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Source: Annals of the Entomological Society of America, 96(4):458-471.

Published By: Entomological Society of America

DOI: [http://dx.doi.org/10.1603/0013-8746\(2003\)096\[0458:ISABSO\]2.0.CO;2](http://dx.doi.org/10.1603/0013-8746(2003)096[0458:ISABSO]2.0.CO;2)

URL: [http://www.bioone.org/doi/](http://www.bioone.org/doi/full/10.1603/0013-8746%282003%29096%5B0458%3AISABSO%5D2.0.CO%3B2)

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Immature Stages and Breeding Sites of Some Neotropical Saprophagous Syrphids (Diptera: Syrphidae)

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Ann. Entomol. Soc. Am. 96(4): 458–471 (2003)

ABSTRACT The larva and/or puparium of the Neotropical syrphids *Habromyia coeruleithorax* Williston, 1888, *Palpada furcata* (Wiedemann, 1819), and six species of *Meromacrus* Rondani, 1848, are figured, described, and compared with other similar larvae. All of these larvae are similar in external form, having mouthparts adapted for filtering suspended items of food, retractile anterior spiracles, prolegs with crochets, and extended anal segments (=long-tailed larvae). Each species varied in the size and distribution of integumental setae and spicules and in the size and form of the pupal spiracles. Keys are provided to identify genera of Neotropical long-tailed syrphid larvae and to separate the six species of *Meromacrus*: *M. acutus* (Fabricius, 1805), *M. currani* Hull, 1942, *M. draco* Hull, 1942, *M. laconicus* (Walker, 1852), *M. loewii* (Williston, 1892), and *M. obscurus* Hine, 1924. Larvae of all these species were found in tree holes, except for *M. draco*, which was associated with decaying bananas, and *P. furcata*, which occurred in a waste heap of decaying coffee pulp.

KEY WORDS Syrphidae, *Meromacrus*, *Habromyia*, *Palpada*, larva, puparium

AMONG THE DIPTERA: SYRPHIDAE are outstandingly diverse larvae (Vockeroth and Thompson 1987, Rotheray and Gilbert 1999). However, only a small proportion of syrphid larvae is known, with the best known region being the Palearctic, followed by the Nearctic (Thompson 1990). Less than 3% of Neotropical syrphid larvae are known, even though some of the most species-rich syrphid lineages occur in this region (Thompson, personal communication).

Over the past 4 yr, we have been finding and rearing syrphid larvae in Central and South America (Rotheray et al. 2000a, b; Marcos-García and Pérez-Bañón, 2001, 2002). This work deals with reared material of one species each of *Habromyia* Williston, 1888, and *Palpada* Macquart, 1834, and six species of *Meromacrus* Rondani, 1848 (Diptera: Syrphidae).

The three genera studied in this work are endemic to the New World. *Meromacrus* includes ≈40 species, ranging from southern United States to northern Argentina (F. C. Thompson, personal communication). Although the species of *Meromacrus* are common, widespread, and well known in some countries such as Argentina (Lagrange 1990), the biology of the immature stages is poorly known. Only the im-

mature stages of *Meromacrus pratorum* (Fabricius, 1775) (= *Meromacrus laconicus* [Walker, 1852], F. C. Thompson, personal communication) have been described briefly (Sack 1921). Published rearing records indicate that the larvae of *Meromacrus* occur in various kinds of decaying matter. Sack (1921) reported that larvae of *M. pratorum* live in sediment of wet tree holes and have been also collected in fluid and debris of upright flower bracts of *Heliconia* sp. (Heliconiaceae) (Maier 1987). Snow (1958) found larvae of *Meromacrus acutus* (Fabricius, 1805) in tree stumps filled with water.

Habromyia comprises ≈12 species, ranging from south of Central America to northern Chile and Argentina (Thompson 1999). *Palpada* with >100 species constitutes one of the five largest genera in the New World, ranging from United States to Chile and Argentina (Thompson 1999). These genera are common and widespread, and some species, such as *Palpada vinetorum* (Fabricius, 1798), have been reported as pollinator (Ewel et al. 1982), and the only reference to early stages is that of van Doesburg (1962), who figures, but does not describe, the puparium of *Eristalis* (= *Palpada*) *scutellaris* Fabricius. Larvae of this species were found in refuse dumps (detritus) of nests of leaf-cutter ants (*Atta cephalotes*, Formicidae).

The objectives of the current study are: 1) to provide a key to identify genera of Neotropical long-tailed syrphid larvae and to separate the six species of *Meromacrus*; 2) to describe the preimaginal stages of one species each of *Habromyia* and *Palpada* and six

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species of *Meromacrus*; and 3) to give details of breeding sites of all these species.

Materials and Methods

Larvae were either obtained by searching in the field or borrowed from the institutions named in the acknowledgments. Many specimens were collected by the Diptera parataxonomists employed by the Instituto Nacional de Biodiversidad, Costa Rica (INBio), after a training course in 1999. Larvae were reared by placing them in plastic pots or boxes with some of the material in which they were found and stored under cool, dark conditions. Water was added to maintain wet conditions. Containers were inspected regularly, and each puparium was removed to a separate container so that adults could be associated with their puparia.

Some third instars were preserved; third stage larvae were recognized by the presence of a pair of discs of differentiated cuticle on the dorsal surface of the first abdominal segment. In the puparium, pupal spiracles protrude through these discs (Hartley 1961). Larvae were fixed by immersion in cold water and boiling gently for ~4 min to extend them. Afterward, they were preserved in 70% alcohol. Cephalopharyngeal skeletons were studied by removing them from puparia, and placing them in warm potassium hydroxide for 3–4 min. Afterward, they were washed in distilled water and preserved and examined in glycerine.

Descriptions are based on preserved larvae and/or puparia. Illustrations and dimensions (mean \pm SE) were measured on preserved material using a stereo microscope with an eyepiece micrometer and drawing tube. The photographs were taken with a scanning electron microscope operated at 20 kV. Terminology follows Rotheray and Gilbert (1999). Depositories for material are as follows: INBio = Instituto Nacional de Biodiversidad, Costa Rica; NMS = National Museums of Scotland, Edinburgh; SI = Smithsonian Institution, Washington, DC.

Results

Identification

Key to the genera of Neotropical long-tailed syrphid larvae (third instar)

- 1) Anterior spiracles small, flat tipped, and not retractile into pockets on the thorax.
 *Sericomyia* Meigen*
 Anterior spiracles pointed at tip and retractile into pockets on the thorax 2
- 2) Abdominal prolegs with crochets arranged in two main transverse rows 3
 Abdominal prolegs with crochets in three or more distinct semicircular rows (arranged in a curved, not a transverse row) 7
- 3) Transverse row of spicules just in front of last pair of prolegs *Eristalinus* Rondani*

No transverse row of spicules just in front of last pair of prolegs, although a few scattered spicules may be present between the prolegs 4

- 4) Abdominal segments 2–7 with sensilla 4–6 in the same horizontal plane. Abdomen smooth, not coated in setae
 *Mallota* Meigen*

Abdominal segments 2–6 with sensilla 4 above 5 and 6 (segment 7 with sensilla 4–6 in the same horizontal plane). Abdomen usually coated in setae 5

- 5) Anterior margin of prothorax with five pairs base bearing hooks *Quichuana* Knab
 Anterior margin of prothorax without hooks 6

- 6) Anterior fold with a band of backwardly directed, hooked spicules that become abruptly completed sclerotized and suddenly shorter posteriorly. These small spicules go into the longitudinal grooves. Last pair of prolegs with the curved tips of most of the primary crochets facing forward to the front of the larva *Quichuana* Knab

Anterior fold with a band of backwardly directed, hooked, and only apically sclerotized spicules that become progressively shorter. These small spicules go into the longitudinal grooves and folds, and also reach the mesothoracic lateral patches of spicules. Last pair of prolegs with the curved tips of most of the primary crochets facing out to the lateral margin of the larva *Palpada* Macquart

- 7) Last pair of prolegs with the curved tips of most of the primary crochets facing out to the lateral margin of the larva 8

Last pair of prolegs with the curved tips of most of the primary crochets facing forward to the front of the larva. Ventral surface with three pairs of projections between the anal opening and the "tail" *Helophilus* Meigen*

- 8) Vento-lateral surface of abdominal segments bearing two lines of long setae, first one with long and densely aggregated setae at level of sensilla 7–8, and second one with shorter and more scarce setae extended along the lateral margins of the prolegs 9

Vento-lateral surface of abdominal segments without two lines of long setae
 *Eristalis* Latreille*

- 9) Anterior fold of the prothorax with a narrow band of backwardly directed, slightly hooked, and moderately sclerotized spicules that become suddenly shorter posteriorly. Maximum width of the "tail" is about two times the distance between the first dorsal sensilla of the seventh abdominal segment *Meromacrus* Rondani

Anterior fold of the prothorax with a broad band of backwardly directed, slightly hooked, and only apically sclerotized spicules that become progressively shorter pos-

* Based on early stages from the Palaearctic or Nearctic region.

teriorly. Maximum width of the "tail" is ≈ 1 and one-third the distance between the first dorsal sensilla of the seventh abdominal segment *Habromyia* Williston*

Key to *Meromacrus* puparia

- 1) Pupal spiracles with the tubercle bands reach the ventral surface (Fig. 3C) 2
Pupal spiracles with the tubercle bands do not reach the ventral surface (Fig. 2B) 4
- 2) Tubercle bands reach the base of the pupal spiracle on the dorsal surface (Fig. 3B). Bands clearly separated on the dorsal surface even on the basal part *Meromacrus currani*
Tubercle bands do not reach the base of the pupal spiracle (Fig. 4, B and C) 3
- 3) Anterior larval spiracles two times longer than broad (Fig. 4A). Pupal spiracles with the tubercles only arranged in bands at the edges of the spiracles *Meromacrus draco*
Anterior larval spiracles three times longer than broad (Fig. 5A). Pupal spiracles with the tubercles arranged in bands not only at the edges of the spiracles, but also on the dorsal surface; the bands are not clear on the basal part *M. laconicus*
- 4) Pupal spiracles clearly tapering apically (Fig. 2, A and B) *M. acutus*
Pupal spiracles only slightly tapering apically (Fig. 5, B and C) 5
- 5) Anterior larval spiracles two times longer than broad (Fig. 6A) *Meromacrus loewii*
Anterior larval spiracles three times longer than broad (Figs. 5A and 7A) 6
- 6) Anterior larval spiracles slightly swollen apically. Ventral surface of pupal spiracles furrowed for many deep longitudinal carinae (Fig. 7, C and F) *Meromacrus obscurus*
Anterior larval spiracles not swollen apically. Ventral surface of pupal spiracles smooth or with very superficial longitudinal ridges (Fig. 5, C and F) *M. laconicus*

Description of the Immature Stages

Habromyia coeruleithorax Williston, 1888 Third Instar

Overall Size and Shape. Body length 16–17 mm (anterior fold to sensilla four of seventh segment), tail length 24–26 mm (sensilla four of seventh segment to tip of posterior respiratory process), maximum width 5 mm. A long-tailed larva with internal mouth hooks and retractile anterior spiracles. Subcylindrical in cross section, truncate anteriorly, and tapering and slightly flattened posteriorly. Dorsal body surface coated in fine and well-developed pubescence backwardly directed, which becomes longer around the dorsal and lateral sensilla (0.15–0.7 mm). Setae on ventral surface are shorter, except for the anal segment. Anterior fold coated in sclerotized spicules,

which become progressively shorter posteriorly. Ventro-lateral margin of abdominal segments bearing two lines of long setae (0.7–0.8 mm). Prolegs bearing crochets in three or more rows.

Head. Mandibles and mandibular lobes internal, mandibles supporting the expanded mandibular lobes, mouthparts adapted for filter feeding (Roberts 1970). Dorsal lip broad, lacking a medial groove and covered with a conspicuous tuft of long setae. Basal section of the papilla supporting antennomaxillary organs divided to the base.

Thorax. Lateral lips rounded and well developed (in profile projecting forward from the anterior part of the prothorax), coated in short and fine setae at base and longer thick setae at tip. Dorsal surface of the prothorax with longitudinal grooves. Anterior fold coated with a band of backwardly directed, slightly hooked, and moderately sclerotized spicules, i.e., sclerotized setae about as tall as broad, which become progressively shorter posteriorly. Dorsal surface of the prothorax with a pair of two times longer than broad anterior spiracles light brown in color, sclerotized, with pointed, slightly recurved tips (Fig. 1a). These spiracles retractile into inverted integumental pockets. Spiracular openings on a clear area of the ventral surface, extending along the distal three-fourths of spiracle length. Clear area is about three times longer than broad. Desclerotized area almost entirely obliterated by facets; only a small part on the apical end without facets. Facets arranged in three rows. Lateral margin of mesothorax with two patches of sclerotized spicules arranged, as follows: a group with 15–20 spicules just anterior to fourth sensilla of mesothorax and another group located with 15–20 spicules in front of the fifth sensilla of mesothorax. Mesothorax bearing well-developed prolegs with ≈ 60 crochets arranged in multiple rows.

Abdomen. Prolegs well developed on segments 1–6, in ventro-lateral view, appearing as small cones that are broader at the apex than the base. Crochets in three semicircular rows, below which are several rows of spicules. Approximately 12 primary crochets with the distal two-thirds sclerotized. Last two pairs of prolegs differ from the first four, in that most of the primary crochets face toward the lateral margins of the body. Between the sixth pair of prolegs appears an incomplete spicule row. On the segment seven, sensilla 4 is aligned horizontally with sensilla 5 and 6. Ventro-lateral margin of abdominal segments 1–7 with two lines of setae. First line setae at level of sensilla 7–8 with setae longer and more densely aggregated than second line near prolegs. On the seventh segment, this line of setae turns inward across the posterior part of the segment just anterior to the anal opening. Anal segment extended as in long-tailed larvae, with three pairs of weakly developed lappets. Maximum width of the "tail" is $\approx 1.3\times$ the distance between the first dorsal sensilla of the seventh abdominal segment. On the anal segment, the pubescence around the lateral sensilla 4, 5, and 6 is obviously longer and more compact than the pubescence around the second sensilla (0.2–0.8 mm).

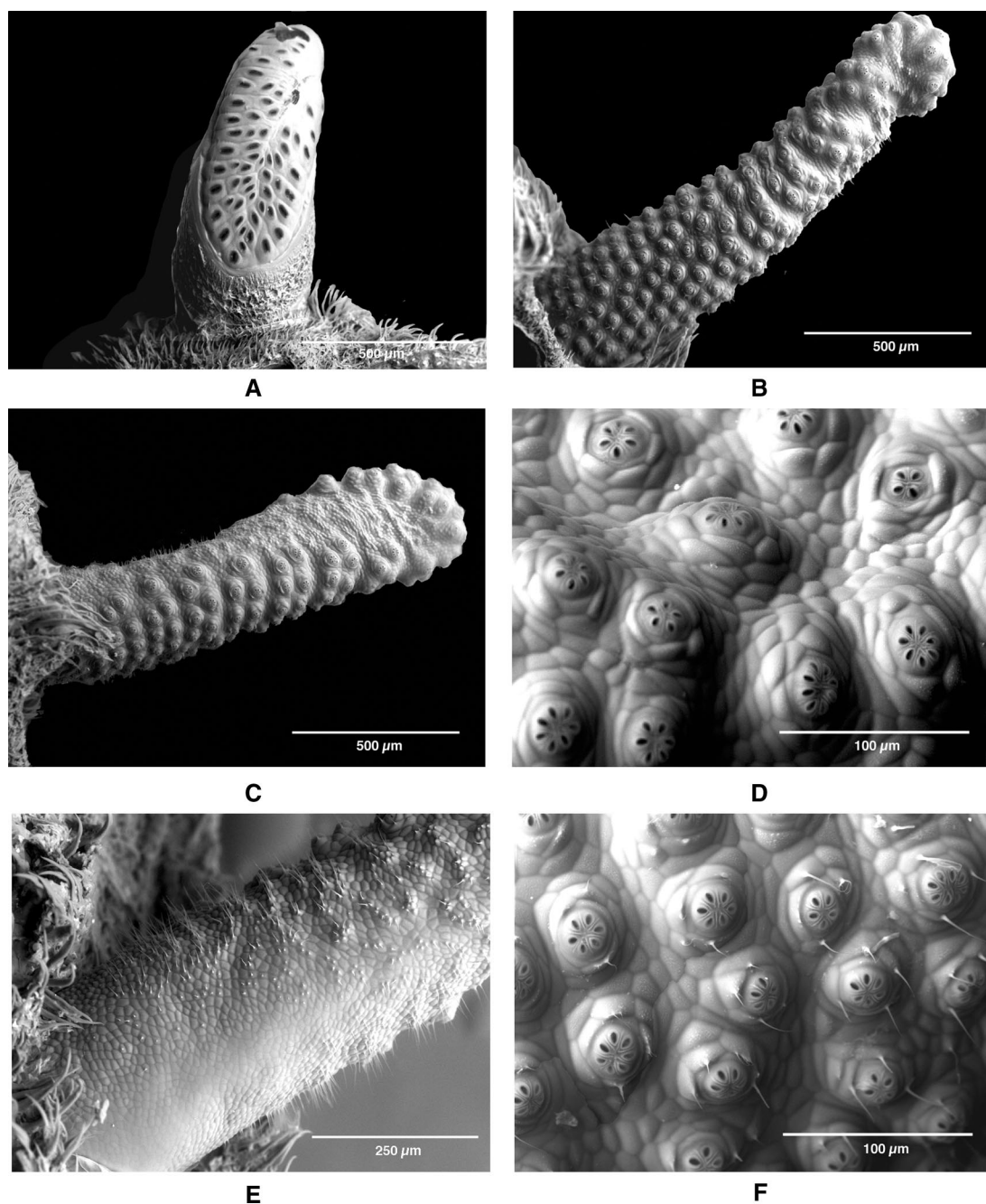


Fig. 1. (a-f) *H. coeruleithorax* Williston, 1888. (a) Anterior spiracle, dorso-lateral view; (b-f) pupal spiracle; (b and c) dorso-lateral views; (d and f) spiracular openings; (e) ventral view.

Posterior respiratory process lustrous, sclerotized, and brown in color.

Chaetotaxy. Distribution and number of sensilla following pattern of other syrphid larvae (Rotheray and Gilbert 1999). Prothorax (P) with 12 pairs of sensilla; mesothorax (Ms) and metathorax (Mt) with 9 pairs; abdominal segments 1-7 with 10 pairs (sensilla 10 inconspicuous); anal segment with 3 pairs of sensilla

(sensilla 9, 10, and 11); and the apices of 3 pairs of lappets bearing sensilla.

Puparium. Subcylindrical in cross section. Anterior end truncate, tapered posteriorly and flattened ventrally. Dark brown in color. Pupal spiracles projecting from middle of upper part of operculum, separated by distance similar to the length of one spiracle. These processes are subcylindrical structures, ≈ 1.6 mm in

length (length: breadth ratio of spiracle 4:1), stout, strongly forward sloping, and slightly twisted (Fig. 1b). Dark brown in color. Dorsal and lateral surface bearing irregularly spaced and oval-shaped tubercles usually extending along the greater part of spiracle length. These tubercles are arranged in 9–11 vague bands that are more defined at the edges of the spiracles (Fig. 1c). These bands are not reaching the ventral surface (Fig. 1e). Each tubercle has from 6 to 10 oval openings (Fig. 1d). Entire surface, including the space between tubercles finely granulated or reticulated; some of these projections bearing apical setae (Fig. 1f).

Material Examined. 2m, 2f, three puparia, two larvae, Costa Rica, Alajuela, Guanacaste, estación San Gerardo, 600 m, LN-318000, 384400, coll. 13.IX.2000 Duvalier Briceño, ex wet decaying roots of fallen unidentified tree. 1f, one puparium, Costa Rica Puntarenas, Coto Brus, Sabalito, 1400 m., LS-318300, 596600, coll. 3.IX.2000 Braulio Hernández Bogantes, ex wet decaying material in hole of unidentified tree (INBio).

Meromacrus Rondani, 1848: Characters Shared by Third Instars and Puparia of All Species Examined

Overall Shape. A long-tailed larva with internal mouth hooks and retractile anterior spiracles. Subcylindrical in cross section, truncate anteriorly, tapering posteriorly. Dorsal body surface coated in fine and well-developed pubescence backwardly directed, which becomes longer around the dorsal and lateral sensilla. Setae on ventral surface are shorter, except for the anal segment. Anterior fold coated in sclerotized spicules, which become abruptly shorter posteriorly. Ventro-lateral margin of abdominal segments bearing two lines of conspicuous setae. Prolegs bearing crochets in three or more rows.

Head. Mandibles and mandibular lobes internal, mandibles supporting the expanded mandibular lobes, mouthparts adapted for filter feeding. Dorsal lip broad, lacking a medial groove and covered with a conspicuous tuft of long setae. Basal section of the papilla supporting antennomaxillary organs divided to the base.

Thorax. Lateral lips rounded and well developed (in profile projecting forward from the anterior part of the prothorax), coated in short and fine setae at base and longer setae at tip. Dorsal surface of the prothorax with longitudinal grooves. Anterior fold with band of backwardly directed, slightly hooked, and moderately sclerotized spicules that become abruptly shorter posteriorly. Dorsal surface of the prothorax a pair of spiracles, sclerotized, elongated, with pointed and slightly curved tips and retractile into inverted integumental pockets. Lateral margin of mesothorax with two patches of sclerotized spicules arranged, as follows: a group of 15–20 just anterior to fourth sensilla of mesothorax and another group of ≈ 25 –30 located in front of the fifth sensilla of mesothorax. Mesothorax bearing well-developed prolegs with ≈ 50 crochets arranged in multiple rows.

Abdomen. Six pairs of ventral prolegs on segments 1–6. Prolegs well developed, in ventro-lateral view, appearing as small cones broader at the apex than the base, with crochets in three distinct semicircular rows. Approximately 12 primary crochets with the distal two-thirds sclerotized. Last two pairs of prolegs differ from the first four, in that most of the large primary crochets facing toward the lateral margins of the body. Between the sixth pair of prolegs appears an incomplete spicule row. On the segment 7, sensilla 4 is aligned horizontally with sensilla 5 and 6. Ventro-lateral margin of the abdominal segments 1–7 with two lines of setae. First line setae at level of sensilla 7–8 with setae longer and more densely aggregated than second line near prolegs. On the seventh segment, this line of setae turns inward across the posterior part of the segment just anterior to the anal opening. Anal segment extended as in long-tailed larvae, with three pairs of weakly developed lappets. Maximum width of the “tail” is about two times the distance between the first dorsal sensilla of the seventh abdominal segment. On the anal segment, pubescence around the lateral sensilla 4, 5, and 6 is slightly longer than the pubescence around the second sensilla (0.4–0.6 mm). Posterior respiratory process lustrous, sclerotized, and brown in color. Six spiracular slits arranged around two central scars. Spiracular slits with a clearly semicircular shape. Four pairs of spiracular setae.

Chaetotaxy. Distribution and number of sensilla following pattern of other syrphid larvae (Rotheray and Gilbert 1999). Prothorax (P) with 12 pairs of sensilla; mesothorax (Ms) and metathorax (Mt) with 9 pairs; abdominal segments 1–7 with 10 pairs (sensilla 10 inconspicuous); anal segment with 3 pairs of sensilla (sensilla 9, 10, and 11) and 3 pairs of lappets.

Puparium. Subcylindrical in cross section. Anterior end truncated, tapering posteriorly and flattened ventrally. Cream to dark brown in color. Pupal spiracles projecting from middle of upper part of operculum, separated by distance clearly more than the length of one spiracle. Spiracles are subcylindrical structures, 1–1.5 mm in length, bearing irregularly spaced and rounded tubercles on the dorsal surface. Tubercles usually arranged in bands that sometimes reach the ventral surface. Entire surface, including the space between tubercles, finely granulated or reticulated. Ventral surface sometimes with longitudinal ridges.

M. acutus (Fabricius, 1805)

Size of Puparium. Maximum width 7 mm; length not including prp 16 mm.

Pupal Spiracles. Subcylindrical structures ≈ 1.5 mm in length (length: width ratio of spiracle 4:1), slightly curved back, tapering, and flattened apically (Fig. 2a). Light brown in color. On $\approx 75\%$ of the dorsal and lateral surfaces with 6–8 bands, indistinct dorsally, clearer laterally. These bands clearly separated even at the base and not reaching the ventral surface (Fig. 2b). On each band are irregular spaced and oval-shaped tubercles each bearing 6–10 spiracular openings. En-

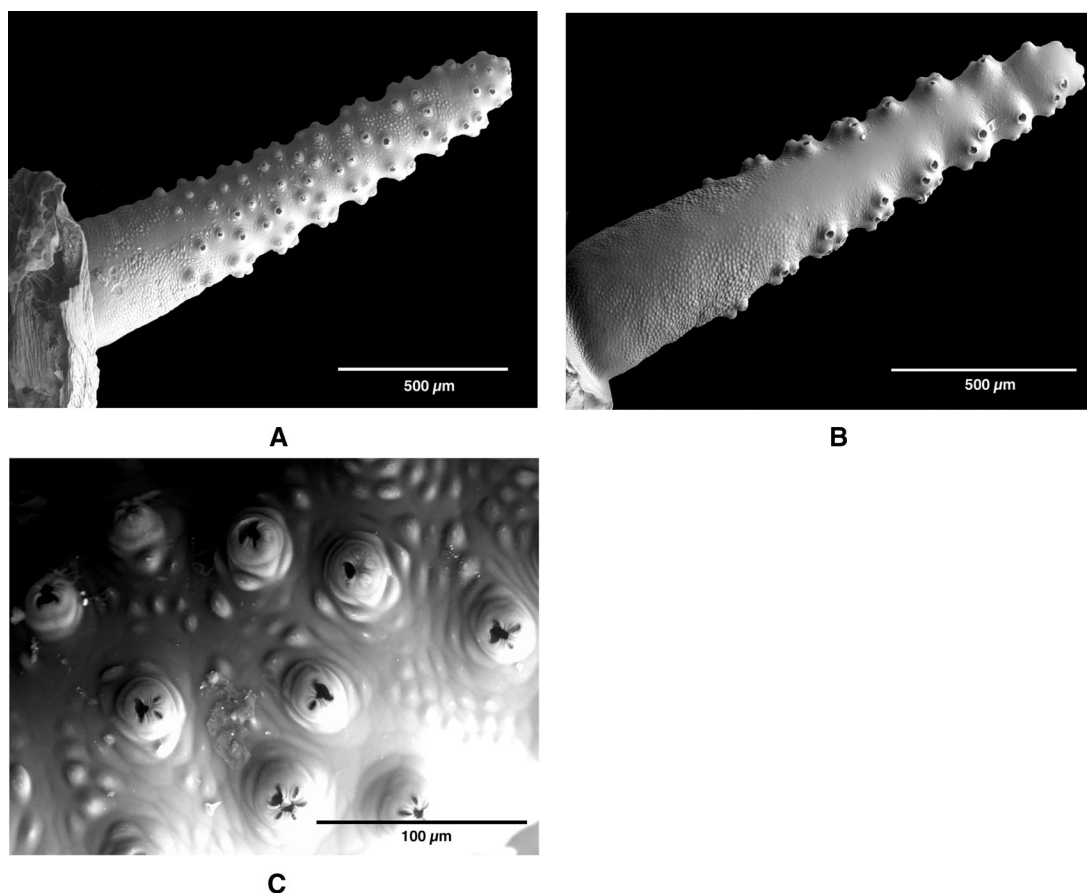


Fig. 2. (a-c) *M. acutus* (Fabricius, 1805), pupal spiracle. (a) Dorsal view; (b) ventral view; (c) spiracular openings.

tire surface, including the space between tubercles, finely granulated or reticulated (Fig. 2c).

Material Examined. One male, one puparium, United States, FL, Putnam County 23.ii.1930 Mark Dodd, ex rotten wood of unidentified tree (SI).

M. currani Hull, 1942

Size of Puparium. Maximum width: 7–8 mm; length not including prp 16–17 mm.

Anterior Larval Spiracles. Spiracles stout, about three times taller than broad. Light reddish brown in color. Spiracular openings on a clear area of the ventral surface, extending on the distal third of the spiracle. Clear area is about two times longer than broad, with the fold at the middle of its length. Upright part of facet band arranged in two rows, the inner one with elongated facets (Fig. 3a).

Pupal Spiracles. Subcylindrical structures ≈ 1.2 mm in length (length:breadth ratio of spiracle 4:1), stout, slightly curved back, and with the end slightly flattened (Fig. 3b). Dark brown in color. On $\approx 90\%$ of the dorsal and lateral surfaces with 9–11 bands, vague dorsally, clearer laterally. The upper and medium bands reaching the ventral surface (Fig. 3c). On each

band are two lines of ≈ 8 –12 densely aggregated tubercles, each bearing 6–10 oval spiracular openings (Fig. 3d). Entire surface, including the space between tubercles, finely granulated or reticulated. Ventral surface sometimes with longitudinal ridges on the two basal thirds.

Material Examined. 2 f, two puparia, two larvae, Costa Rica, Limón, Talamanca, Sixaola, 10–30 m, LS-390000, 612000. coll. 25.II.1999 Braulio Hernández Bogantes, ex wet decaying material in hole at the base of a *Carapa guianensis* Aubl. (Meliaceae) tree (INBio).

M. draco Hull, 1942

Size of Puparium. Maximum width 6 mm; length not including prp 11–12 mm.

Anterior Larval Spiracles. Spiracles about two times longer than broad, with the distal half curved back (Fig. 4a). Reddish brown in color. Spiracular openings on a clear area of the ventral surface, extending to the distal half of the spiracle. Clear area is about two times longer than broad, with a horizontal fold above the base. Below this fold, the clear area is semicircular. Clear area almost entirely obliterated by facets, only

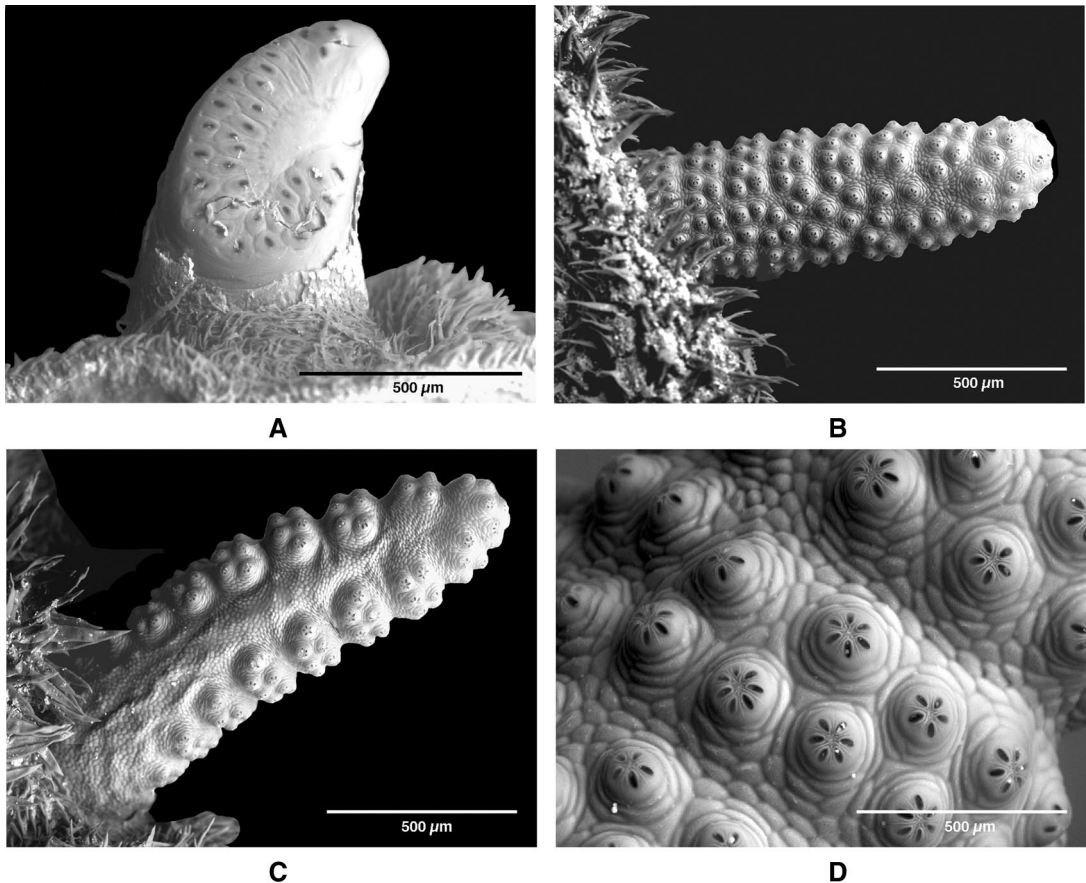


Fig. 3. (a–d) *M. currani* Hull, 1942. (a) Anterior spiracle dorso-lateral view; (b–d) pupal spiracle, (b) dorsal view; (c) ventral view; (d) spiracular openings.

a small part on the apical end without facets. Facet band with very elongated facets arranged in one/two rows.

Pupal Spiracles. Subcylindrical structures with ≈ 1.2 mm in length (length:breadth ratio of spiracle 4:1), slightly curved back, and with the end slightly flattened (Fig. 4b). Shiny to dark brown in color. On $\approx 80\%$ of the dorsal and lateral surface are 5–7 bands, indistinct dorsally, clearer laterally (Fig. 4, b and c). Upper and medium bands reaching the dorsal surface. On each band are irregular spaced and oval-shaped tubercles each bearing 6–10 oval spiracular openings. Entire surface, including the space between tubercles, finely granulated or reticulated (Fig. 4d).

Material Examined. 1f, one puparium, Costa Rica, Guanacaste, Cañas, Palmira, 200 m., LN-280500, 418650. coll. 5.v.1999 José Daniel Gutiérrez, ex cavity in the ground containing a banana plant (INBio).

M. laconicus (Walker, 1852)

Size of Puparium. Maximum width 4–6 mm; length not including prp 9–14 mm.

Anterior Larval Spiracles. About three times longer than broad, with the distal half curved back and thin

(Fig. 5a). Light brown in color. Spiracular openings on a clear area of the ventral surface, extending to the distal half of the spiracle. Clear area is about three times longer than broad, with a fold on the apical third. Unsclerotized area with a rectangular shape. Facets arranged in one or two rows.

Pupal Spiracles. Two different morphologies and intermediates exist. In one, the spiracles are subcylindrical ≈ 1.1 mm in length (length:breadth ratio of spiracle 5:1), straight or slightly curved back (Fig. 5b). On $\approx 65\%$ of the dorsal and lateral surface are 4–6 bands, indistinct dorsally, clear laterally. These bands are not reaching ventral surface (Fig. 5c). On each band are irregular spaced and oval-shaped tubercles, each bearing 6–10 oval spiracular openings. Entire surface, including the space between tubercles, finely granulated or reticulated (Fig. 5d). Ventral surface sometimes with superficial longitudinal ridges (Fig. 5c).

Alternatively, the pupal spiracles are subcylindrical and ≈ 1 mm in length (length:breadth ratio of spiracle 3.5:1), stout, and slightly curved back. On $\approx 90\%$ of the dorsal and lateral surfaces are 7–9 bands, vague dorsally, clearer laterally (Fig. 5e). These bands are not clearly separated at the base. The upper and medium

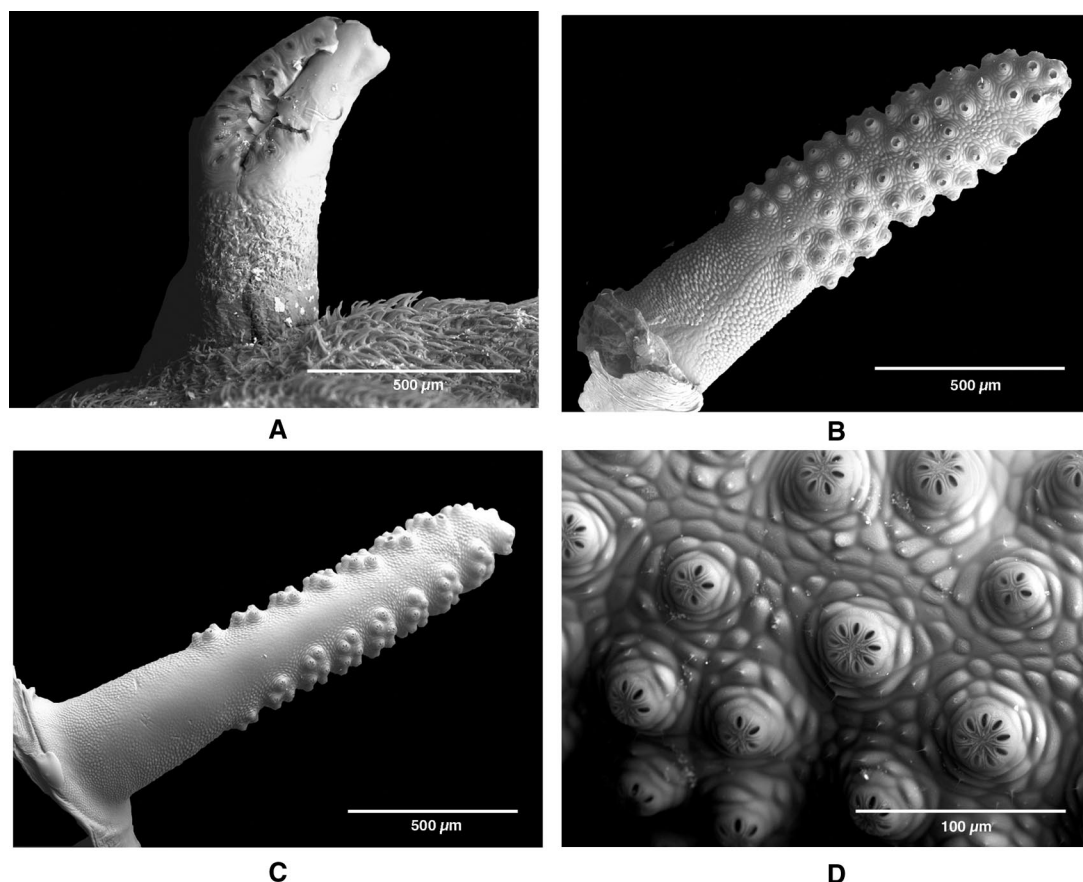


Fig. 4. (a–d) *M. draco* Hull, 1942. (a) Anterior spiracle dorso-lateral view; (b–d) pupal spiracle; (b) dorsal view; (c) ventral view; (d) spiracular openings.

bands are reaching the ventral surface. On each band are two lines of ≈ 8 –12 densely aggregated tubercles, each bearing 6–10 oval spiracular openings. Entire surface, including the space between tubercles, finely granulated or reticulated. Ventral surface sometimes with superficial longitudinal ridges (Fig. 5f). Specimens with intermediate characters, in particular, lack of longitudinal ridges on the ventral surface also exists (Fig. 5, g and h).

Material Examined. First morphology: 2m, 1f, three puparia, Costa Rica, Guanacaste, Bagaces, P. N. Palo Verde, 15 m., LN-257000, 398400. coll. 21.IX.2000 Braulio Hernández Bogantes, ex wet decaying material in hole of mango (Anacardiaceae: *Mangifera indica* L.) tree (BHB-341s). Second morphology: 1m, 1f, two puparia, Costa Rica, Guanacaste, P. N. Santa Rosa, 300 m., LN-313000, 359800. coll. 27.VI.2000 Duvalier Briceño, ex wet decaying material in hole of a *Enterolobium cyclocarpum* (Jacq.) Griseb. (Fabaceae: Mimosoideae) tree. 1m, one puparium, Costa Rica, Heredia, Santa Rosa de Santo Domingo, 1100 m., LN-217300, 526200. coll. 7.v.1999 Annia Picado, ex wet decaying material in hole of an *Erythrina poeppigiana* (Walp.) O.F. Cook (Fabaceae: Papilionoideae) tree (INBio). Specimens with intermediate character

states: 2m, 3f, five puparia, Costa Rica, Guanacaste, Bagaces, P. N. Palo Verde, estación Catalina, 15 m., LN-257000, 398400. coll. 21.IX.2000 Braulio Hernández Bogantes, ex wet decaying material in hole of mango (Anacardiaceae: *M. indica* L.) tree (INBio). 4m, 1f, five puparia, two larvae, British West Indies, Trinidad, Northern Range, Lopinot, coll. 6.VII.1998 Rotheray, G. ex cut, water-filled *Carica papaya* L. stems (Caricaceae) (NMS). 2m, two puparia, Mexico, Oaxaca, Cuicatlán, coll. 14–18.VIII.1999 Valerio Trujano, ex wet decaying material in a hole of a mango tree (NMS). 1m, 2f, three puparia, Brazil, Bahia. Rockefeller Foundation Laboratory iv.1929, Shannon, R.C. ex tree hole (SI). Specimens with pupal spiracles not well developed: 2m, 1f, three puparia, Costa Rica, Guanacaste, estación Santa Rosa, coll. 24.X.2000 Duvalier Briceño, ex wet decaying material in hole of unidentified tree (INBio).

M. loewii (Williston, 1892)

Size of Puparium. Maximum width 5–6 mm; length not including prp 10–12 mm.

Anterior Larval Spiracles. About two times longer than broad, with the tips slightly pointed and curved

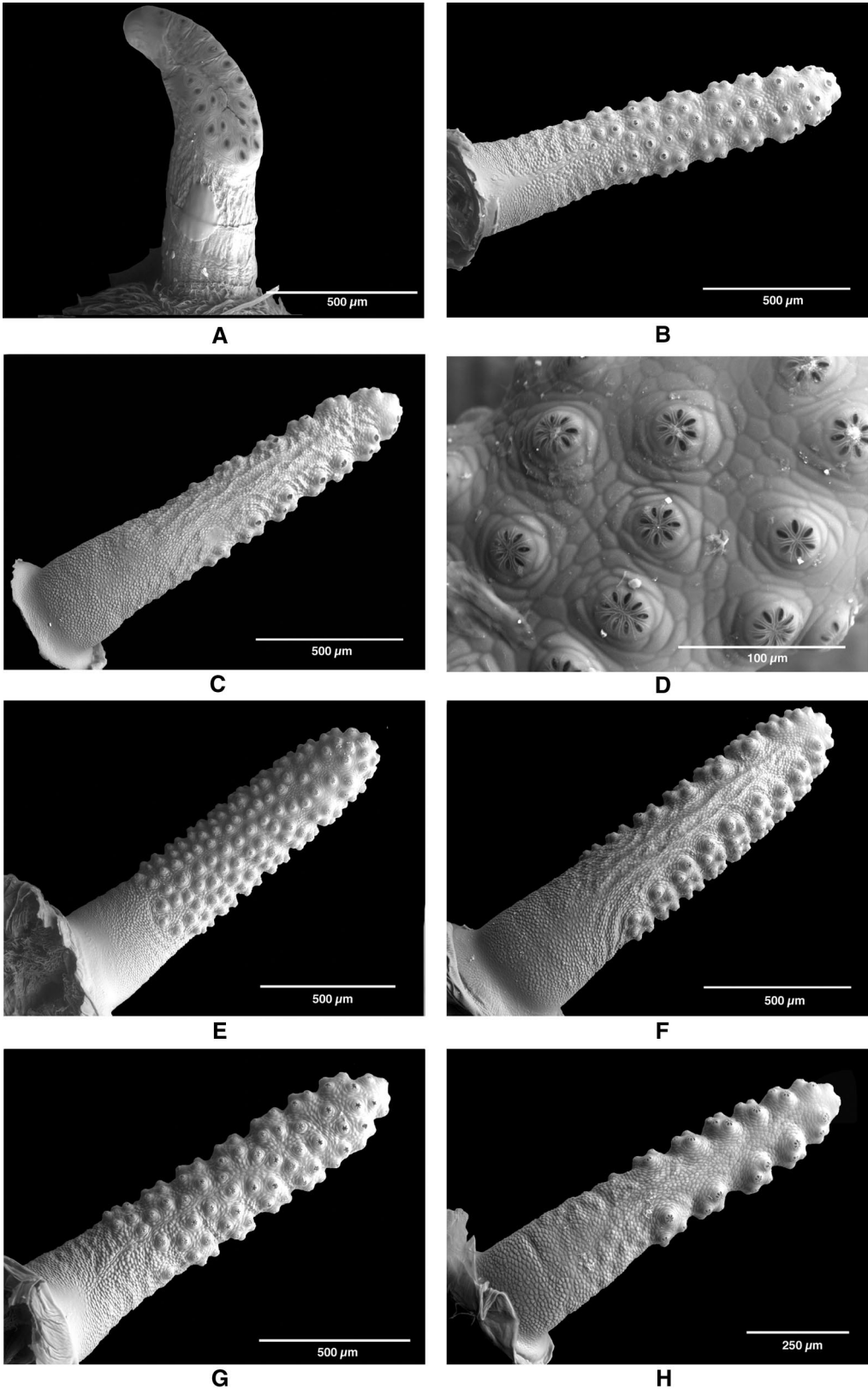


Fig. 5. (a-h) *M. laconicus* (Walker, 1852). (a) Anterior spiracle dorso-lateral view; (b-h) pupal spiracle; (b) dorsal view; (c) ventral view; (d) spiracular openings; (e-h) variations in morphology; (e and g) dorsal views; (f and h) ventral views.

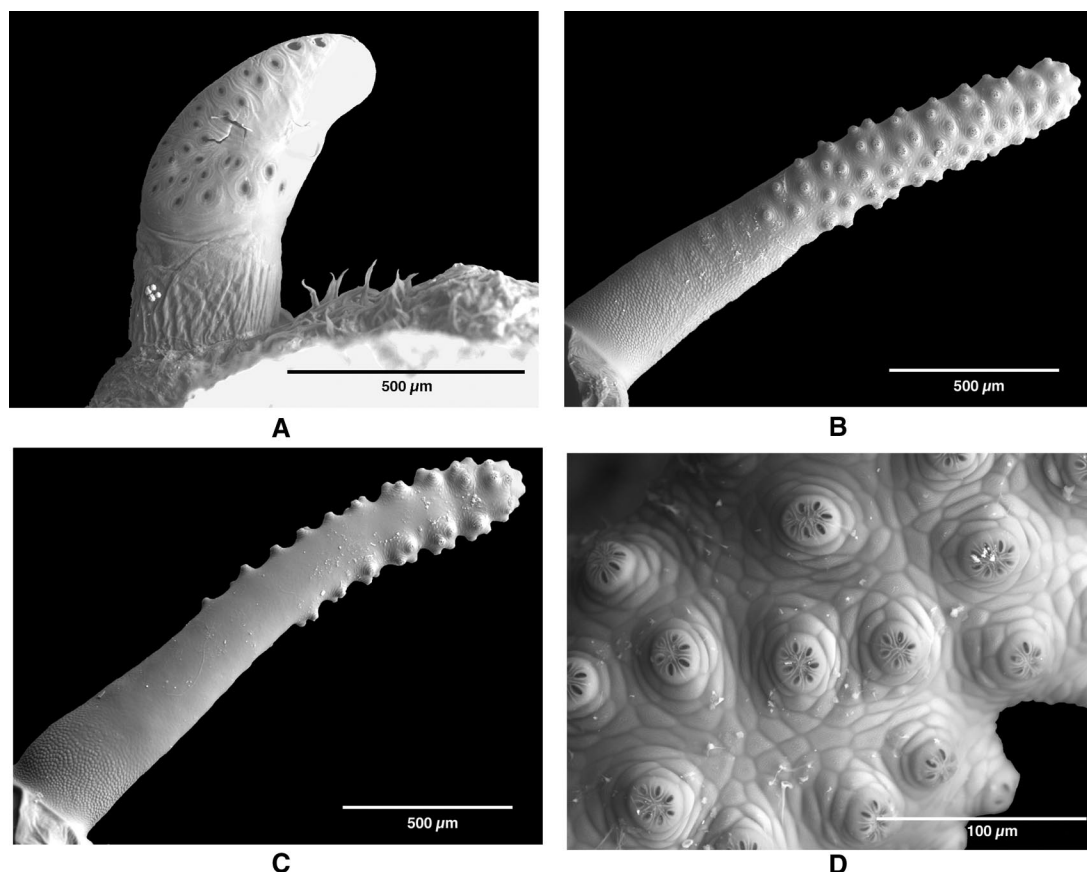


Fig. 6. (a-d) *M. loewii* (Williston, 1892). (a) Anterior spiracle dorso-lateral view; (b-d) pupal spiracle; (b) dorsal view; (c) ventral view; (d) spiracular openings.

back (Fig. 6a). Light brown in color. Spiracular openings on a clear area of the ventral surface, extending on the distal half of the spiracle. Clear area is ≈ 1.5 times longer than broad, with a triangular shape. Ventral part with the facets arranged in a double or triple row, inner ones with smaller facets. Upright part with the facets arranged in a double row.

Pupal Spiracles. Subcylindrical structures ≈ 1.3 mm in length (length:breadth ratio of spiracle 6:1), very slightly curved toward the lateral margins (Fig. 6b). Light brown in color. On $\approx 60\%$ of the dorsal and lateral surface are 6–7 bands, indistinct dorsally, vague laterally. These bands are not reaching ventral surface (Fig. 6c). On each band are irregular spaced and oval-shaped tubercles, each bearing 6–10 oval spiracular openings (Fig. 6d). Entire surface, including the space between tubercles finely granulated or reticulated, some of these projections bearing a single apical seta.

Material Examined. 1f, one puparium, Costa Rica, Puntarenas, Coto Brus, Sabalito, Estación Progreso, 1780 m., LS-317400, 599100. coll. 7.VI.2000 Milady Alfaro, ex wet decaying material in a hole of fallen unidentified tree (INBio). 1f, one puparium, Costa

Rica, San José, Escazú, Alto Tapezco, 1760 m., LN-209000, 518900. coll. 2.VIII.2001 Marcos-García, M. A. ex wet decaying material in a cavity of an unidentified tree (NMS).

M. obscurus Hine, 1924

Size of Puparium. Maximum width: 4–6 mm; length not including prp: 10–14 mm).

Anterior Larval Spiracles. About three times longer than broad, with the distal half curved back and slightly swollen (Fig. 7a). Light brown in color. Spiracular openings on a clear area of the ventral surface, extending on the distal half of the spiracle. Clear area is ≈ 2.5 times longer than broad, with the fold slightly beyond midpoint. Below a semicircular unsclerotized area. Facets arranged in one or two rows.

Pupal Spiracles. Two different morphologies exist. In one, the pupal spiracles are subcylindrical structures ≈ 1.2 mm in length (length:breadth ratio of spiracle 4.5–5:1), slightly flattened, with the distal two-thirds usually curved toward the lateral margins and the apex curved inward. On $\approx 65\%$ of the dorsal and lateral surface are 5–7 bands, indistinct dorsally,

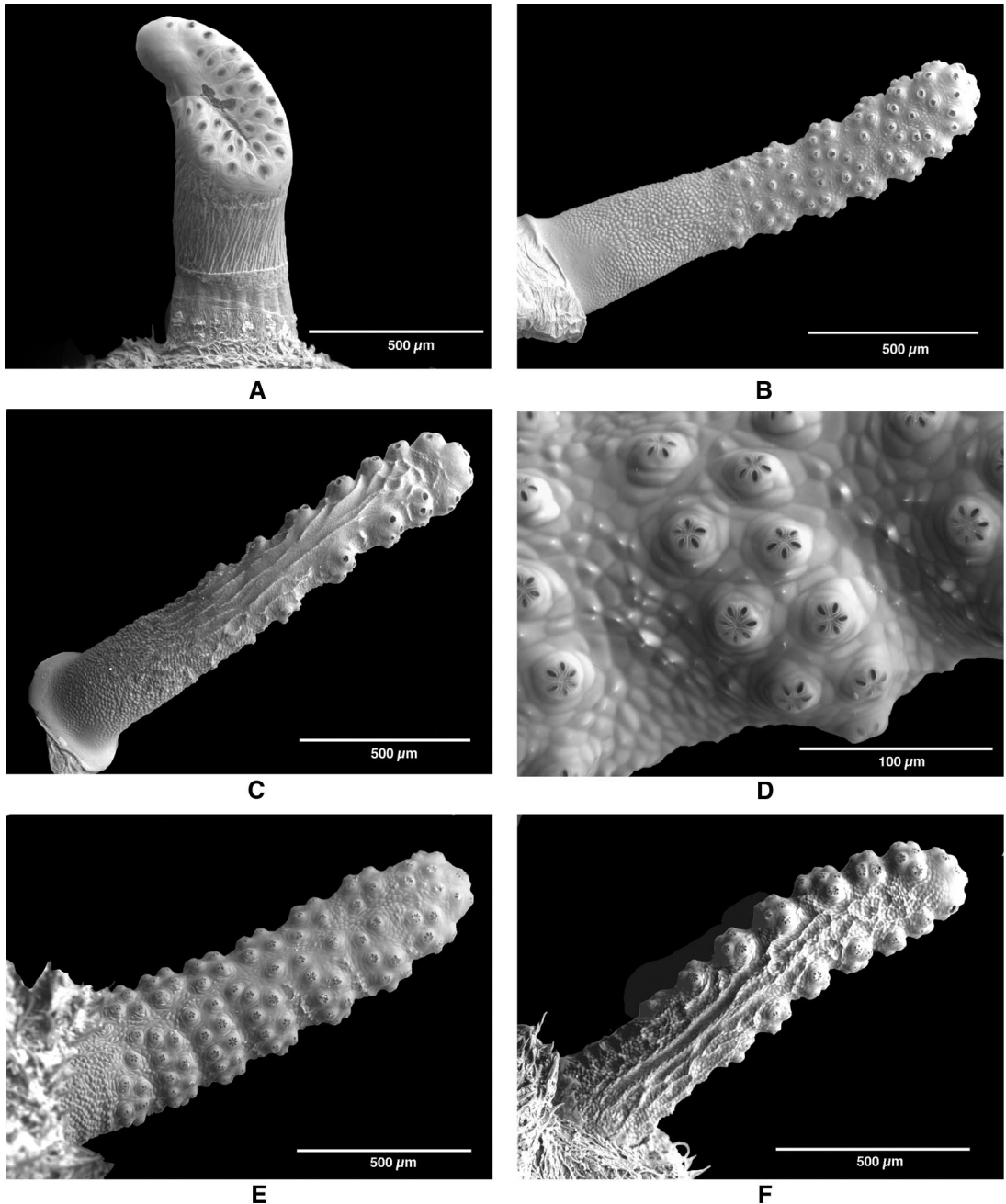


Fig. 7. (a–f) *M. obscurus* Hine, 1924. (a) Anterior spiracle dorso-lateral view; (b–f) pupal spiracle; (b) dorsal view; (c) ventral view; (d) spiracular openings; (e and f) variation in morphology; (e) dorsal view; (f) ventral view.

clearly laterally (Fig. 7, b and c). These bands not reaching ventral surface. On each band are irregularly spaced and oval-shaped tubercles, each bearing 6–10 oval spiracular openings (Fig. 7d).

In the other, the pupal spiracles are subcylindrical structures ≈ 1.2 mm in length (length:breadth ratio of spiracle 3.5:1), stout, and slightly flattened apically. On

$\approx 90\%$ of the dorsal and lateral surface are 7–9 bands, indistinct dorsally, clearly laterally (Fig. 7, e and f). These bands are not reaching ventral surface. On each band are irregular spaced and oval-shaped tubercles, each bearing 6–10 oval spiracular openings.

In both types, the pupal spiracles share the following characters: 1) entire surface, including the space

between tubercles finely granulated or reticulated, and 2) the greater part of the ventral surface is furrowed with deep longitudinal ridges (Fig. 7, c and f).

Other differences between the two types are that, in the first type, the puparium has a very long posterior respiratory process, more than two times the body length. In the latter type, the posterior respiratory process is about as long as the body length.

Material Examined. First type: 4m, 4f, eight puparia, Costa Rica, Guanacaste, Liberia, Mayorga, A. C. Guanacaste, 700 m., LN-318600, 375400. coll. 28.VI.2001 Duvalier Briceño, ex wet decaying material in a hole of *Enterolobium cyclocarpum* (Jacq.) Griseb. (Fabaceae: Mimosoideae) tree. 6m, 2f, eight puparia, Costa Rica, Limón, Talamanca, Sixaola, 10–30 m, LS-390000, 612000., coll. 25.II.1999 Braulio Hernández Bogantes, ex wet decaying material in hole of *Carapa guianensis* Aubl. (Meliaceae) tree. Second type: 3m, 3f, six puparia, Costa Rica, Guanacaste, P. N. Santa Rosa, 300 m., LN-313000, 359800. coll. 10.VII.2000 Duvalier Briceño, ex wet decaying material in a hole of a *Spondias mombin* L. (Anacardiaceae) tree. 1m, one puparium, Costa Rica, Guanacaste, La Cruz, A. C. Guanacaste, sector Santa Elena, LN-320000, 359300. coll. 17.XI.2000 Duvalier Briceño, ex wet decaying material of a *Hymenaea courbaril* L. (Fabaceae: Caesalpinioideae) tree (INBio).

Palpada furcata (Wiedemann, 1819): Third Instar

Overall Size and Shape. Length, 14–15 + 7–8 mm; maximum width, 3.5–4 mm. A long-tailed larva with internal mouth hooks and retractile anterior spiracles. Subcylindrical in cross section, truncate anteriorly, and tapering posteriorly. Dorsal body surface coated in fine and well-developed pubescence backwardly directed, which becomes shorter and scarce on the ventral surface, except for the anal segment. Anterior fold coated in sclerotized spicules, which become progressively shorter posteriorly. Prolegs bearing crochets in two main rows.

Head. Mandibles and mandibular lobes internal, mandibles supporting the expanded mandibular lobes. Mouthparts adapted for filter feeding. Basal section of the papillae supporting antennomaxillary organs divided to the base. Dorsal lip broad, lacking a medial groove and without setae.

Thorax. Lateral lips rounded and well developed (in profile projecting forward from the anterior part of the prothorax), coated in short and fine setae at base and longer setae at tip. Dorsal surface of the prothorax with longitudinal grooves. Anterior fold with a broad spicule band reaching to sensilla two and extending to lateral margins of mesothorax. These spicules are densely aggregated, backwardly directed, apically sclerotized, and become progressively shorter posteriorly. Dorsal surface of the prothorax with a pair of spiracles, sclerotized, elongated (length:breadth ratio of spiracle 5–6:1), with pointed and slightly curved tips, and retractile into inverted integumental pockets. Spiracular openings on a clear area of the ventral surface, extending on the distal fourth of the spiracle.

Spiracles narrowed just before the clear area; below this point the color is distinctly darker than apex. Facets are arranged in one row around the periphery of the clear area. Lateral margin of mesothorax with two patches of only apically sclerotized spicules arranged as follows: a group of 15 just anterior to fourth sensilla of mesothorax and another group of ≈ 25 in front of the fifth sensilla. Mesothorax bearing well-developed prolegs with ≈ 40 –50 crochets arranged in multiple rows. Antero-ventral margin of metathorax with two patches of spicules behind the mesothoracic prolegs.

Abdomen. Pupal spiracles obvious on the dorsal surface of first abdominal segment. Abdominal segments 1–6 each with a pair of prolegs. Prolegs, in ventro-lateral view, appearing as small cones that are shorter than broad, with crochets in two main transverse rows. Approximately 5–6 large primary crochets with only the distal third sclerotized. Crochets arrangement gradually change from posterior penellipse (i.e., crochets complete around posterior margin of the prolegs) on abdominal segment one to lateral penellipse (i.e., crochets complete around outer margin). On the segment 7, sensilla 4 is aligned horizontally with sensilla 5 and 6. Anal segment extended to $\approx 55\%$ length of thorax and first seven abdominal segments, with three pairs of weakly developed lappets. Posterior respiratory process lustrous, sclerotized, and brown in color. Six spiracular slits arranged around two central scars. Four pairs of spiracular setae.

Chaetotaxy. Distribution and number of sensilla following pattern of other syrphid larvae (Rotheray and Gilbert 1999). Prothorax (P) with 12 pairs of sensilla; mesothorax (Ms) and metathorax (Mt) with 9 pairs; abdominal segments 1–7 with 11 pairs; anal segment with 3 pairs of sensilla (sensilla 9, 10, and 11) and 3 pairs of lappets.

Puparium. Subcylindrical in cross section. Dark brown in color. Pupal spiracles projecting from middle of upper part of operculum, separated by distance clearly less than a third of the spiracle length. These are subcylindrical ≈ 1.9 mm in length (length:breadth ratio of spiracle 5–6:1), with the distal two-thirds usually curved toward the lateral margins of the puparium and slightly flattened apically (Fig. 8, a–c). On $\approx 80\%$ of the dorsal and lateral surface with irregular spaced and oval-shaped tubercles, each bearing 6–10 oval spiracular openings (Fig. 8d). The tubercles are arranged in vague bands laterally. Dorsal surface with a narrow tapering gap that disappears at the base. Entire surface, including the space between tubercles, finely granulated or reticulated and coated in dense setae that become longer basally.

Material Examined. 2m, 1f, three puparia, Costa Rica, Cartago, Paraíso, Río Macho, 1200 m., LN-193500, 553800, coll. 12.XI.1999 Rotheray, G., Hancock, G. & Zumbado, M. ex coffee waste (NMS).

Discussion

The larvae of all studied species have been found living in very wet vegetal decaying matter or sub-

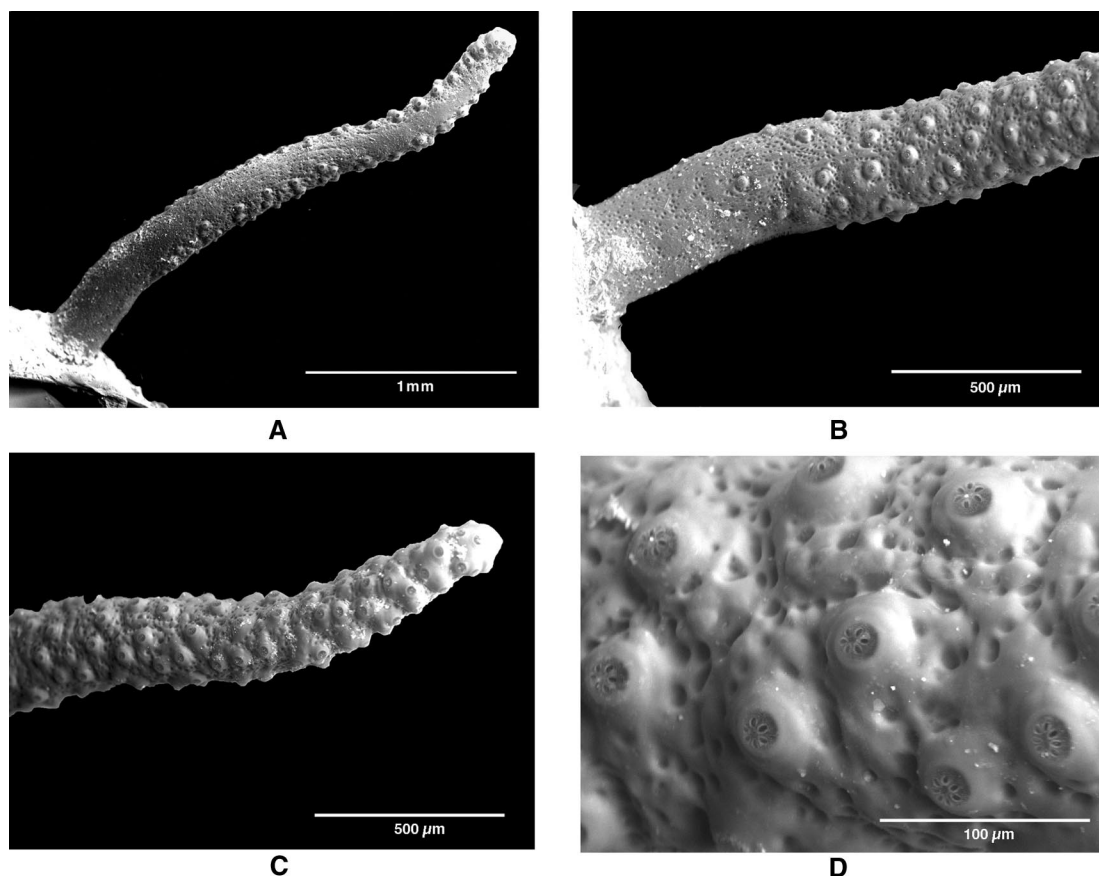


Fig. 8. (a-d) *P. furcata* (Wiedemann, 1819), pupal spiracle. (a) Ventral view; (b) basal view; (c) distal view; (d) spiracular openings.

merged in stagnant water on hole trees. As to be expected, they have an extendable breathing tube and seem similar to the long-tailed larvae of the Old World: *Sericomyia* Meigen, 1803; *Anasimya* Schiner, 1864; *Eristalinus* Rondani, 1845; *Eristalis* Latreille, 1804; *Helophilus* Meigen, 1822; *Mallota* Meigen, 1822; *Myathropa* Rondani, 1845; *Parhelophilus* Girschner, 1897. In all of these larvae, the long anal segment is a result of an extension in the first ring (i.e., the second and third pairs of lappets are together at the end of the anal segment, with the first pair about halfway along its length), which distinguishes them from other larvae with extended anal segment (Rotheray 1993).

The mouthparts of the larvae of *H. coeruleithorax*, *Meromacrus* spp., and *P. furcata* are similar to those of other saprophagous syrphids, which feed by filtering micro-organisms from fluids. For example, in all of these taxa: the thorax is broad and the anterior fold is coated in spicules; the dorsal lip is firm, not fleshy; the lateral lips are large and coated in variously sized setae; behind the mouth, a feeding channel is present and the mandibular lobes are within the mouth.

The larvae of *Meromacrus* and *H. coeruleithorax* show striking similarities. Both of these genera share a number of characters, such as two lines of setae

located on the ventro-lateral margin of the abdominal segments 1-7; prolegs with crochets in three main rows; last two pairs of prolegs with most of the large primary crochets facing to the lateral margins of the body. However, they may be separated readily by the characters in the key to Neotropical long-tailed larvae. *H. coeruleithorax* puparia are very distinctive. They can be recognized by the characteristic twist shape of the pupal spiracle, which may be a character of phylogenetic importance. These puparia may be mainly separated by the ornamentation of the pupal spiracles. However, we found in *M. laconicus* and *M. obscurus* slight variation in the ornamentation of these spiracles. The material examined is not enough to determine whether these variations are related to the existence of more than one species. The study of additional specimens will help to resolve whether these differences respond to intraspecific or interspecific variation. This fact may complicate the identification of these species. In this case, the shape of the anterior spiracle is the main diagnostic character between both species.

The larva of *P. furcata* can be separated from other long-tailed larvae by the following characters: spicules on the prothorax reaching to second sensilla of the

prothorax and the mesothoracic patches of spicules; antero-ventral margin of metathorax with two patches bearing spicules; prolegs with crochets in two main rows. However, with the immature stages of only one species described, many more will need to be studied before we can characterize and distinguish *Palpada* larvae.

Acknowledgments

We are very grateful to F. Christian Thompson (United States Department of Agriculture, Agricultural Research Service, Systematic Entomology Laboratory) for not only arranging loans of specimens from the Smithsonian Institution, but also for access to unpublished manuscripts, keys, and for general guidance and encouragement. We are also grateful to the team of parataxonomists from the Instituto Nacional de Biodiversidad (INBio), for support and help in Costa Rica through a cooperative agreement with the CIBIO (Alicante, Spain), and to D. Briceño and B. Hernández, who enthusiastically collected and reared many of the species in this paper. Financial support was partially provided by the following Research Programmes: CONABIO K038 (Instituto de Ecología de Xalapa, Veracruz, México), CONABIO Y035 (Colegio de la Frontera Sur, Chiapas, México), and GR02-09 (Alicante University, Spain). G.E.R. and E.G.H. thank members of the 1998 Glasgow University Exploration Society expedition to Trinidad for their help in the field, and finally, to the Leverhulme Fund for funding.

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Received for publication 18 July 2002; accepted 24 February 2003.