*Zootaxa* 4012 (1): 135–155
www.mapress.com/zootaxa/


**Article**

ISSN 1175-5326 (print edition)
**ZOOTAXA**
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.4012.1.7
http://zoobank.org/urn:lsid:zoobank.org:pub:82F22029-9046-4859-A732-D2B7EFD01F4A

# Revision of the Neotropical genus *Eschatocerus* Mayr (Hymenoptera, Cynipidae, Eschatocerini) with biological notes and the first description of the terminal larva

JOSÉ LUIS NIEVES-ALDREY[1] & GERMÁN SAN BLAS[2]

[1]*Museo Nacional de Ciencias Naturales (CSIC), Departamento de Biodiversidad y Biología Evolutiva, C/ José Gutiérrez Abascal 2, ES-28006 Madrid, Spain. E-mail: aldrey@mncn.csic.es*
[2]*Laboratorio de Entomología, Instituto Argentino de Investigación de las Zonas Áridas (IADIZA, CCT Mendoza CONICET). Av. A. Ruiz Leal s/n, Pque. Gral. San Martin*
*CC: 507, CP: 5500. Mendoza. Argentina. E-mail: gsanblas@mendoza-conicet.gob.ar*
*Author for correspondence: Jose Luis Nieves-Aldrey; E-mail: aldrey@mncn.csic.es*

## Abstract

The gall wasp genus *Eschatocerus* (Hymenoptera, Cynipidae, Eschatocerini), a cynipid genus of gall inducers on *Prosopis* and *Acacia* species (Fabaceae), endemic to southern South America, is revised. Complete descriptions of the external morphology of the genus and its three known species, illustrated with scanning electron photographs, are given for the first time, and an updated key for the identification of the species is provided. The biology of the species of *Eschatocerus* and their galls is described. Host plant associations are given, and the terminal larva of *Eschatocerus niger* is described for the first time. Preliminary notes on the inquiline and parasitoid community associated with the galls of *Eschatocerus* species are also given.

**Key words:** gall wasps, life history, South America, Argentina, *Prosopis*, *Acacia*

## Introduction

Cynipidae and Figitidae are the two largest families of Cynipoidea, a species rich superfamily of predominantly parasitic Hymenoptera. However, the Cynipidae family is different from the remaining Cynipoidea families in that it comprises only specialized herbivores capable of inducing complex galls on plants or of modifying existing galls as inquilines, either of other Cynipidae or, in some cases, of Chalcidoidea or Lepidoptera (Nieves-Aldrey *et al*. 2009; van Noort *et al*. 2007). The family has traditionally been divided into six tribes: Aylacini, Eschatocerini, Cynipini, Diplolepidini, Pediaspidini and Synergini (Ashmead 1903; Nieves-Aldrey 1994, 2001; Ronquist 1999; Csóka *et al*. 2005), while two additional tribes were described in recent years: Paraulacini and Qwaqwaini (Nieves-Aldrey *et al.* 2009; Liljeblad *et al.* 2011).The classification of the Cynipidae has been just adjusted in light of the more recent combined, morphological and molecular, phylogenetic analysis (Ronquist *et al.* 2015). In this study, it is shown that the Aylacini and the Synergini are not monophyletic and the classification of the Cynipidae is modified accordingly, with the erection of four new tribes: Aulacideini, Diastrophini, Ceroptresini and Phanacidini. As a result of this reclassification, the Cynipidae are now divided into twelve monophyletic tribes (Ronquist *et al.* 2015).

The great majority of the *circa* 1500 gall wasp species occur in the temperate regions of the Northern Hemisphere. These species are mainly cynipines, commonly known as oak gall wasps (Stone & Cook 1998; Nieves-Aldrey 2001; Liljeblad *et al.* 2008); the tribes Paraulacini and Eschatocerini are peculiar because they are endemic of temperate areas of the Neotropics (Nieves-Aldrey *et al.* 2009; Medianero & Nieves-Aldrey 2111), whereas the Qwaqwaini have a southern Afrotropical distribution. The Cynipidae were recorded as absent in Australia and the Oceanian region, but a species of the tribe Synergini has recently been described from Papua New Guinea (Nieves-Aldrey & Butterill 2014).

In the present paper, we address one of the two cynipid tribes endemic to the Neotropical Region, the Eschatocerini. The Eschatocerini comprises one genus, *Eschatocerus* Mayr, with three described species:

*Accepted by I. Miko: 10 Jul. 2015; published: 2 Sept. 2015*

*Eschatocerus acaciae* Mayr, *E. niger* Kieffer & Joergensen and *E. myriadeus* Kieffer & Joergensen (Mayr 1881; Kieffer & Joergensen 1910).

The tribe Eschatocerini was erected by Ashmead (1903) based on the type species *Eschatocerus acaciae* Mayr, 1881. The gall associated with this genus was illustrated in Houard (1933), while a morphological diagnosis of the adult with some line drawings of this species was given by Weld (1953) in his identification key for Cynipoidea throughout the world. Díaz & De Santis (1975) provided further diagnostic data for adults, including a description of the male, with figures of the antenna, fore wing and genitalia and further data and illustrations of the gall. Later, Diaz (1980) presented an identification key for the three described species, mainly based on the coloration of adults, and redescribed *Eschatocerus myriadeus* Kieffer & Joergensen, illustrating the female fore wing and the gall. More recently, Melika (2006) included some additional line drawings of *Eschatocerus acaciae* in his monograph of gall wasps of Ukraine. The detailed morphological information of the same species, based on scanning electron micrographs, was included in the morphological phylogenetic analysis of Liljeblad *et al*. (2008). Finally, metal-enrichment in the ovipositor and mandibles, and antennal morphology and sensillar equipment of *Eschatocerus acaciae* were studied in recent analyses (Polidori *et al*. 2013; Polidori & Nieves-Aldrey 2014). Despite this available taxonomic information on the species of *Eschatocerus*, the genus as a whole has not been revised yet and the taxonomic knowledge of this tribe is still poor and fragmentary.

The classification of the Eschatocerini in its own tribe has just been reinforced after the recent study by Ronquist *et al*. (2015) that found strong support for the monophyly of this group. The tribe is unique within the Cynipidae in many ways: morphological, biological and biogeographical. It is one of the two cynipid tribes endemic to the Neotropical Region, and the only one whose species are gall inducers on Fabaceae plants. Regarding morphology, the tribe exhibits a large number of unique or highly unusual features. However, despite this high number of autapomorphies, the tribe shares numerous morphological traits with the Diplolepidini tribe. Liljeblad *et al*. (2008), found that Diplolepidini + Eschatocerini were the sister groups of a monophyletic Cynipini. With the Pediaspidini, Diplolepidini, and Qwaqwaiini, the Eschatocerini form a group of species-poor but highly distinctive lineages, suggesting that they are the products of a long period of evolution in isolation (Ronquist *et al.* 2015).

In recent years, the junior author of this paper was able to collect fresh materials in Argentina, of both galls and adult insects, of the three known species of *Eschatocerus.* Based on these materials, we studied the skeletal morphology of the insects in detail using SEM. In light of the new descriptive information gathered in the present study, we revise the genus, including a new, richly illustrated key for the identification of the three known species of *Eschatocerus*. Furthermore, we include the first description of the mature larva of one species of *Eschatocerus*.

## Materials and methods

### *Field work*

Field work was carried and material was collected by the junior author of this study, mainly during summers, from February 2011 to March 2013, at four sites in the Mendoza province in the Cuyo Region (Western Central Argentina). The galls were collected on *Prosopis flexuosa* D.C. Additionally, samples of the galls of *E. acaciae* were collected on *Prosopis alba* Griseb., in September 2011 and 2012, by J. Martín Cano in the provinces of Santiago del Estero and Formosa (at the National Park Rio Pilcomayo), and sent to the first author of the study. Galls were collected and dissected in the laboratory. Wasps were mainly obtained by rearing in emergence cages. Larvae, pupae and adults were also obtained by dissection of the freshly collected galls.

Materials were deposited in the Museo Nacional de Ciencias Naturales (Madrid, Spain; MNCN) and Instituto Argentino de Investigación de las Zonas Áridas (IADIZA, CCT Mendoza CONICET).

Terminology of the anatomical structures, sculpture and abbreviations follow Ronquist & Nordlander (1989), Nieves-Aldrey (2001) and Liljeblad *et al.* (2008).

For observation under scanning electron microscope (SEM), adults were dissected in 90% ethanol, air dried, mounted on a stub, and coated with gold; micrographs were taken with a SEM Inspect S (high vacuum technique) for several standardized views based on Liljeblad and Ronquist (1998). Images will be deposited at MorphBank (http://www.morphbank.net).

The forewings and dissected ovipositor were mounted in Euparal on microscope slides and were examined with a Wild MZ8 stereo-microscope. Images of the intact and dissected galls were obtained with a Nikon Coolpix

P6000 digital camera. Measurements were made with a calibrated micrometer scale attached to the ocular of a light microscope (Wild MZ8).

## Tribe ESCHATOCERINI

Eschatocerini Ashmead, 1903. *Psyche* (Cambridge Mass.), 10: 147.
Type genus *Eschatocerus* Mayr, 1881

***Diagnosis***

This morphologically distinctive tribe differs from other cynipid tribes by many morphological features. The following diagnostic characters can be observed: Toruli situated very high on the head; presence of a median carina between the antennal sockets extended to median ocellus (Fig. 1A); occiput concave, often with visible lateral occipital carinae (Figs 1B, 4A); sensillae coeloconic type A very large and situated far from distal margin of the flagellomeres (Fig. 2C). Maxillary palps three-segmented and reduced; fifth and fourth maxillary palps apparently fused (Fig. 1B). Notauli absent (Fig. 3A). Scutellar foveae absent; dorsal axillar area large, triangular and situated in the same plane as mesoscutellum (Fig. 3C). Pubescence on mesopleural triangle absent. Propodeal carinae absent (Fig. 4C). Fore wing veins reduced; R1 virtually absent and Rs ending well before anterior margin of wing; cross medial vein absent and Rs+M vein addressed to the meeting point between medial and MCu1 (Figs 5A–C). Terebra of female ovipositor extremely short. Association with Fabaceae (*Acacia* and *Prosopis*). The tribe can also be distinguished by a combination of the following characters which are not unique as the above mentioned: Subocular (malar) furrow present, sometimes weak; female antenna filiform, with 11 flagellomeres; male antenna without sexual modified flagellomeres (Figs 2B, 2F); clypeus distinct, large, trapezoidal, ventral margin projected over mandibles (Fig. 1E); clypeo-pleurostomal lines deeply impressed. Pronotum dorsally very short; without pronotal plate, lateral margins of pronotum with reticulate sculpture and glabrous; mesopleura reticulate, without mesopleural impression (Fig. 3D).

**Biology:** Gall inducer on *Prosopis* spp. and *Acacia* spp. (Fabaceae).

**Diversity and distribution:** A single genus, *Eschatocerus*, with 3 species. South Neotropical. Recorded from Argentina and Uruguay.

***Included species***

*Eschatocerus acaciae* Mayr, 1881
*Eschatocerus niger* Kieffer & Joergensen, 1910
*Eschatocerus myriadeus* Kieffer & Joergensen, 1910

## Key to species of *Eschatocerus*

**1.** Genae expanded behind compound eyes. Subocular furrow more or less indicated by rugose sculpture (Figs 1A, 1C). Frons and vertex rugose (Figs 1A, 1C). Lateral occipital carinae conspicuous (Figs 1B, 1D). Median mesoscutal impression indicated, although very short (Fig. 3A). Propodeum medially with reticulate sculpture (Figs 4C, 4D). Scuto-scutellar suture (inner margin of axillae) marked. Setae on disc and basal cell of forewing not very dense (Figs 5A, 5B). Females contrasting strongly in color with males or, if not, both sexes black (Figs 8A–D). Galls more or less regularly spherical (Figs 9A–D). . . . . **2**

• Genae not expanded behind compound eyes (Fig. 1E). Subocular furrow very weak or indistinct. Frons and vertex reticulate (Fig. 1A). Lateral occipital carinae inconspicuous. Median mesoscutal impression absent (Fig. 3E). Propodeum medially with very weak reticulate sculpture, almost smooth (Fig. 4E). Scuto-scutellar suture (medial margin of dorsal axillar areas) indistinct, weakly marked (Fig. 3E). Setae on fore wing disc and basal cell of fore wing dense (Fig. 5C). Both sexes with mesosoma black and metasoma brown (Figs 8E, 8F). Galls plurilocular internally on twigs (Figs 9E–F) . . . . . ***E. myriadeus***

**2.** Genae more heavily expanded behind eyes (Fig. 1A). Frons and vertex with sculpture more strongly rugose (Fig. 1A); inner margin of compound eyes inflexed. Female F1 shorter than F2 and 1.7 times as long as pedicel (Fig. 2A). Females yellowish, males blackish (Figs 8A, 8B). Galls large up to 35 mm (Fig. 9A).. . . . . ***E. acaciae***

• Genae only slightly expanded behind eyes (Fig. 1C). Frons and vertex with sculpture only weakly rugose (Fig. 1C); inner margin of compound eyes straight. Female F1 1.3 times as long as F2, and only 1.3 times as long as pedicel (Fig. 2E). Both sexes black (Figs 8C, 8D). Galls smaller, usually 8–15 mm (Fig. 9D) . . . . . ***E. niger***

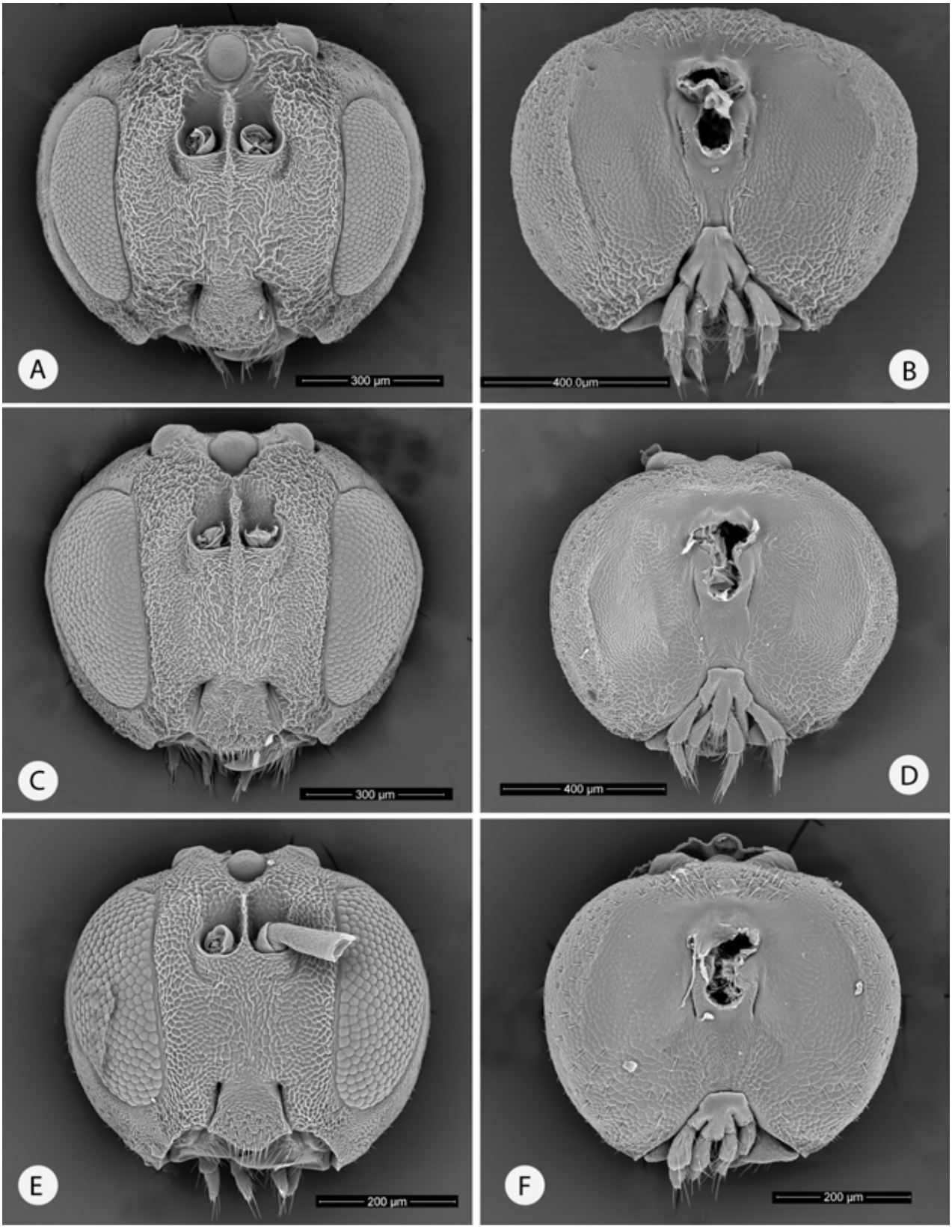


**FIGURE 1.** Head, anterior and posterior view of species of *Eschatocerus:* (A) Anterior view and (B) Posterior view of *E. acaciae.* (C) Anterior view and (D) Posterior view of *E. niger.* (E) Anterior view and (F) Posterior view of *E. myriadeus*.

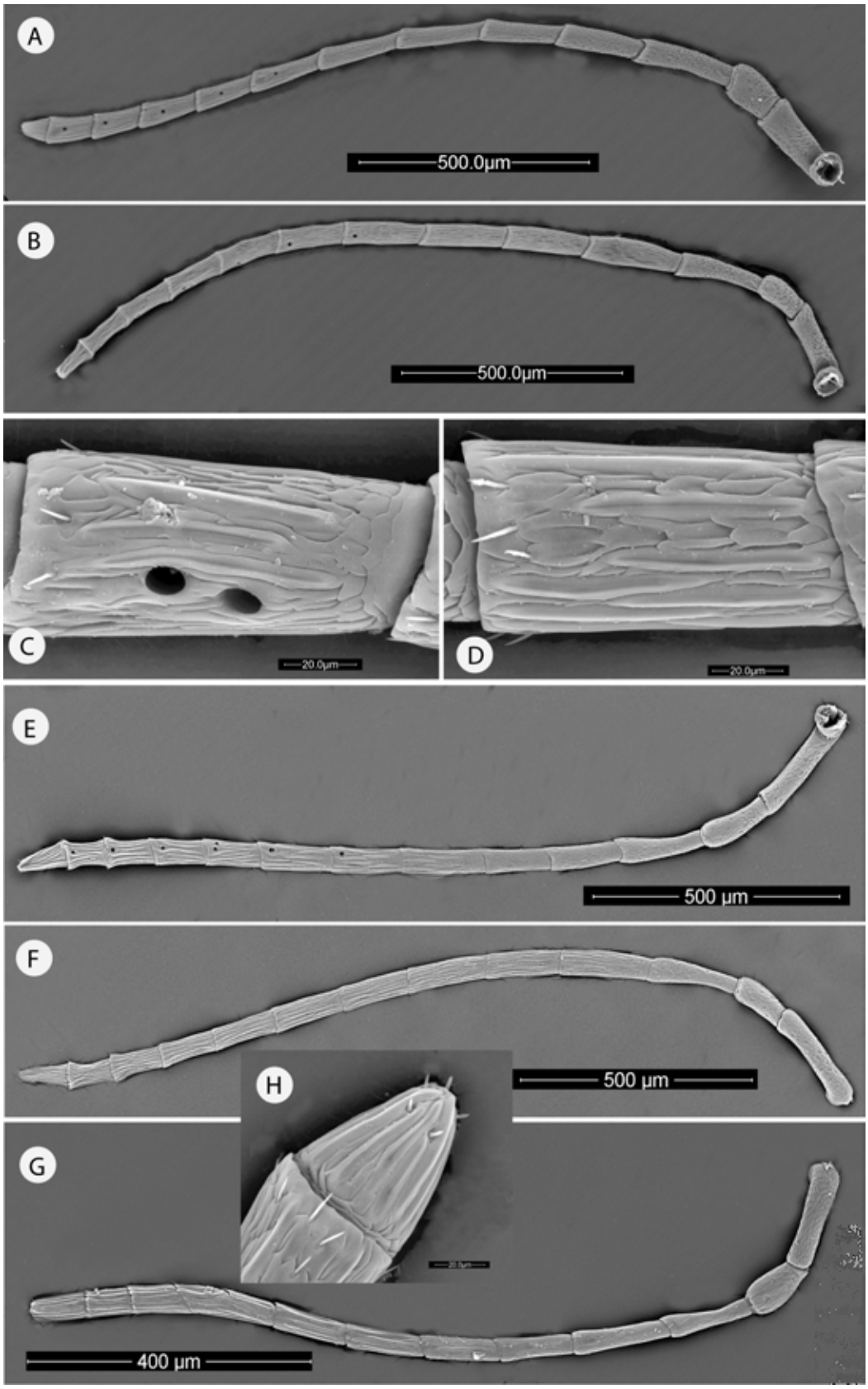


**FIGURE 2.** Antennae of species of *Eschatocerus*: (A) Female antenna of *E. acaciae.* (B) Male antenna of *E. acaciae.* (C) Detail of large sensilla coeloconic type A on antennal flagellomere of *E. acaciae.* (D) Detail of sensilla placoidea on antennal flagellomere of *E. acaciae*. (E) Female antenna of *E. niger.* (F) Male antenna of *E. niger.* (G) Female antenna of *E. myriadeus.* (H) Detail of last flagellomere of female antenna of *E. acaciae.*

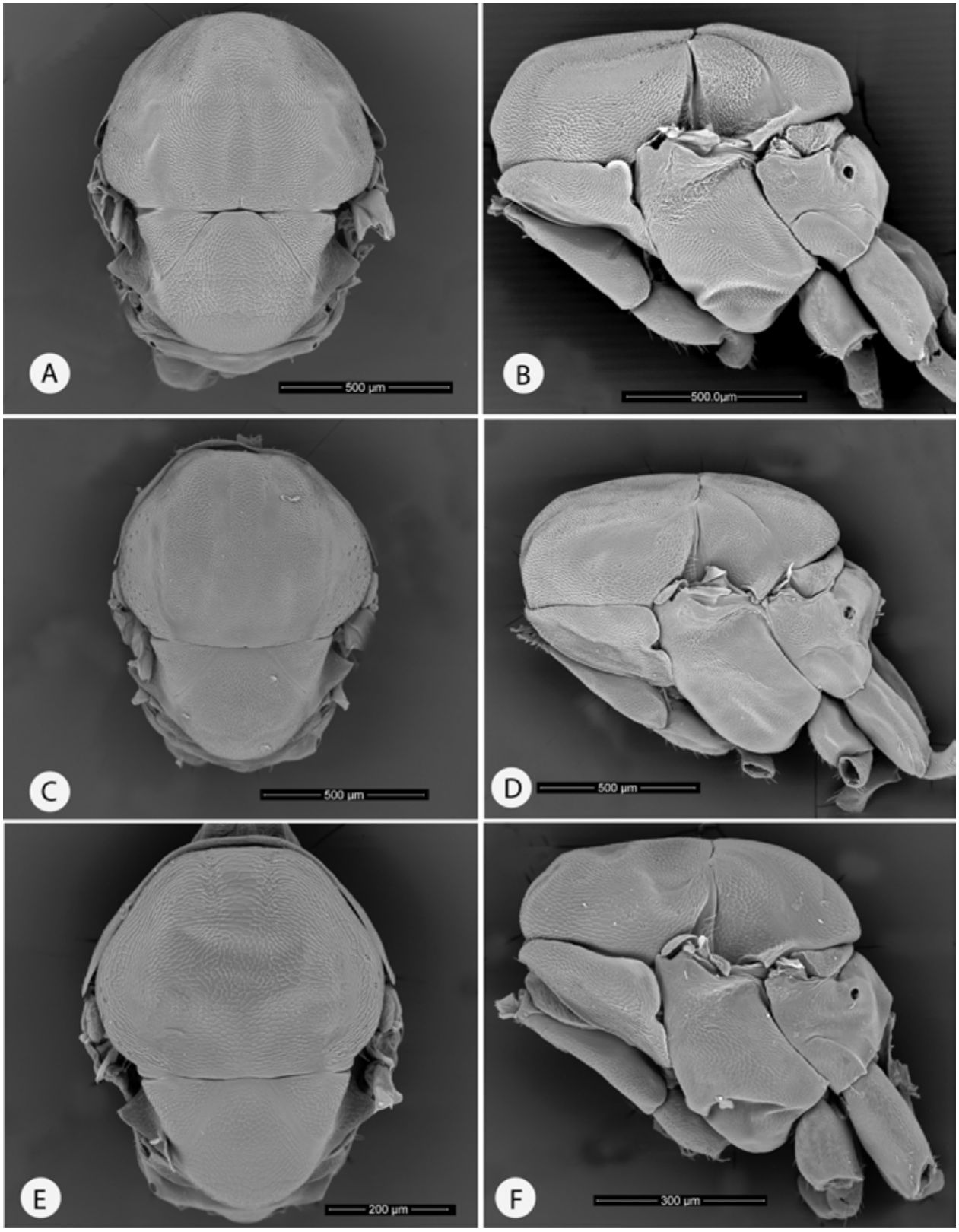


**FIGURE 3**. Mesosoma, dorsal and lateral view of species of *Eschatocerus*: (A) Dorsal view and (B) lateral view of *E. acaciae.* (C) Dorsal view and (D) Lateral view of *E. niger*. (E) Dorsal view and (F) Lateral view of *E. myriadeus*.

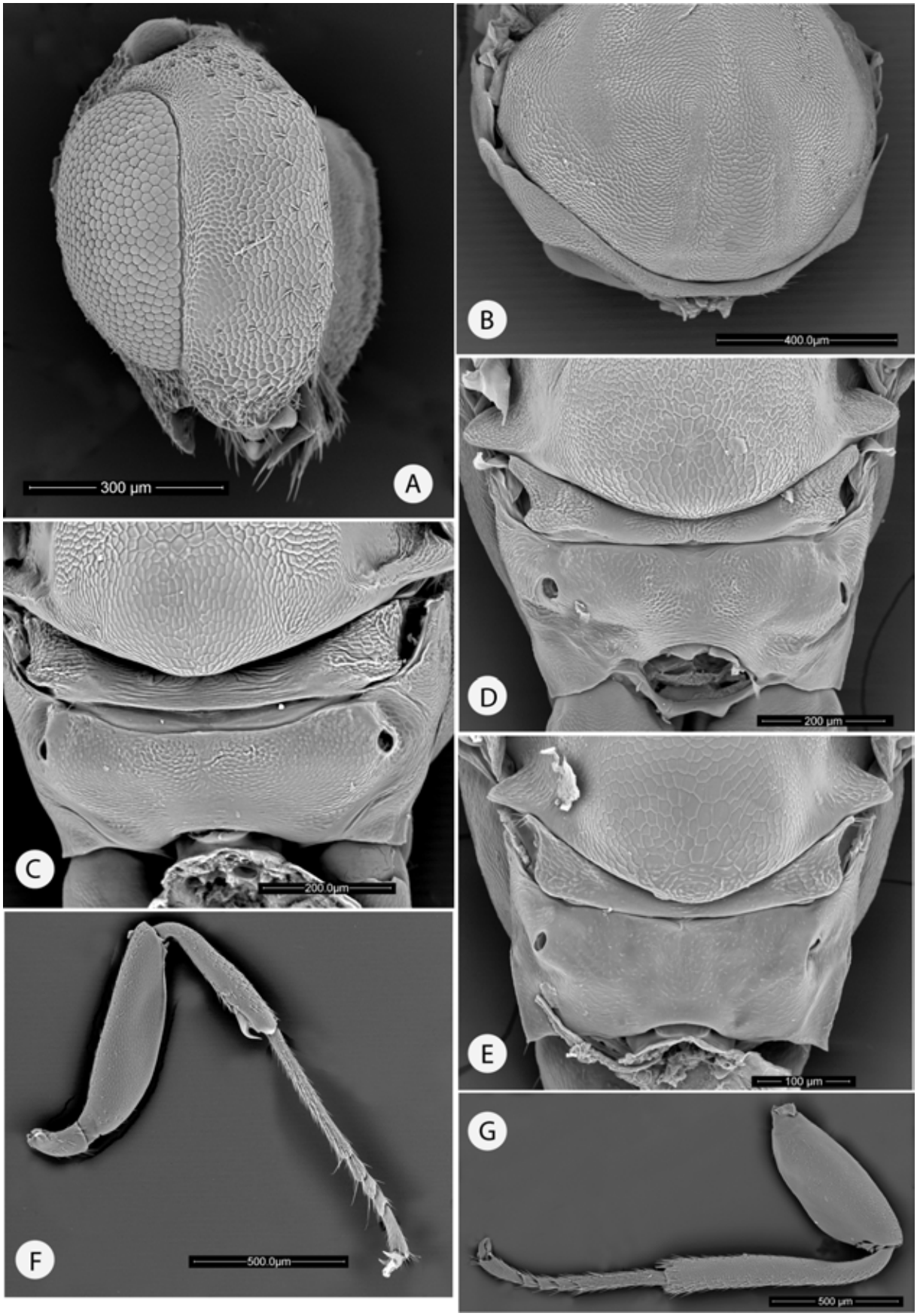


**FIGURE 4.** (A) *Eschatocerus acaciae*, head lateral view (B) *E. niger*, pronotum anterior view. (C) Propodeum of *E. acaciae* (D) Propodeum of *E. niger.* (E) Propodeum of *E. myriadeus*. (F) Fore leg of *E. acaciae*. (G) Hind leg of *E. niger.*

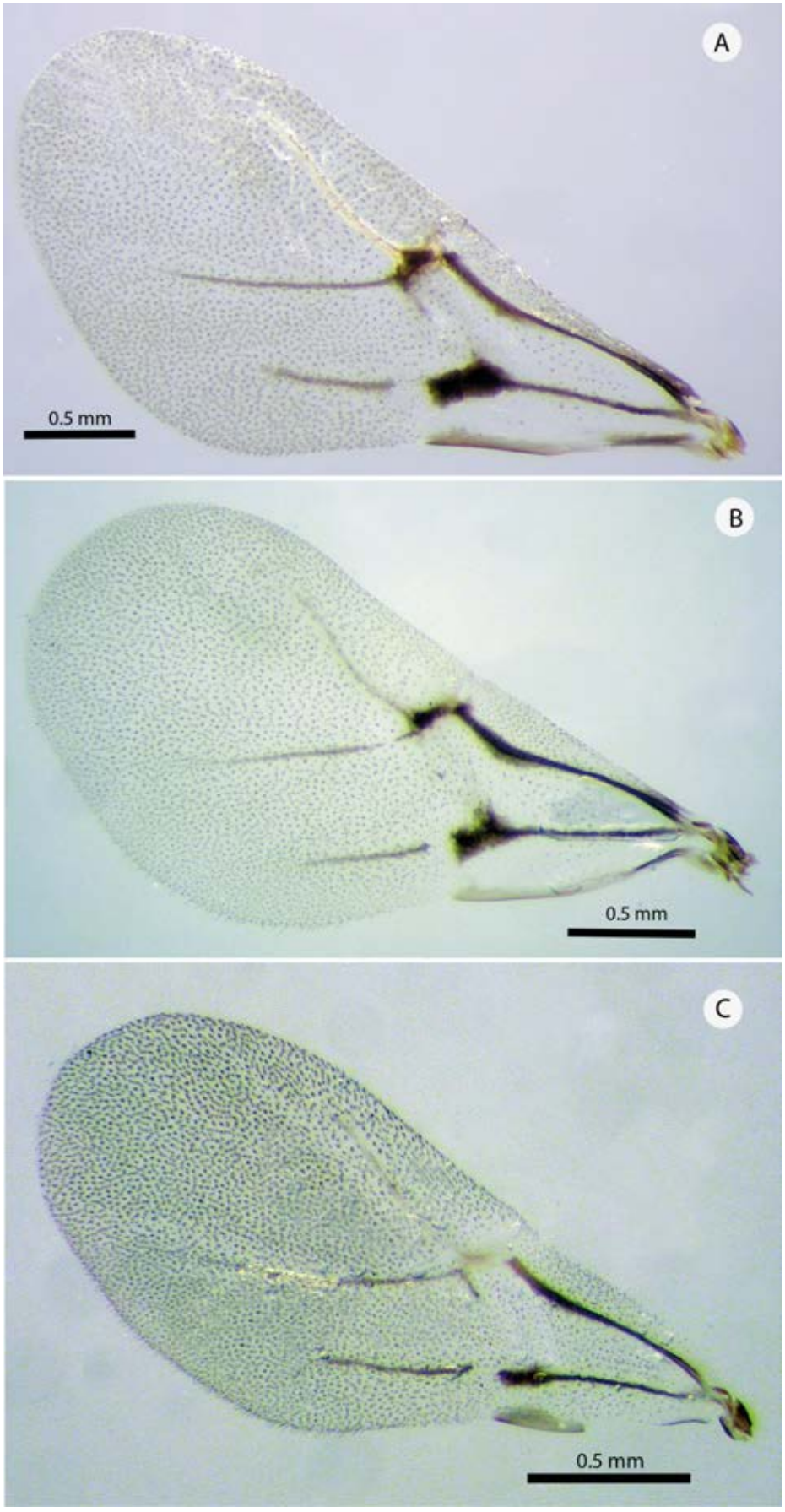


**FIGURE 5**. Forewing of species of *Eschatocerus*: (A) *E. acaciae* (B) *E. niger* (C) *E. myriadeus.*

### *Eschatocerus acaciae* Mayr, 1881

(Habitus Figs 8A, 8B)

*Eschatocerus acaciae* Mayr, 1881. *Gen. Gall. Cynip*., p.14

**Type material.** The type material of this species is deposited in the Naturhistorische Museum of Vienna and was revised by Melika & Bechtold (2001) who designed lectotype and paralectotypes (not herein examined). According to them, types consist of 11 males and 3 females on 11 pins; all labelled as "Collect. G. Mayr" and "Esch. acaciae G. Mayr. Type;" 8 pins with additional red label "TYPUS," which, however, do not originate from Mayr. The type material also includes approximately 40 galls. All specimens are damaged in some way and lack some parts of the body. The type locality is unknown.

**Material examined.** 4 males, 6 females, "ARGENTINA, Santiago del Estero, ex galls *Prosopis alba* (Fabaceae), galls collected 23/IX/2011, adults emerged X/2011. J. Martin Cano leg". 50 males, 78 females, "ARGENTINA, Mendoza, Luján de Cuyo, ex galls *Prosopis flexuosa*, collected 27/XI/2011, adults emerged XII/2011. G. San Blas leg". Additionally, we examined the galls of this species, collected at the National Park Rio Pilcomayo (Formosa province) on *Prosopis alba* (24/IX/2012). J. Martin Cano leg.

#### *Diagnosis*

*Eschatocerus acaciae* differs from *E. niger* and *E. myriadeus* by the genae more heavily expanded behind eyes; frons and vertex with sculpture more strongly rugose; concave inner margin of compound eyes and female F1 shorter than F2 and 1.7 times as long as pedicel. The females are easily identifiable by their yellowish coloration in contrast to the brown and black coloration of other species in the tribe.

A redescription of this species was done by Diaz & De Santis (1975). However they included only illustrations for the female antenna, forewing and male genitalia. Additional morphological data were given for this species in the phylogenetic morphological analysis of Liljeblad *et al*. (2008).

#### *Description*

Length 2.6 mm (range 2.3–2.9; N = 5) for females; 2.4 mm (range 2.2–2.6; N = 3) for males. Coloration: female body entirely yellowish; apex of mandibles, parts of propodeum and metasoma distally slightly darker; distal antennal flagellum gradually darkening. Fore wing hyaline, veins brown, with darkened smoky areas around veins 2r and cubitalis. Male differ from female in the darker coloration of head, mesosoma, and metasoma which are blackish or dark brown; antenna and legs, excepting the brownish coxae, yellow.

*Female.* Head. In dorsal view 2 times as wide as long. Inner margin of compound eyes slightly curved inwards. Genae moderately expanded behind compound eye. POL 1.8 times as long as OOL, posterior ocellus separated from inner orbit of eye by about 1.2 times its diameter. In anterior view (Fig. 1A), head more or less rounded, 1.2 times as wide as high. Face weakly pubescent, with only some sparse setae; facial strigae radiating from clypeus absent. Face reticulate, the reticulate sculpture being more irregular and rugose on frons and vertex; ocellar plate slightly raised; malar space 0.2 times height of compound eye. Clypeus distinct, more or less trapezoidal, with reticulate sculpture; anterior tentorial pits visible, epistomal sulcus indistinct and clypeo-pleurostomal lines deeply impressed; ventral margin broadly projecting over mandibles (Fig. 1A). Subocular impression present although not well marked, visible as a transition between two different sculptures. Genae expanded behind compound eyes (Fig. 1A). Toruli situated at upper half of compound eye; transfacial line 1.1 times height of eye; distance between antennal rim and compound eye 1.1 times width of antennal socket including rim. Ventral margin of toruli deeply excavated and a strong median raised vertical carina is present between toruli and the median ocellus (Fig. 1A). Head posterior view (Fig. 1B). Occiput weakly pubescent, pubescence present only on dorsal and lateral areas; with reticulate sculpture, without dorsal occipital carina; occiput medially concave, with a pair of vertical lateral carinae present, separating the concave area of the lateral raised areas (Figs 1B, 4A). Posterior tentorial pits narrow, slit-like. Hypostomal sulci, weak and incomplete, free, not united, meeting or converging at hypostoma (Fig. 1B). Distance between dorsal cranial margin and occipital foramen 0.7 as long as occipital foramen height; distance between occipital and oral foramina 0.75 as long as occipital foramen height.

Mouthparts (Fig. 1B). Mandibles in anterior view hidden by the exposed and projected ventral clypeal margin (Fig. 1A); both mandibles with two teeth; but a small basal secondary tooth present on right mandible. Cardo of maxilla invisible posteriorly; maxillary stipes short, not reaching base of labial palpus. Maxillary palp with only three visible segments. Labial prementum distally broadening; labial palp with three segments.

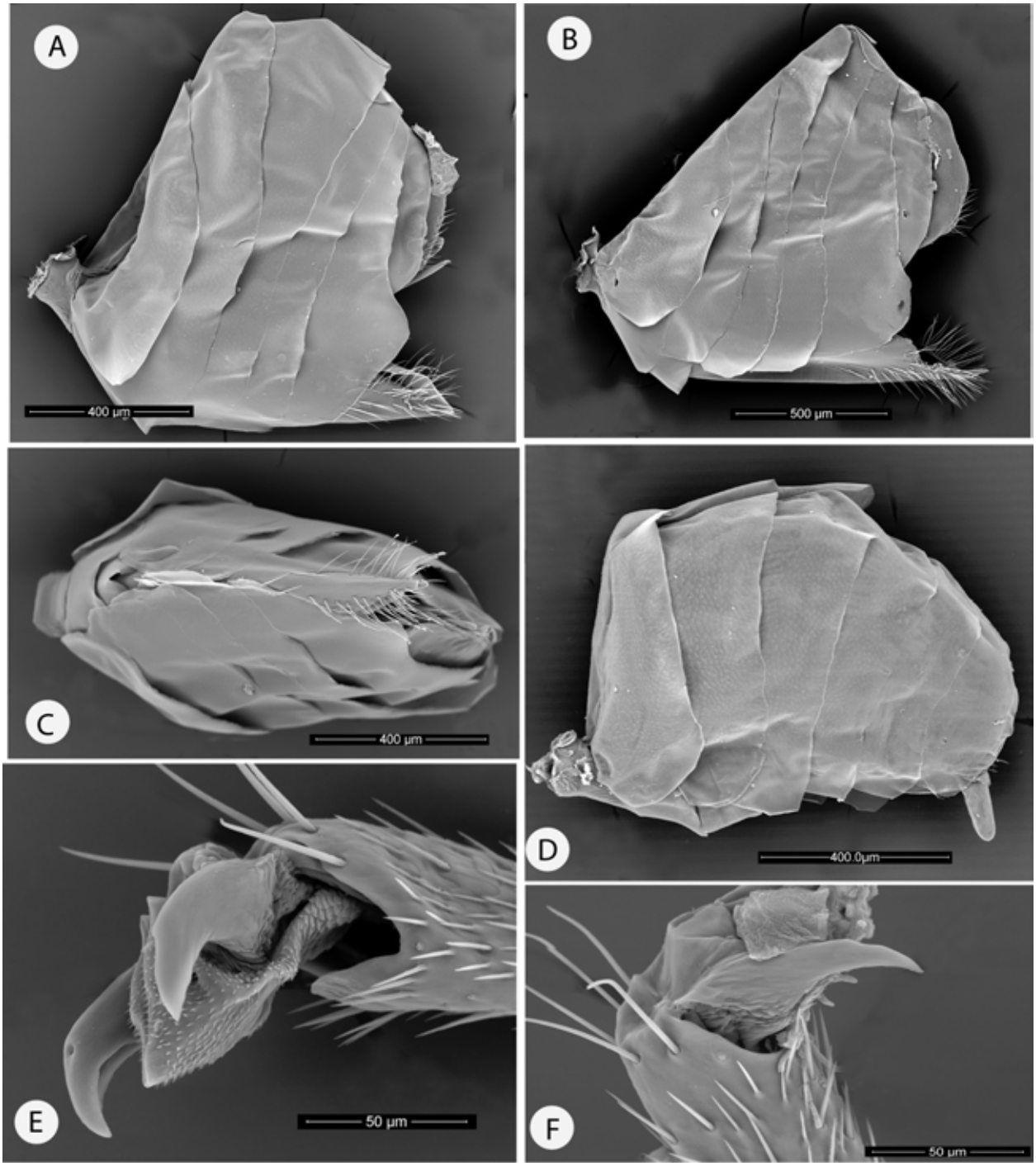


**FIGURE 6.** (A) Lateral view of female metasoma of *Eschatocerus acaciae*. (B) Lateral view of female metasoma of *E. niger*. (C) Ventral view of female metasoma of *E. acaciae*. (D) Lateral view of male metasoma of *E. niger*. (E) Metatarsal claw of *E. niger.* (F) Metatarsal claw of *E. acaciae*.

Antenna (Fig. 2A) 0.6 times as long as body, with 13 segments, filiform, flagellum not widening towards apex; antennal segments with weak alutaceous sculpture and weakly pubescent. Placodeal sensilla present from F4 to last flagellomere (Fig. 2D); large coeloconic sensilla type A visible on flagellomeres F5–F10 and situated not close distal margin of flagellomere (Fig. 2C). Relative lengths of antennal segments: 22:15:28:25:20:22:21:19:16:17:12: 11:09; pedicel 1.9 times as long as wide; F1 1.7 times as long as pedicel. Ultimate flagellomere shorter than penultimate, with some trichoidea sensilla at apex (Fig. 2H).

Mesosoma. Pronotum anterior view (Fig. 4B) very short medially; ratio of median to lateral length of pronotum < 0.3; almost glabrous and with reticulate sculpture. Admedian depressions of pronotum and pronotal

plate absent. In lateral view (Fig. 3B) spiracular incision of pronotum distinct, moderately deep. Lateral surface of pronotum reticulate (Fig. 3B).

Mesonotum. Mesoscutum (Fig. 3A) 1.4 times wider than long; with regular reticulate sculpture and almost glabrous. Notauli absent and median mesoscutal impression extremely short (Fig. 3A). Anteroadmedian signa inconspicuous. Mesoscutum and mesoscutellum separated by narrow transscutal fissure. Scutellar foveae absent. Mesoscutellum, in dorsal view with regular reticulate sculpture; dorsalaxillar area large, triangular and situated in same plane as mesoscutellum in lateral view. Mesopleuron (Fig. 3B) with regular reticulate sculpture, without mesopleural impression; ventral margin of mesopleural triangle only indicated by a change in curvature of mesopleural surface.

Metanotum (Fig. 4C). Metascutellum without distinct median constriction; almost smooth and glabrous medially and with reticulate sculpture laterally.

Metapectal-propodeal complex. Metapleural sulcus (Fig. 3B) incomplete, meeting posterior margin of mesopectus at about mid height of metapectal-propodeal complex. Lateral propodeal carinae absent (Fig. 4C). Lateral and median propodeal areas glabrous and with very weak reticulate sculpture. Nucha very short.

Legs. Protibia longer than protarsus; calcar simple, strongly curved and glabrous, broad basally (Fig. 4F); metafemur 2.7 as long as wide; metatibia 1.4 as long as metatarsus; metatarsal claw simple, without basal lobe or tooth (Fig. 6F).

Fore wing (Fig. 5A. 1.2 times longer than body. Radial cell open along anterior margin; R1 depigmented, weakly visible; radius (Rs) bowed, stopping far reaching anterior margin of wing. Areolet absent; vein Rs+M and basalis almost invisible. Two infuscate areas around veins 2r and at the end of Cu1 vein. Wing margin without distinct cilia.

Metasoma (Fig. 6A) shorter than head plus mesosoma; in lateral view about as long as high, laterally compressed. Abdominal petiole about as long as high. T2 smooth, covering about 1/4 of metasoma; anteromedian area of T2 glabrous. Projecting part of hypopygial spine keel shaped; lateral margins with long setae, the subapical ones projected beyond apex of spine (Fig. 6C).

*Male.* Similar to female except as described below (size and coloration already discussed). Antenna (Fig. 2B) with 13 flagellomeres. F11 as long as F10; placodeal sensillae present since F2. F1 not modified. Metasoma (Fig. 6D), T2 covering 1/3 of length of metasoma.

***Distribution***

A species distributed in temperate or dry semiarid areas of southern South America, in Argentina and Uruguay. In Argentina, this species was recorded in the provinces of Catamarca, Córdoba, Santa Fe, Tucumán (Díaz & De Santis 1975), and also from Salta and San Luis (Díaz 1980). Galls of this species were also recorded in a study in the province of Santiago del Estero (Carabajal de Belluomini *et al*. 2009). We add here records from the provinces of Mendoza and Formosa. The species may potentially be distributed in a larger area of Argentina, and also in the neighboring countries of Chile, Bolivia, and Paraguay, following the distribution areas of their host plants in the genera *Prosopis* and *Acacia.*

***Biology***

A gall inducer species on plants in the Fabaceae family. It has been recorded on *Acacia caven* (Mol.), *A. aroma* Gill., *Prosopis chilensis* (Mol.) Stuntz, and *P. nigra* Hieron (Diaz & De Santis 1975; Diaz 1980). Here we add *Prosopis alba* and *P. flexuosa.* The life cycle is bisexual, and univoltine. Adults fly in one generation, from late winter to late spring. The adult insects we studied from Mendoza emerged from galls in December, but in the studied material from Santiago del Estero, the adults were fully developed inside the galls as early as September, a month that corresponds with late winter in Argentina.

The gall has been described and illustrated by Houard (1933) and later by Diaz & de Santis (1975). It is subspherical or ovoidal, large, up to 35 mm in diameter, often only 13–18 mm, of spongy consistency becoming hard when mature, developing in twigs (Fig. 9A). It is plurilocular, enclosing many larval ellipsoidal cells disposed radially (Figs 9B, 9C).

The galls we studied from Santiago del Estero and Formosa were fully developed in September. However, the galls collected in Mendoza matured later, in November or December.

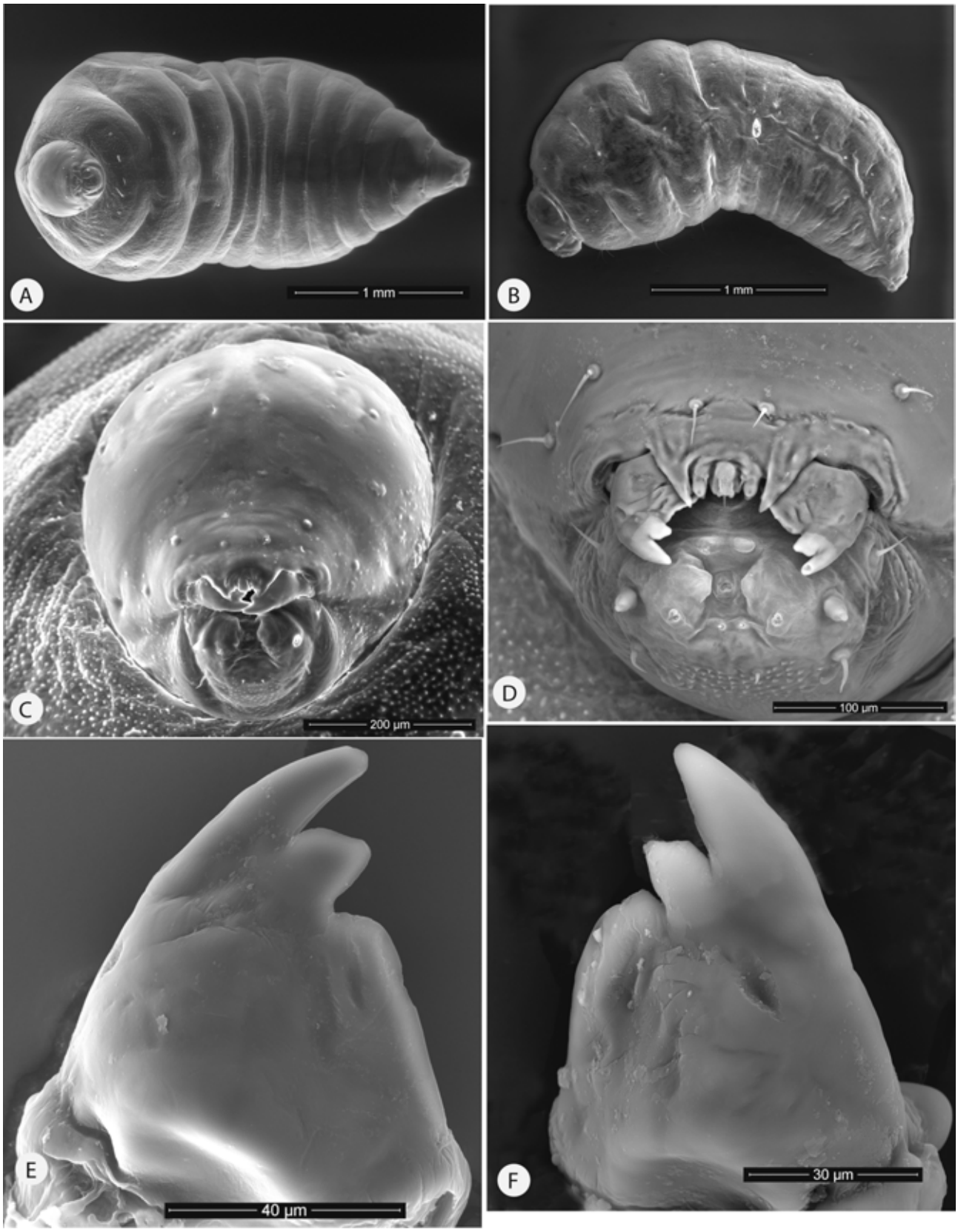


**FIGURE 7.** Mature larva of *Eschatocerus niger*. (A) Body ventral view. (B) Body lateral view. (C) Head anterior view. (D) Detail of mouth parts. (E) Left mandible, anterior view. (F) Right mandible, anterior view.

### *Eschatocerus niger* Kieffer & Joergensen, 1910

(Habitus Figs 8C, 8D)

*Eschatocerus niger* Kieffer & Joergensen, 1910. *Centralbl. Bakter. Parasit. Infekt*., 2(27): 418.

**Type material.** The type material of this species is apparently lost, as is the case with the majority of Kieffer types (Gagne 1994). Joergensen's collection is deposited in the Museo de La Plata, Argentina, although it mostly comprises higher Hymenoptera and does not hold the types described in Kieffer and Joergensen (1910) (Martínez *et al*. 2008). However, non-type materials of *E. niger* are deposited in the Cynipoidea collection of the Museo de la Plata (Argentina) (Díaz & Loiácono 1995; Díaz *et al.* 2011).

**Material examined.** 3 males, 4 females, "ARGENTINA, Mendoza, Las Heras, Cancha Chacra, ex galls *Prosopis flexuosa*, collected 21/I/2013, emerged I/2013"; 9 males, 4 females, "Cerro Petaca (10/III/2013), emerged III/2013. G. San Blas leg".

**Diagnosis.** Closely similar to *Eschatocerus acaciae*. Differs easily from this species, aside from the characters given in the identification key, by the black coloration of the females.

**Redescription.** Length 2.7 mm (range 2.5–2.8; N = 4) for females; 2.3 mm (range 2.2–2.5; N = 4) for males. Coloration: female body entirely black; face medially dark reddish; antennae pale yellow or whitish, legs blackish, excepting tibiae and tarsi yellowish. Forewing hyaline, veins brown, with darkened smoky areas around veins 2r and cubitalis. Male similar to female in the black coloration; dorsal parts of mesopleuron reddish; legs mainly yellow, excepting coxae which are darker.

*Female.* Head. In dorsal view 2 times as wide as long. Gena slightly expanded behind compound eye. POL 1.7 times as long as OOL, posterior ocellus separated from inner orbit of eye by about 1.1 times its diameter. In anterior view (Fig. 1C) head slightly wider than high. Inner margin of compound eyes straigth. Face weakly pubescent and with irregular reticulate sculpture, only slightly coarse on frons and vertex; ocellar plate slightly raised; malar space 0.17 times height of compound eye. Clypeus distinct, more or less trapezoidal with reticulate sculpture; anterior tentorial pits conspicuous; epistomal sulcus indistinct and clypeo-pleurostomal lines deeply and widely impressed (Fig. 1C); ventral margin of clypeus broadly projecting over mandibles. Genal furrow not well impressed, but present as an area of transition between two different sculptures. Genae slightly expanded behind compound eyes (Fig. 1C). Torulus situated at upper height of compound eye; transfacial line 0.9 times height of eye; distance between antennal rim and compound eye 1.1 times width of antennal socket including rim. Ventral margin of toruli deeply excavated; a strong median raised vertical carina present between toruli and the median ocellus (Fig. 1C). Head posterior view (Fig. 1D). Occiput weakly pubescent and with regular reticulate sculpture, without dorsal occipital carina; occiput medially concave, with a pair of vertical lateral carinae present, separating the concaves area of the lateral raised areas (Figs 1D). Posterior tentorial pits narrow, slit-like; hypostomal sulci weak and incomplete, free, not united, meeting or converging at hypostoma (Fig. 1D). Distance between dorsal cranial margin and occipital foramen 0.7 as long as occipital foramen height; distance between occipital and oral foramina 0.7 as long as occipital foramen height.

Mouthparts (Fig. 1D). Both mandibles with two teeth, but a small basal secondary tooth present on right mandible. Cardo of maxilla invisible posteriorly; maxillary stipes short, not reaching base of labial palpus. Maxillary palp with only three visible segments. Labial palp with three segments.

Antenna (Fig. 2E) 0.7 times as long as body, filiform, with 13 segments. Placodeal sensilla present in flagellomeres F4–F11; large coeloconic sensilla Type A visible on flagellomeres F5–F10. Relative lengths of antennal segments: 30:22:29:22:20:25:22:20:18:17:16:13:16; pedicel 1.9 times as long as wide; F1 1.3 times as long as pedicel and F2. Ultimate flagellomere longer than penultimate.

Mesosoma. Pronotum anterior view very short medially, almost glabrous and with reticulate sculpture. Admedian depressions of pronotum and pronotal plate absent; spiracular incision of pronotum more deeply incised (Fig. 3D).

Mesonotum. Mesoscutum (Fig. 3C) similar to *E. acaciae;* median mesoscutal impression absent. Mesopleuron (Fig. 3D) with regular reticulate sculpture, without mesopleural impression. Ventral border of mesopleural triangle only indicated by a change in curvature of mesopleural surface.

Metanotum (Fig. 4D). Metascutellum without distinct median constriction; with reticulate sculpture medially and laterally. Metapectal-propodeal complex as in *E. acaciae*. Nucha short, with some longitudinal rugae medially.

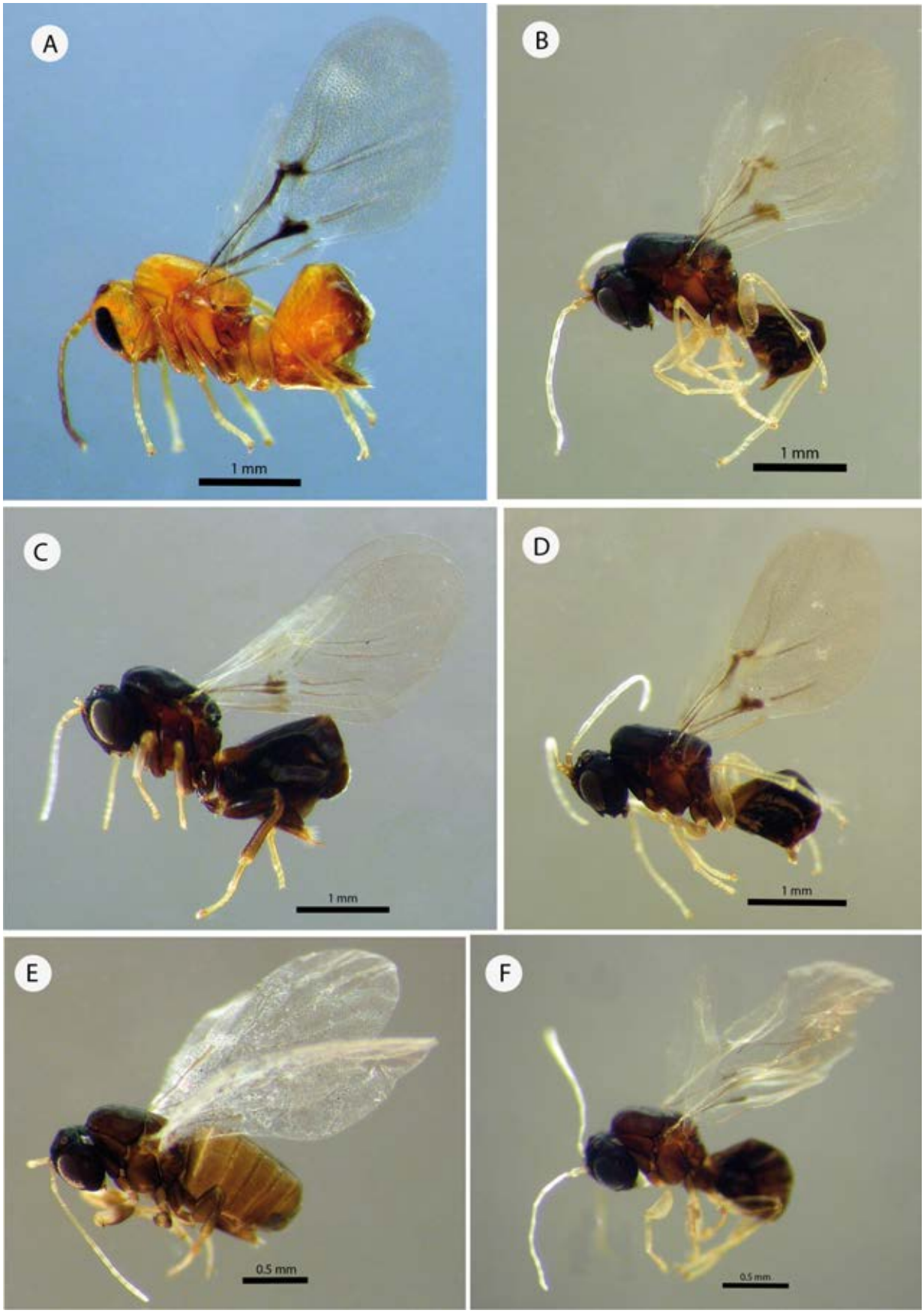


**FIGURE 8.** Habitus female and male of species of *Eschatocerus*: (A) Female (B) Male of *E. acaciae* (C) Female (D) Male of *E. niger* (E) Female (F) Male of *E. myriadeus*.

Legs. Protibia 0.5 as long as protarsus. First protarsomerus 1.3 as long as the joint length of the protarsomerus 2–5; protarsomerus 1 not curved basally. Metafemur 2.6 as wide as long; metatibia 1.2 as long as metatarsus (Fig. 4G). Metatarsal claw simple (Fig. 6E).

Forewing (Fig. 5B) 1.16 times as long as body. Radial cell open along anterior margin; R1 and Rs depigmented, hardly visible; radius (Rs) bowed, stopping far reaching anterior margin of wing. Areolet absent; vein basalis absent; Rs+M incomplete, addressed to junction of basalis with cubitalis. An infuscate area around the end of Cu1 vein. Wing margin without cilia.

Metasoma laterally compressed (Fig. 6B), shorter than head plus mesosoma, in lateral view 1.1 as long as high. Abdominal petiole about as long as high. T2 and following tergites with weak reticulate sculpture and glabrous, covering about 1/4 of metasoma. Hypopygium keel shaped; projected ventral spine about three times as long as wide; its lateral margins with long erect setae, the subapical ones projected far beyond apex of spine (Fig. 6B).

*Male.* Similar to female except as described below (size and coloration already discussed). Antenna (Fig. 2F) with 13 flagellomeres. F1 as long as F2; placodeal sensillae present since F2. F1 not modified, only slightly enlarged towards apex.

***Distribution***

Argentina. It has been recorded in the provinces of Chaco, Catamarca and Mendoza (De Santis 1967; Díaz 1980). New records are here given from the Mendoza province.

***Biology***

Induce galls on *Prosopis alpataco* Phil. and *P. campestris* Gris (Fabaceae). The life cycle is bisexual, and univoltine. Adults flight in one generation, from late winter to late spring. Houard (1933), reported that the adults emerge in January but our studied adult materials from Mendoza emerged from the galls in December.

The gall, besides its original mention by Kieffer & Joergensen, has been described and illustrated in Houard (1933). It is similar to the *E. acaciae* gall but is usually not as large, measuring only 8–15 mm. It is globular, sometimes solitary and other times clustering in three or four units, growing from buds situated laterally on twigs (Fig. 9D). The surface is smooth and glabrous and the color yellowish. As with the *E. acaciae* galls, they are plurilocular enclosing several small larval cells.

***Description of the terminal larva***

***Final-instar larva.*** *Size.* Body length 2.6 mm (range 2.5–2.8); body width 1.4 mm (1.3–1.5) (n=3).

*Habitus*. Larval type hymenopteriform (Quicke 1997; Nieves-Aldrey *et al*. 2005), maggot-like, segmented, without appendages.

Body ventral view (Fig. 7A) spindle shaped, narrower at the first abdominal segment, and more or less abruptly tapering posteriorly. Integument whitish, smooth and bare, except for a few short setae concentrated on the head, and a few longer setae on the thoracic segments. Body consisting of head and 13 visible segments: 3 thoracic, 9 abdominal and one caudal segment. In lateral view (Fig. 7B), spiracles visible laterally on TS2–AS7.

TS1, in ventral view, not narrowed medially under ventral part of head; with minute blister-like sculpture and a few moderately long setae ventrally and laterally on the head. TS2 longer than TS1 and TS3 in lateral view; AS1-AS8 slightly increasing in length; last two segments elongate, trapezoid, 1.5 times as wide as they are long in ventral view. Head (Fig. 7C) more or less rounded in anterior view. Antennae and antennal areas indistinct. Pairs of lateral clypeal setae and ventral clypeal setae present. Genal setae visible. Mouth parts (Fig. 7D). Ventral margin of clypeus prolonged into a more or less trapezoid labrum which is ventrally divided into five irregular lobes, two shorter central lobes, and two lateral lobes slightly longer. Maxillae rounded, well differentiated from labium; a pair of conspicuous cylindrical palps visible laterally on the maxillae; a pair of maxillary setae also visible. Labium with a pair of short dorsomedial labial setae visible; ventrally with blister like sculpture and two pairs of long setae visible laterally on dorsal and ventral parts of labium. A salivary opening visible between the maxillae. Mandibles (Figs 7E, 7F) partially visible below labium, without sculpture or hairs. Both mandibles with three teeth, one larger apical acute tooth, an intermediate broader and blunter tooth and a basal small tooth.

*Remarks.* The larva of *Eschatocerus niger* and likely the larvae of all *Eschatocerus* species, differs from other described cynipid larvae by the labrum, which is partially divided into lobes, whereas it is entire in most other cynipid larvae. In this feature, *E. niger* resembles the larva of chalcidoid species of *Eurytoma* Illiger and *Sycophila* Walker (Eurytomidae), but differs from them in the structure of the mandibles as well as in the divisions of the labrum, which are fewer and not as deep (Gómez *et al.* 2011, 2013). The larva of *Eschatocerus* is most similar to

*Diastrophus rubi* (Bouché) larvae and the Diplolepidini, where the body tapers abruptly posteriorly and the last segment is cylindrical and slightly elongated (Nieves-Aldrey *et al*. 2005). The shape of the teeth of the right mandible, especially the second tooth which is relatively broad and blunt, also resembles the larvae of the gall wasp inquilines Diastrophini and Synergini (Nieves-Aldrey *et al.* 2005).

### *Eschatocerus myriadeus* Kieffer & Joergensen, 1910

(Habitus Figs 8E, 8F)

*Eschatocerus myriadeus* Kieffer & Joergensen, 1910. *Centralbl. Bakter. Parasit. Infekt*., 2(27): 418.

***Type material***

As in the case of types of *E. niger*, the type material of this species is apparently lost. Non-type material of this species is deposited in the Cynipoidea collection of the Museo de la Plata (Argentina) (Díaz & Loiácono 1995; Díaz *et al*. 2011).

***Material examined.***

4 males, 2 females reared from galls collected on 9 December 2012 in Las Heras, Mendoza province (Argentina) at 978 m on *Prosopis* sp. (Fabaceae). G. S. Blas leg.
Mendoza, Lujan de Cuyo (25/XI/2012): 28/XI/2012, 1 female
Galls collected in Cerro Petaca were dissected and 19 pupae were extracted.

**Diagnosis.** Differs from *E. acaciae* and *E. niger* by its smaller size, mainly chestnut or brown coloration, and a much weaker head and mesosoma sculpture.

**Redescription.** Length 1.8 mm (range 1.87–1.75; N = 24) for females; 1.5 mm (range 1.4–1.6; N = 4) for males. Coloration: female body entirely dark brown; head black; antenna pale yellow; legs light brown excepting tibia and tarsi yellowish. Forewing hyaline, veins yellowish; a darkened smoky areas around cubitalis. Male similar to female in the head and body coloration; antennae and legs paler.

*Female.* Head. In dorsal view 2 times as wide as long. Gena not expanded behind compound eye. POL 2.4 times as long as OOL, posterior ocellus separated from inner orbit of eye by about 1.2 times its diameter. In anterior view (Fig. 1E) head 1.1 wider than high. Inner margin of compound eyes straight. Face weakly pubescent and with regular reticulate sculpture, regular reticulate sculpture present also in frons and vertex; lateral ocelli slightly raised; malar space 0.19 times height of compound eye. Clypeus distinct, more or less axe shaped, with reticulate sculpture; anterior tentorial pits conspicuous, epistomal sulcus indistinct and clypeo-pleurostomal lines deeply impressed (Fig. 1E); ventral margin of clypeus broadly projecting over mandibles. Genal furrow not visible. Genae not expanded behind compound eyes. Toruli situated at upper height of compound eye; transfacial line 0.7 times height of eye; distance between antennal rim and compound eye as long as width of antennal socket including rim. Toruli inserted into an excavation of the face and a median raised vertical carina present, between toruli and the median ocellus (Fig. 1E). Head posterior view (Fig. 1F). Occiput weakly pubescent excepting dorsal and lateral areas; with regular reticulate sculpture, much more weak in lateral areas adjacent to the occipital foramen; occiput medially concave, but the pair of vertical lateral carinae separating the concave area of the lateral raised areas are virtually absent (Figs 1F). Posterior tentorial pits and hypostomal sulci as in the other *Eschatocerus* species. Distance between dorsal cranial margin and occipital foramen 0.8 as long as occipital foramen height; distance between occipital and oral foramina 1.3 as long as occipital foramen height.

Mouthparts (Fig. 1F). Mandibles with two teeth, but a small basal secondary tooth present on right mandible. Cardo of maxilla invisible posteriorly, maxillary stipes short, not reaching base of labial palpus. Maxillary palp with only three visible segments. Labial palp with three segments.

Antenna (Fig. 2G) 0.6 times as long as body, filiform, with 13 segments. Placodeal sensilla present in flagellomeres F4–F11; large coeloconic sensillae type A visible on flagellomeres F5–F10. Relative lengths of antennal segments: 27:16:25:27:21:21:21:20:17:16:13:13:16; pedicel 1.5 times as long as wide; F1 1.5 times as long as pedicel and 0.9 as long as F2. Ultimate flagellomere 1.2 as long as penultimate.

Mesosoma. Pronotum anterior view very short medially, almost glabrous and with reticulate sculpture. Admedian depressions of pronotum and pronotal plate absent; spiracular incision of pronotum moderately incised (Fig. 3F).

Mesonotum. Mesoscutum similar to *E. acaciae;* median mesoscutal impression absent. Scuto-scutellar suture of mesoscutellum (inner margin of axillae) indistinct, weakly marked (Fig. 3E).

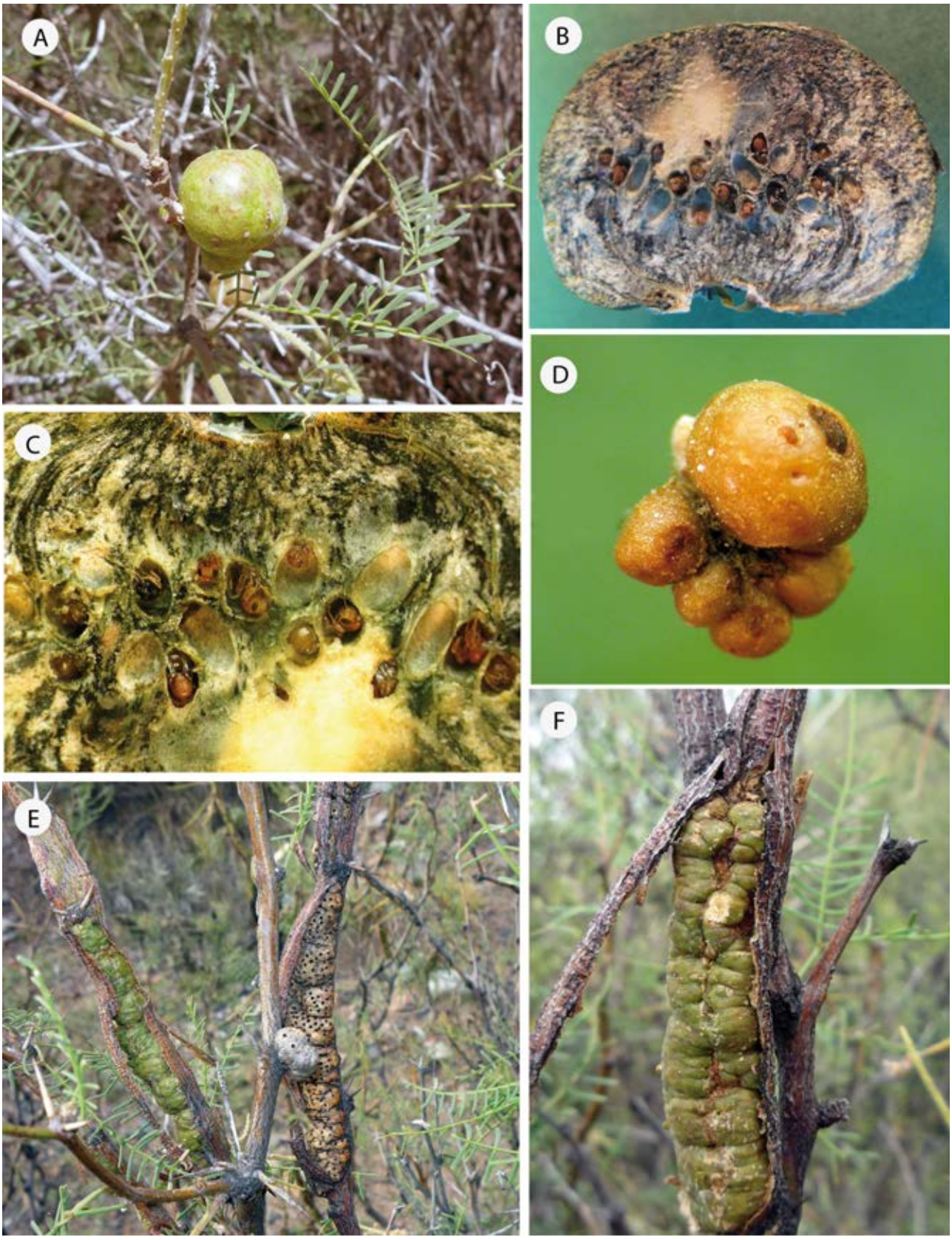


**FIGURE 9.** Galls of *Eschatocerus*, on species of *Prosopis*: (A) Gall of *E. acaciae*. (B) Section of gall. (C) Detail of formed adults inside larval cells. (D) Cluster gall of *E. niger*. (E) Galls of *E. myriadeus* and (F) detail of a gall.

Metanotum (Fig. 4E). Metascutellum without distinct median constriction, glabrous and smooth, without reticulate sculpture, which is only present in lateral areas of metascutellum. Metapectal-propodeal complex glabrous and almost smooth; areas of reticulate sculpture very weak and almost invisible. Nucha very short and smooth.

Legs. As in the related species of *Eschatocerus.*

Forewing (Fig. 5C) 1.2 times as long as body. Radial cell open along anterior margin; R1 and Rs depigmented, hardly visible; radius (Rs) bowed, stopping far reaching anterior margin of wing. Areolet absent; vein basalis absent; Rs+M incomplete, addressed to junction of basalis with cubitalis. An infuscate area around the end of Cu1 smaller than in *E. acaciae* and *E. niger*. Setae on disc of forewing more conspicuous than in the other species of *Eschatocerus;* setae on basal cell and below the cubital vein are more visible and densely spaced.

Metasoma similar to the other species of *Eschatocerus*. Ventral spine of hypopygium broad, as long as wide; subapical setae long extended beyond apex of spine.

*Male.* Similar to female except as described in coloration.

***Distribution***

Recorded only from Argentina. Has been cited in the provinces of Entre Ríos and Mendoza (De Santis 1967; Diaz 1980). New collecting sites are here given from the Mendoza province (Fig. 10).

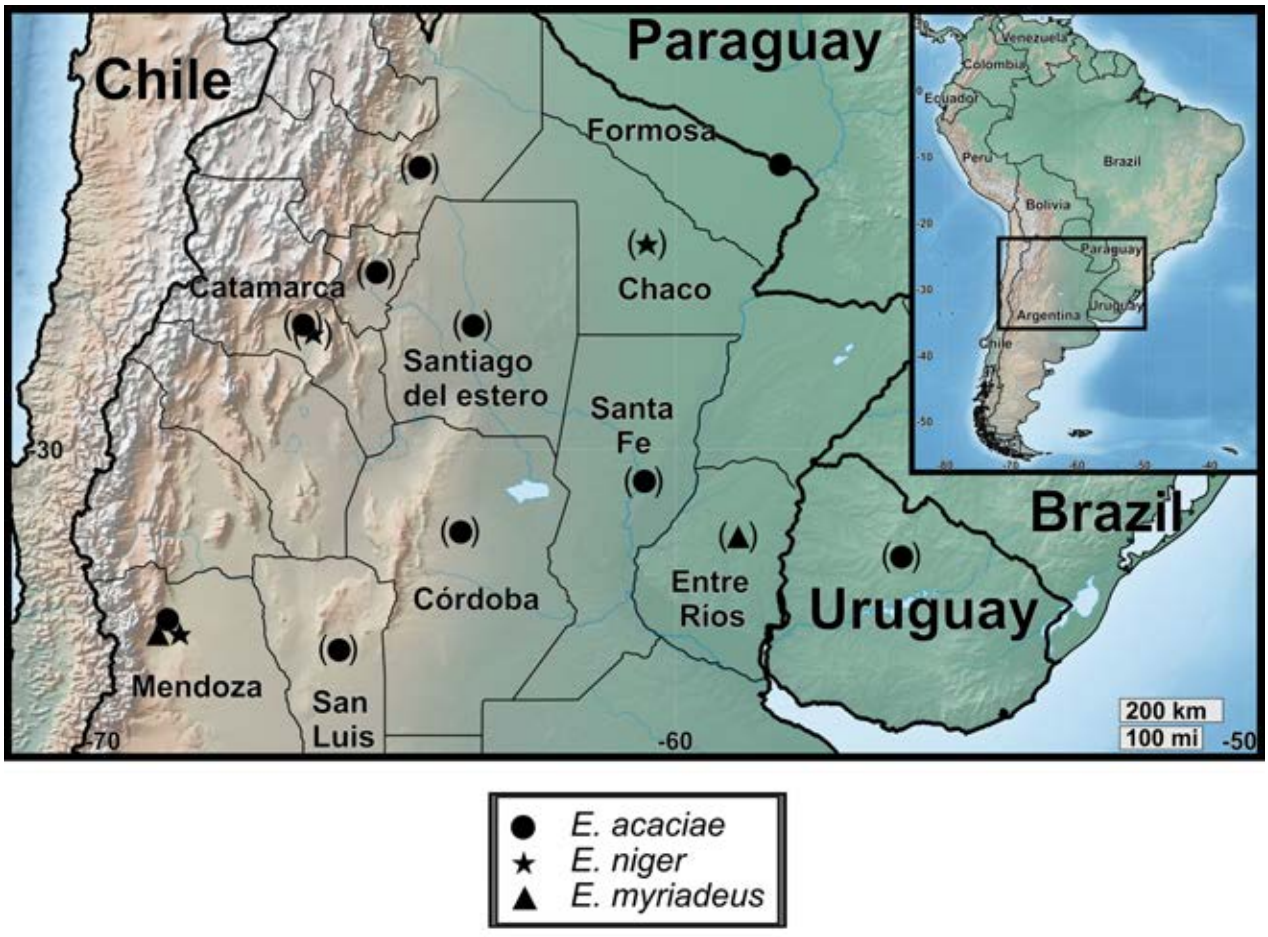


**FIGURE 10.** Distribution of *Eschatocerus* ssp in Argentina and Uruguay.

***Biology***

Induce galls in twigs of *Prosopis alpataco* Phil*,* "alpataco"; *P. campestris* Gris; and *P. vinalillo* Stuck (Fabaceae) (Díaz 1980). The only known parasitoid associated with their galls is *Eudecatoma fastigiata* (Joergensen & Kieffer) (Hymenoptera, Chalcidoidea, Eurytomidae) (De Santis1967). Our studied adult materials from Mendoza emerged from galls in December.

The galls were described and illustrated by Kieffer & Joergensen (1910) and later by Houard (1933) and Díaz (1980). Galls develop inside twigs, consisting of small (approximately 1.5 mm diameter) ovoid or hemispheric cells, up to 300–600, clustering closely, resulting in a compressed or fused enlarged mass gall measuring up to 12 cm long, breaking the bark of the twig (Figs 9E, 9F). The numerous small, circular, adult emergence holes are quite visible on the apical surface of the old galls (Fig. 9E).

**Preliminary notes on the inquiline and parasitoid communities in galls of *Eschatocerus*.**

The parasitoid and inquiline communities associated with cynipid galls have been well studied. In recent years, a catalogue of the communities associated with herb gall wasps and bushes was first published (Askew *et al*. 2006), followed by a catalogue of the communities in oak gall wasps from the Palaearctic (Askew *et al*. 2013). Data on the parasitoid communities associated with oak galls of Panama have also been published (Sánchez *et al*. 2013). However, very little is known about the communities in galls of the endemic Neotropical tribes Paraulacini and Eschatocerini.

The Eschatocerini are morphologically similar and phylogenetically related to the Diplolepidini (Liljeblad *et al*. 2008; Ronquist *et al*. 2015). However, in contrast with the Diplolepidini, whose galls host cynipid inquiline species of the genus *Periclistus*, the galls of the species of *Eschatocerus* do not host cynipid inquiline species. The *Eschatocerus* galls host however inquiline species of at least two other hymenopteran species: the braconid *Bracon prosopidis* Kieffer & Joergensen (Hymenoptera, Braconidae) and one chalcidoid species, *Tanaeostigmodes coeruleus* Kieffer & Joergensen (Chalcidoidea, Tanaeostigmatidae). The biological behavior of these gall associated species has been discussed (Martínez *et al*. 2008; La Salle 2005). We have strong evidence that both species are inquilines and not gall inducers or parasitoids (Nieves-Aldrey unpublished observations). A striking feature of the communities reared from cynipid galls is that the taxonomic composition among them is quite similar, regardless of the geographic distribution of the host galls. Of the six chalcidoid families usually taking part in the gall wasp parasitoid communities, four are present in *Eschatocerus* galls: Torymidae, Pteromalidae, Eupelmidae and Eurytomidae, while two are absent: Ormyridae and Eulophidae. The galls of *Eschatocerus* also host an inquiline apionid phytophagous coleopteran species. In this feature, the *Eschatocerus* galls are similar to the galls induced by species of *Aditrochus* (Pteromalidae) on *Nothofagus*, which also host cynipid species (*Cecinothofagus*) (Nieves-Aldrey *et al*. 2009). The hymenopteran community, including inquiline and parasitoid species, associated with the galls of species of *Eschatocerus* is being studied and it will be published elsewhere (Nieves-Aldrey *et al.* in prep.).

**Acknowledgements**

Thanks to J. Martin Cano for sending us samples of galls of *E. acaciae*. Thanks also to Alberto Jorge for technical assistance with SEM images. We are grateful to two anonymous referees for their useful criticism, notes and comments on the manuscript. Junior author is grateful to IADIZA for the use of facilities and CONICET. This study was financed by Project CGL2010–15786 of the Spanish Ministry of Science and Innovation to J.L. Nieves-Aldrey.

**References**

Ashmead, W.H. (1903) Classification of the gall-wasps and the parasitic cynipoids, of the super-family Cynipoidea. IV. *Psyche*, 10, 210–215.
http://dx.doi.org/10.1155/1903/21809

Askew, R.R., Plantard, O., Gómez, J.F., Nieves, M.H. & Nieves-Aldrey, J.L. (2006) Catalogue of parasitoids and inquilines in galls of Aylacini, Diplolepidini and Pediaspidini (Hym., Cynipidae) in the West Palaearctic. *Zootaxa,* 1301, 1–60.

Askew, R.R., Melika, G., Pujade-Villar, J., Schönrogge, K., Stone, G.N. & Nieves-Aldrey, J.L. (2013) Catalogue of parasitoids and inquilines in cynipid oak galls in the West Palaearctic. *Zootaxa*, 3643 (1), 1–133.
http://dx.doi.org/10.11646/zootaxa.3643.1.1

Carabajal de Belluomini, M.V., Castresana, L., Salim, V. & Notario, A. (2009) The diversity of galls and their occurrence in productive forest systems of *Prosopis alba* (Griseb.) in Santiago del Estero, Argentina. *Boletín de Sanidad Vegetal-Plagas*, 35, 255–265.

Csóka, G., Stone, G.N, & Melika, G. (2005) The biology, ecology and evolution of gall wasps. *In*: Raman, A., Schaeffer, C.W. & Withers, T.M (Eds.), *Biology, ecology and evolution of gall-inducing arthropods.* Science Publishers, Inc. Enfield, New Hampshire, pp. 569–636.

De Santis, L. (1967) *Catálogo de los himenópteros argentinos de la serie Parasitica, incluyendo Bethyloidea*. Comisión de Investigación Científica de la provincia de Buenos Aires. La Plata, 337 pp.

De Santis, L. (1979) *Catálogo de los himénopteros calcidoideos de América al sur de los Estados Unidos*. Publicación Especial Comisión de Investigaciones Cientifícas Provincia de Buenos Aires, 488 pp.

Díaz, N.B. & De Santis, L. (1975) Las agallas esferoidales del algarrobo de Chile. *Neotropica*, 21 (65), 89–93.

Díaz, N.B. (1980) Cinipoideos galígenos e inquilinos de la República Argentina. *Revista de la Sociedad Entomológica Argentina*, 39 (1980), 221–226.

Gagné, R. (1994) *The gall midges of the Neotropical Region*. Cornell University Press, Ithaca, New York, 360 pp.

Gómez, J.F., Nieves-Aldrey, J.L., Hernandez Nieves, M. & Stone, G.N. (2011) Comparative morphology and biology of terminal-instar larvae of some E*urytoma* (Hym., Eurytomidae) species parasitoids of gall wasps (Hym. Cynipidae) in western Europe. *Zoosystema,* 33 (3), 288–323.

Gómez, J.F., Nieves-Aldrey, J.L. & Stone, G.N. (2013) On the morphology and biology of the terminal-instar larvae of some european species of *Sycophila* (Hymenoptera, Eurytomidae) parasitoids of gall wasps (Hymenoptera, Cynipidae). *Journal of Natural History,* 47 (47–48), pp. 2937–2960.
http://dx.doi.org/10.1080/00222933.2013.791937

Houard, C. (1933) *Les Zoocécidies des Plantes de l´Amerique du Sud et de l´Amerique Centrale*. Librairie Scientifique A. Hermann, Paris, 519 pp

Kieffer, J.J. & Joergensen, P. (1910) Gallen und Gallentiere aus Argentinien. *Centralblatt für bakteriologie, parasitenkunde u. infektionskrankheiten*, 27 (2), 362–442.

La Salle, J. (2005) Biology of Gall Inducers and Evolution of Gall Induction in Chalcidoidea (Hymenoptera: Eulophidae, Eurytomidae, Pteromalidae, Tanaostigmatidae, Torymidae). *In:* Raman, A., Schaefer, C.W & Withers, T.M. (Eds.), *Biology, Ecology, and Evolution of Gall-inducing Arthropods*. *Vol 2.* Science Publishers, Inc. Enfield, New Hampshire, & Plymouth, pp. 507–537.

Liljeblad, J., Nieves-Aldrey, J.L., Nesser, S. & Melika, G. (2011) Adding another piece to the puzzle: the description of a South African gall wasp and a new tribe (Hymenoptera: Cynipidae). *Zootaxa*, 2806, 35–52.

Liljeblad, J. & Ronquist, F. (1998) A phylogenetic analysis of higher-level gall wasps relationships (Hymenoptera: Cynipidae). *Systematic Entomology*, 28, 229–252.
http://dx.doi.org/10.1046/j.1365–3113.1998.00053.x

Liljeblad, J., Ronquist, F., Nieves-Aldrey, J.L, Fontal-Cazalla, F., Ros-Farre, P., Gaitros, D. & Pujade-Villar, J. (2008) A fully web-illustrated morphological phylogenetic study of relationships among oak gall wasps and their closest relatives (Hymenoptera: Cynipidae). *Zootaxa*, 1796, 1–73.

Martínez, J.J., Zaldivar-Riverón, A. & Sáez, A.G. (2008) Reclassification of *Bracon mendocinus*, a gall-associated doryctine wasp, and description of a new closely related species of *Allorhogas* (Hymenoptera: Braconidae). *Journal of Natural History*, 42, 2689–2701.

Mayr, G. (1881) Die Genera der gallenbewohnenden Cynipiden. - *Jahresbericht der Rossauer Communal-Oberrealschule, Wien*, 20, 1–38.

Medianero, J.L. & Nieves-Aldrey, J.L. (2011) Primer estudio de las avispas de las agallas de la república de Panamá, incluyendo una lista actualizada de los cinípidos neotropicales (Hymenoptera, Cynipoidea, Cynipidae). *Boletín de la Sociedad Entomólogica Aragonesa (S.E.A.),* 48, 89–104.

Melika, G. (2006) *Gall wasps of Ukraine. Cynipidae. Vol. 1*. Schmalhausen Institute of Zoology, Nacional Academy of Sciences of Ukraine, Ukraine, 300 pp.

Melika, G. & Bechtold, M. (2001) Taxonomic notes and type designations of gall inducing cynipid wasps described by G. Mayr (Insecta: Hymenoptera: Cynipidae). *Ann. Naturhist. Mus. Wien*, 103 (B), 327–339.

Nieves-Aldrey, J.L. (1994) Revision of West-European Genera of the Tribe Aylacini Ashmead (Hymenoptera, Cynipidae). *Journal of Hymenoptera Research,* 3, 175–206.

Nieves-Aldrey, J.L. (2001) Hymenoptera, Cynipidae. *In*: Ramos, M.A., Alba, J., Bellés, X., Gosálbez, J., Guerra, A., Macpherson, E., Martín, F., Serrano, J. & Templado, J. (Eds.), *Fauna Ibérica. Vol. 16*. Museo Nacional de Ciencias Naturales, CSIC, Madrid, pp. 1–636.

Nieves-Aldrey, J.L. & Butterill, P.T. (2014) First evidence of cynipids from the Oceanian Region: the description of *Lithonecrus papuanus* anew genus and species of cynipid inquilines from Papua New Guinea (Hymenoptera: Cynipidae, Synergini). *Zootaxa*, 3846 (2), 221–234.
http://dx.doi.org/10.11646/zootaxa.3846.2.3

Nieves-Aldrey, J.L., Liljeblad, J., Hernández Nieves, M., Grez, A. & Nylander, J.A.A. (2009) Revision and phylogenetics of the genus *Paraulax* Kieffer (Hymenoptera, Cynipidae) with biological notes and description of a new tribe, a new genus, and five new species. *Zootaxa,* 2200, 1–40.

Nieves-Aldrey, J.L., Vårdal, H. & Ronquist, F. (2005) Comparative morphology of terminal-instar larvae of Cynipoidea: phylogenetic implications. *Zoologica Scripta,* 34, 15–36.
http://dx.doi.org/10.1111/j.1463–6409.2005.00175.x

Polidori, C., Jorge García, A. & Nieves-Aldrey, J.L. (2013) Breaking up the wall: metal-enrichment in ovipositors, but not in mandibles, co-varies with substrate hardness in Gall-Wasps and their associates. *PLoS ONE*, 8 (7), e70529. http://dx.doi.org/10.1371/journal.pone.0070529

Polidori, C. & Nieves-Aldrey, J.L. (2014) Diverse Filters to Sense: great variability of antennal morphology and sensillae equipment in Gall-Wasps (Hymenoptera: Cynipidae). *PloS ONE*, 9 (7), e101843. http://dx.doi.org/10.1371/journal.pone.0101843

Quicke, D.J.L. (1997) *Parasitic wasps*. Chapman & Hall, London, 470 pp.

Ronquist, F. (1999) Phylogeny, classification and evolution of the Cynipoidea. *Zoologica Scripta*, 28, 139–164. http://dx.doi.org/10.1046/j.1463–6409.1999.00022.x

Ronquist, F., Nieves-Aldrey, J.L., Buffington, M., Liu, Z., Liljeblad, J. & Nylander, J.A.A. (2015) Phylogeny, Evolution, and Classification of Gall Wasps: The Plot Thickens. *PLoS ONE,* 10 (5), e0123301. http://dx.doi.org/10.1371/journal.pone.0123301

Ronquist, F. & Nordlander, G. (1989) Skeletal morphology of an archaic cynipoid, *Ibalia rufipes* (Hymenoptera: Ibaliidae). *Entomologica scandinavica Supplements*, 33, 1–60.

Sánchez, V., Cambra, R.A., Nieves-Aldrey, J.L. & Medianero, E. (2013) Parasitoides asociados a cecidias inducidas por avispas Cynipidae (Hymenoptera) en plantas del género *Quercus* (Fagaceae) en Panamá. *Scientia (Panamá)*, 2 3(1), 25–56.

Stone, G.N. & Cook, J.M. (1998) The structure of cynipid oak galls: patterns in the evolution of an extended phenotype. *Proceedings of the Royal Society of London B*, 265, 979–988. http://dx.doi.org/10.1098/rspb.1998.0387

Van Noort, S., Stone, G.N., Whitehead, V.B. & Nieves-Aldrey, J.L. (2007) Biology of *Rhoophilus loewi* (Hymenoptera: Cynipoidea: Cynipidae), with implications for the evolution of inquilinism in gall wasps. *Biological Journal of the Linnaean Society*, 90, 153–172. http://dx.doi.org/10.1111/j.1095–8312.2007.00719.x

Weld, L.H. (1952) *Cynipoidea (Hymenoptera) 1905–1950*. Privately printed [L.H. Weld], Ann Arbor, Michigan, 351 pp.