅. Discal cell closed, while dci being nontubular. M₁ and M₂ arising independently in upper region of discal cell, and M₃ being separate from M₁ and M₂, initiating in lower region of discal cell, with proximal third curved upward. Conformation of veins CuA₁ and CuA₂ similar to forewing. Anal veins separated from discal cell at their bases, with 2A ending at anal angle of wing; 3A ending in median third of anal margin. In males, odoriferous scales long and projected parallel to veins, originating between CuA₂ and 2A.

Prothoracic leg (Fig. 7A, B) atrophied and smallest in relation to others. Tarsus unisegmented in males and pentasegmented in females, both without terminal claw. Coxa elongated, wider at base and gradually narrowing distally. Trochanter subrectangular, and smallest of leg sclerites. Femur and tibia elongated, with approximately the same length. In females, tarsus composed of five tarsomeres, of which proximal longer than others, which have similar lengths and spines at their distal end. Male having single tarsus, which is thin and lacks spines or setae.

Meso- and metathoracic legs (Fig. 7C, D) having similar conformation. Coxae II and III longitudinally divided into eucoxa and meron by coxal suture. Eucoxa and meron II similar in size, whereas meron III about four times larger than eucoxa III. Trochanters II and III irregular in shape. Femurs II and III elongated. Meso- and metathoracic tibiae covered with setae, featuring pair of spurs articulated at inner distal end. Tarsi II and III pentamerous; proximal tarsomere larger than others. Distal portion of distitarsus (Fig. 7E, F) having membranous projected area that contains tarsal claws, pulvilli, and medially placed, rounded, and cushion-like arolium.

***Archaeoprepona licomedes licomedes* (Cramer, 1777)**

Prothorax. In dorsal (Fig. 1B), lateral (Fig. 2B), and ventral (Fig. 3B) views, prothorax having morphological pattern similar to that of *A. d. demophon*. In *A. l. licomedes*, paraplatagium longer, approximately three times as long as wide; spinasternum subtriangular.

Mesothorax. In dorsal view (Fig. 1B), prescutum broad and lozenge-shaped, occupying median portion of anterior margin of hourglass-shaped scutum. Scutellum lozenge-shaped, with median anterolateral projections.

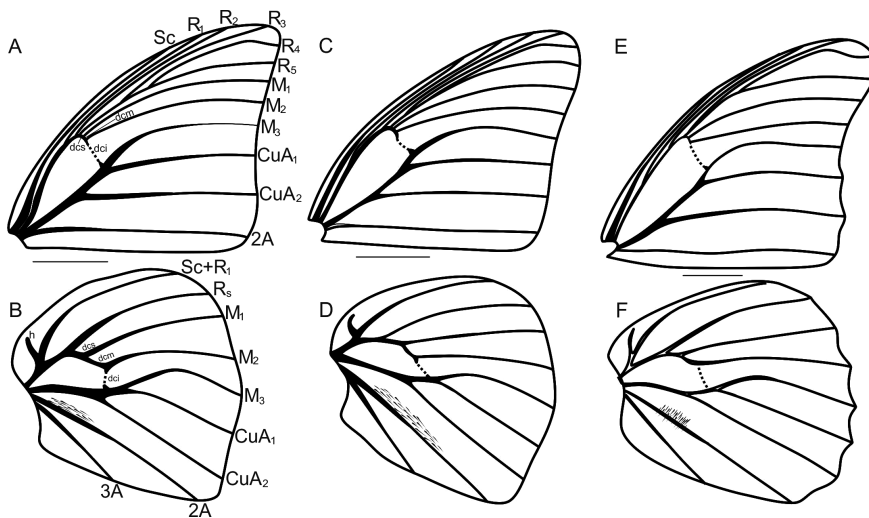


Fig. 6. Wings; (A), (B) *Archaeoprepona demophon demophon* (Linnaeus, 1758); (C), (D) *Archaeoprepona licomedes licomedes* (Cramer, 1777); (E), (F) *Prepona pylene pylene* Hewitson, [1854]; (A, C, E) forewing, (B, D, F) hindwing. Scale bar: 1 mm.

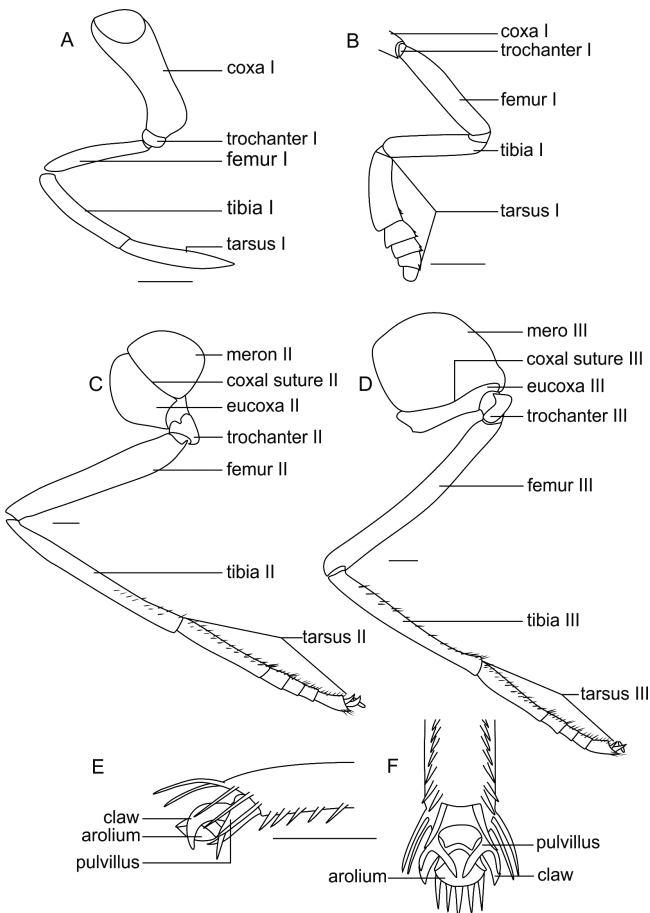


Fig. 7. *Archaeoprepona demophon demophon* (Linnaeus, 1758); (A) prothoracic leg, males; (B) prothoracic leg, female; (C) mesothoracic leg; (D) metathoracic leg; (E), (F) distitarsus; (E) lateral view, (F) ventral view. Scale bars: 1 mm.

Other structures similar to those of *A. d. demophon*.

In lateral (Fig. 2B) and ventral (Fig. 3B) views, mesothorax having same morphological pattern as in *A. d. demophon*, except for subquadrangular basalare, proepisternum being partially divided from katepisternum by pre-episternal suture, and discrimen extending to furcal pit.

Metathorax. In dorsal (Fig. 1B), lateral (Fig. 2B), and ventral (Fig. 3B) views, conformation being virtually identical to that of *A. d. demophon*, although only scutellum III having trapezoidal shape and katepisternum being longer, about five times as long as wide.

Thoracic appendages. Tegula (Fig. 4B), axillary sclerites (Fig. 5B), and legs (Fig. 8A–F) having morphological characteristics similar to those of *A. d. demophon*. In thoracic

appendages, these two species differing in venation of forewing (Fig. 6C), such as the bifurcation of R_1 and R_5 (R_2 , R_3 , R_4 and R_5) at the end of the median third of the discal cell, and the bifurcation of R_2 and R_3 , $R_4 + R_5$ at the distal third of the discal cell; although hindwing (Fig. 6D) similar to that of *A. d. demophon*.

***Prepona pylene pylene* Hewitson, [1854]**

Prothorax. In dorsal (Fig. 1C), lateral (Fig. 2C), and ventral (Fig. 3C) views, prothorax having morphological pattern similar to that of *A. d. demophon* and *A. l. licomedes*, although parapatagium being narrow, about seven times as long as wide, and spinasternum being subtriangular.

Mesothorax. In dorsal view (Fig. 1C), prescutum small, triangular, occupying median portion of anterior margin of scutum; latter being subrectangular, having bulged outer margin; scutellum semicircular, having anteromedian salience. Other structures similar to those of *A. d. demophon* and *A. l. licomedes*.

In lateral (Fig. 2C) and ventral (Fig. 3C) views, mesothorax having the same morphological pattern as *A. d. demophon* and *A. l. licomedes*, except for basalare being elongated; proepisternum completely separated from katepisternum by preepisternal suture; epimeron with laterally projected lobe; and discrimen extending to furcal pit.

Metathorax. In dorsal view (Fig. 1C), morphological pattern similar to that of *A. d. demophon* and *A. l. licomedes*, except for medially narrowed scutum and elongated scutellum.

In lateral (Fig. 2C) and ventral (Fig. 3C) views, metathorax similar to that of *A. d. demophon* and *A. l. licomedes*, except for subtriangular scutum; elongated scutellum and katepisternum being twice as long as wide; epimeron as single sclerite, therefore without divisions; and transverse inclination of coxal suture.

Thoracic appendages. Tegula (Fig. 4C), axillary sclerites (Fig. 5C), and legs (Fig. 8G–L) having morphology similar to *A. l. licomedes*. Forewing (Fig. 6E) similar to that of

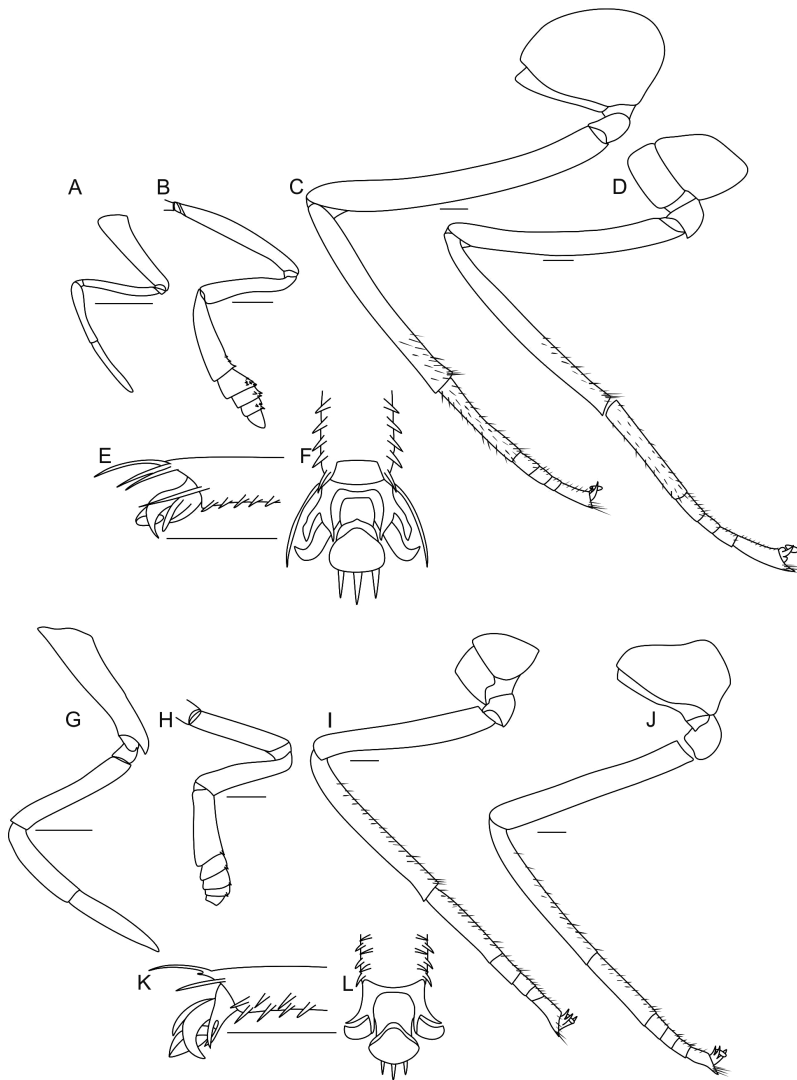


Fig. 8. *Archaeoprepona licomedes licomedes* (Cramer, 1777); (A) prothoracic leg, males; (B) prothoracic leg, female; (C) mesothoracic leg; (D) metathoracic leg; (E), (F) distitarsus; (E) lateral view, (F) ventral view. *Prepona pylene pylene* Hewitson, [1854]; (G) prothoracic leg, males; (H) prothoracic leg, female; (I) mesothoracic leg; (J) metathoracic leg; (K), (L) distitarsus; (K) lateral view; (L) ventral view. Scale bars: 1 mm.

A. d. demophon. Among thoracic appendages, differences include hindwing (Fig. 6F) in form and arrangement of odoriferous scales, latter being short and perpendicular to venation.

DISCUSSION

As expected, the thorax and appendages have several interesting features. Among these is the mesothoracic prescutum, which is well developed in *Archaeoprepona*, occupying at least half of the anterior margin of the scutum II, in addition to the metathoracic epimeron divided into two distinct sclerites, and the shape of the scutum III. All these characters can be easily observed and are useful in the diagnosis of this genus. This contrasts with the head and appendages, which in the first part of this study (Bonfantti et al., 2015) proved to show no morphological patterns useful in distinguishing as the thorax.

The two genera, *Archaeoprepona* and *Prepona*, showed quite similar morphological patterns for this tagma. As in the first part of this study (Bonfantti et al., 2015), the individual species with the most distinct morphological pattern was *Prepona p. pylene*. This species differs in having the semicircular scutellum II, a medially narrowed scutum III, and a lobe on the epimeron II, which can easily be observed with the specimen in ventral view, without the need for specimen dissection or damage.

Even with so many similarities, the odoriferous scales have different conformations among the species of *Archaeoprepona* Fruhstorfer, 1915 and *Prepona* Boisduval, 1836, and can be widely used as a diagnostic character for the genera. Although these scales are located in the same region, on the dorsal surface of the posterior wing of males between veins CuA₁ and 2A, *Archaeoprepona* has long scales oriented parallel to the venation, while *Prepona* has short scales oriented perpendicular to the venation.

The thorax in Lepidoptera is relatively unexplored for use in higher-level taxonomy, although it has great importance in the characterization of species (Leite et al., 2010). For Charaxinae, this tagma deserves attention considering that it is where most synapomorphies among adults are concentrated, all of which were corroborated in this study. Moreover, this tagma may show some very interesting characters for diagnosis of Preponini, which should be analyzed in the future in a phylogenetic context to test whether they are synapomorphies for this group, as besides being easily observable, they are well established among other species of this tribe that were not analyzed in this study. One of these characters, the dci vein of the forewing, was shown to be of a nontubular type, differing from what was previously reported for Charaxinae, where only the dci vein of the hindwing was nontubular. Further important characters

include the divisions of the mesothoracic epimeron into three distinct sclerites, by the dorsal and ventral sutures; the wing venation, which is generally similar; and the consistent presence of odoriferous scales on the wings of males. The thorax and appendages in general showed several characters that are important for the diagnoses of genera and tribes. Use of these characters will aid in advancing understanding of the phylogeny of these groups. The abdomen, examined in the third and last part of this study, will provide further important characters for understanding the morphological pattern as a whole.

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