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Description of *Fumariphilus* Nieves-Aldrey, gen. nov., a new genus of herb gall wasps, with a key to genera of the tribe Aulacideini (Hymenoptera: Cynipidae)

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Abstract

A new genus of herb gall wasps, *Fumariphilus* Nieves-Aldrey **gen. nov.**, (Hymenoptera, Cynipidae, Aulacideini), is described. Previous molecular phylogenetic analyses, and resulting systematic changes at the tribe level, have shown that the related species *Aylax hypecoi* Trotter and *Neaylax versicolor* Nieves-Aldrey have been incorrectly placed within their respective genera. In order to reflect their monophyletic lineage and to accommodate these species within the tribe Aulacideini, it is necessary to erect a new genus. The two species, *Fumariphilus versicolor* (Nieves-Aldrey, 1985) **n. comb.** and *Fumariphilus hypecoi* (Trotter, 1913) **n. comb.** placed in the new genus induce galls in fruits of species of, respectively, *Hypecoum* L. (Papaveraceae: Fumarioideae: Hypecoeae) and *Fumaria* L. (Papaveraceae: Fumarioideae: Fumarieae), reflecting a host-plant association that is unique among all the cynipids. Diagnostic morphological features of both the adult and the larvae and an identification key to the species of the new genus are provided. Adults of *Fumariphilus versicolor* **n. comb.**, are also re-described and, for both species of *Fumariphilus*, the terminal instar larva is described and illustrated with SEM images. Following the erection of the new genus *Fumariphilus*, *Aylax* Hartig, *sensu* Nieves-Aldrey, 1994 is now sufficiently delimited within the tribe Aylacini *sensu stricto* Ashmead, 1903, which comprises species associated with only plants of the genus *Papaver* (Papaveraceae). Likewise, *Neaylax* Nieves-Aldrey, 1994, which now includes only the gall wasp species that associate with species of *Salvia* (Lamiaceae), is sufficiently delimited within the tribe Aulacideini Nieves-Aldrey, Nylander & Ronquist, 2015. Also provided in this work is an updated and illustrated identification key to the genera of the Aulacideini.

Key words: Herb gall wasps, Aylacini, *Aylax*, *Neaylax*, Papaveraceae, *Fumaria*, *Hypecoum*

Introduction

The family Cynipidae, commonly known as gall wasps, constitutes one of the main lineages within the predominant parasitic group of cynipoids (Hymenoptera: Cynipoidea). Our knowledge of the phylogenetic relationships of the Cynipoidea has increased greatly in recent years due to molecular-based studies, whose results have led to several accepted (Ronquist *et al.* 2015) or proposed changes (Blaimer *et al*. 2020) in the classification and systematics of this group of hymenopterans at the higher taxonomic levels (for a synthesis of the historical changes in the classification of the Cynipoidea, see Nieves-Aldrey & Sharkey (2014).

Cynipids, which have been classified into 12 tribes, grouping different monophyletic lineages (Ronquist *et al.* 2015), are peculiar by being mostly phytophagous, either inducing galls on plants or living as inquilines in the galls of other cynipids, or occasionally those of other insects such as gall midges and lepidopterans (van Noort *et al*. 2007). The most important cynipid hosts are trees or bushes, usually oaks (*Quercus*) and other trees of the family Fagaceae (e.g., *Lithocarpus*, *Chrysolepis, Castanopsis* and *Castanea*) or roses (*Rosa*). However, cynipid species traditionally classified within the tribe "Aylacini", called herb gallers or herb gall wasps, induce galls on herbs and shrubs of the families Asteraceae, Papaveraceae, Lamiaceae, Valerianaceae and Rosaceae (Nieves-Aldrey 2001, Liljeblad 2002). In the molecular phylogenetic study by Ronquist *et al.* (2015), the recovered paraphyletic assemblage representing this tribe was revised and subdivided into four monophyletic tribes: Aylacini *sensu stricto*, Aulacideini, Diastrophini and Phanacidini.

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The distribution of herb gallers is restricted to the Holarctic region, except for a species described from South Africa (Melika & Prinsloo 2007; Van Noort *et al*. 2015). A total of 18 genera and around 130 species of herb gallers has been recorded from the Palearctic (Liljeblad 2002; Melika 2006, Melika & Karimpour 2012), and 48 species, from the Nearctic (Nastasi *et al*. 2021).

Genera comprising Western European herb gallers were revised by Nieves-Aldrey (1994), who also revised the species found in the Iberian Peninsula, of which 33 were listed (Nieves-Aldrey 2001). Since then, new Iberian species have been recorded and added to the list, increasing the total number of herb gall species in Iberia to 40 (Nieves-Aldrey 2012).

In Ronquist *et al.*'s (2015) phylogenetic study, taxa associated with plants of the family Papaveraceae were recovered in two distant clades. The species *Aylax papaveris* (Perris, 1840), *Barbotinia oraniensis* (Barbotin, 1964) and *Iraella luteipes* (Thomson, 1877), all associated with the host genus *Papaver*, constituted a monophyletic clade that was named Aylacini *sensu stricto*. However*, Aylax hypecoi* Trotter, 1913, a gall inducer species on *Hypecoum* (a plant genus now in the Papaveraceae, Angiosperm Phylogeny Group 2009), unexpectedly nested within the tribe Aulacideini with high support (Ronquist *et al*. 2015; Fig. 1). Its closest relative being *Neaylax versicolor* (Nieves-Aldrey, 1985), a species that, as shown by Nieves-Aldrey (2003), forms galls on plants of the genus *Fumaria* (which was previously classified in the Fumariaceae but is now included in the Papaveraceae (Angiosperm Phylogeny Group 2009).

Aylax hypecoi can be clearly distinguished morphologically from the other species of *Aylax* (*sensu* Nieves-Aldrey 1994), as was previously emphasized in its redescription (Nieves-Aldrey & Melika 2005). Taken altogether, these results indicate that the current generic placements of *A. hypecoi* and *N. versicolor* are incorrect and that both should be transferred to another genus. However, the morphological diagnostic characters of these two species do not fit with any of the described genera of Aulacideini; consequently, it is necessary to erect a new genus to accommodate them within this tribe.

The main objective of the present study is to describe a new genus of Aulacideini, *Fumariphilus* Nieves-Aldrey **gen. nov.,** with two species: *F. hypecoi* (Trotter) and *F. versicolor* (Nieves-Aldrey), which were previously misplaced within the genera *Aylax* Hartig and *Neaylax* Nieves-Aldrey, respectively. As secondary objectives, the adults of *F. versicolor* are re-described, the terminal instar larva of *F. versicolor* is described for the first time and an updated key for the identification of the genera of Aulacideini is given.

Material and methods

Study material

Main studied materials were reared from galls collected in the field in Spain by the author and from those collected in Bulgaria by Anelia Stojanova. Adults emerged in rearing cages from galls maintained under laboratory conditions. Voucher specimens and their galls were deposited in the entomological collection of the Museo Nacional de Ciencias Naturales (MNCN) in Madrid, Spain. Additional studied materials included specimens from the Cabrera y Díaz historical entomological collection, also housed in the MNCN.

Specimen preparation

Freshly collected galls were dissected and their contents (larvae and adults) identified and photographed. Adult insects were dissected in 70% ethanol, air dried, mounted on a stub and coated with gold. Micrographs in different standardized views were taken with a scanning electron microscope (SEM) FEI QUANTA 200 (high vacuum technique) (Liljeblad *et al*. 2008). Larvae were transferred directly from absolute alcohol onto a SEM-stub and into the microscope at low vacuum without prior fixation or coating. Larval mandibles were dissected, mounted and observed as morphological parts of the adult following the protocol described by Nieves-Aldrey *et al.* (2005).

The forewings were mounted in Euparal on slides. The wings and adult habitus were examined and imaged using a Wild MZ8 stereomicroscope fitted with a NIKON Coolpix 4500 digital camera. Measurements were taken using a micrometric eyepiece calibrated to a Wild M5A stereomicroscope.

Morphological descriptions

The terminology used for the morphological structures and abbreviations follow that of Ronquist and Nordlander

(1989), Nieves-Aldrey (2001) and Liljeblad *et al.* (2008). The terminology used for wing venation and cuticular sculpture followed Ronquist and Nordlander (1989) and Harris (1979), respectively. Structure measurements were made according to Nieves-Aldrey (2001). The following abbreviations were used: F1–F12, for the antennal flagellomeres; POL, for the post-ocellar length (distance between the inner margins of the posterior ocelli); OOL, for the ocellar-ocular length (distance from the outer margin of a posterior ocellus to the inner margin of a compound eye) and DOL, for the diameter of a lateral ocellus. The width of the forewing radial cell was measured from the margin of the wing to the Rs vein.

Molecular phylogenetics

Available DNA sequence data and previous phylogenetic analysis were used to delimit the genus *Fumariphilus* **gen. nov.** and to place it in a broader phylogenetic context with respect to the other herb gall wasps (Aulacideini + Aylacini). Three gene fragments of individuals of the two species included in the newly erected genus *Fumariphilus*, *Aylax hypecoi* Trotter and *Neaylax versicolor* (Nieves-Aldrey), were amplified and sequenced: mitochondrial cytochrome oxidase c subunit I (COI, 1,078 bp), nuclear protein-coding elongation factor 1-alpha, F1 copy (EF1aF1, 367 bp) and nuclear ribosomal 28S (1,246 bp). The protocols and primers used for amplification were described by Nylander *et al*. (2004a, b) and Ronquist *et al.* (2015). Their results provided the phylogenetic framework for the current study and are partially reproduced here (Fig. 1).

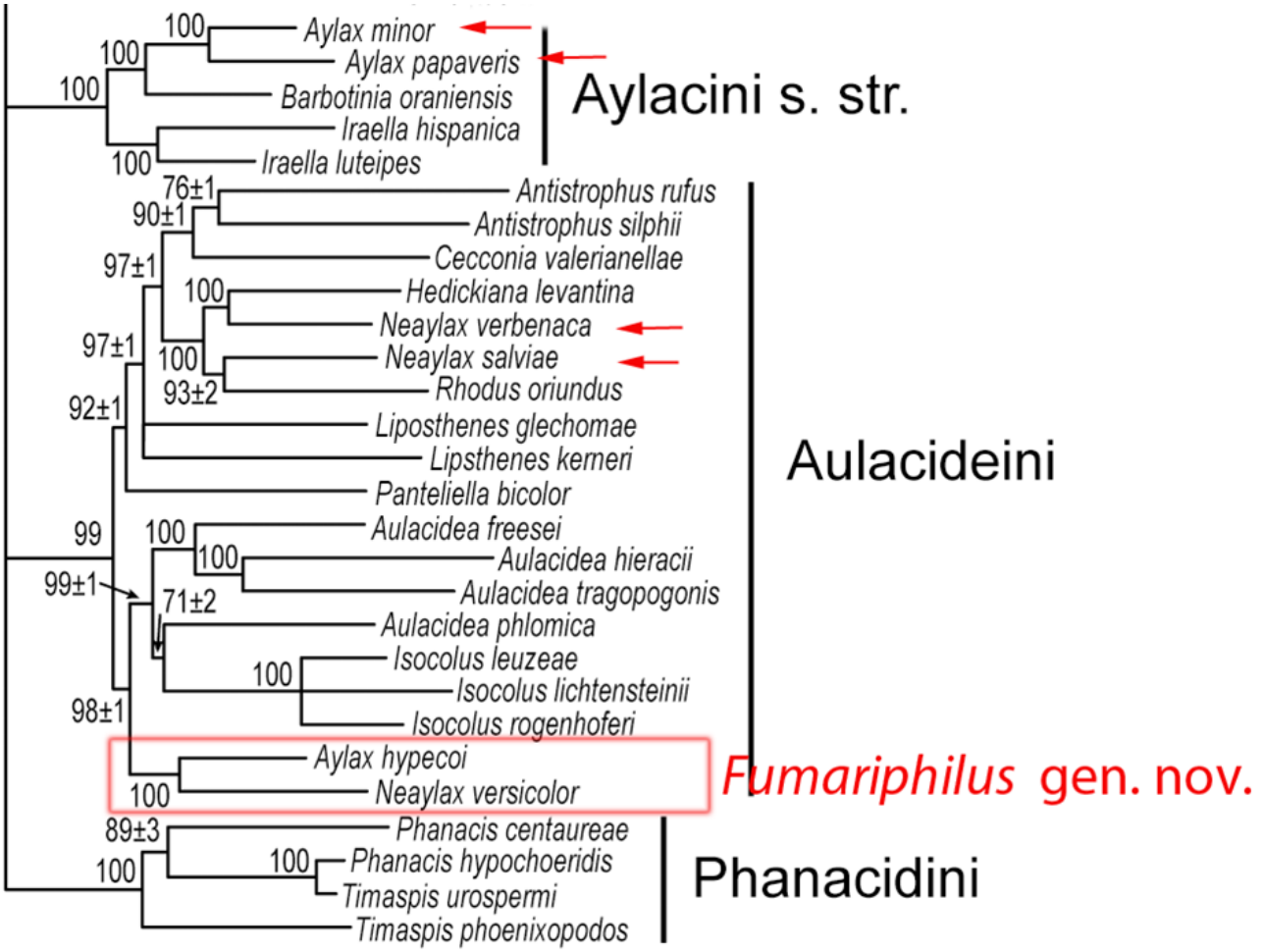

FIGURE 1. Portion of the phylogeny related to herb gall wasps, modified from Fig. 3 in Ronquist *et al*. (2015). This analysis was based on a combined molecular data set of three genes Numbers on branches indicate posterior clade probabilities (in % units) ± Monte Carlo error (errors less than 1% not shown) across four separate analyses. Only groups with a posterior probability above 70% are shown. The red box indicates the monophyletic clade containing the two species with an incorrect genus identification, evidence that supports the erection of the new genus *Fumariphilus* to accommodate them. The red arrows point to the phylogenetic positions of the species correctly assigned to *Aylax* Hartig and *Neaylax* Nieves-Aldrey.

Results

Fumariphilus Nieves Aldrey, gen. nov.

Figs. 2–8

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Type species: *Fumariphilus versicolor* (Nieves-Aldrey, 1985), designated herein.

Etymology. The name is composed of two words: "*Fumari*" refers to the first part of the name of the host plant subfamily of the two cynipid species and "*philus*", to the Greek for "love or fondness". More generally, the name refers to the association of the new genus with plants of the genera *Fumaria* and *Hypecoum* in the subfamily Fumarioideae Eaton, 1836 (Papaveraceae) (Angiosperm Phylogeny Group 2009).

Gender. Masculine

Diagnosis. *Fumariphilus* **gen. nov.**, differs from the other Aulacideini genera by having the following combination of morphological characters: female antennae with 10 flagellomeres, notauli weakly impressed in the anterior third of the mesoscutum, vertex and mesoscutum weakly coriaceous with scattered piliferous punctures, radial cell open on the anterior margin of the forewing and a R1 vein that reaches the anterior margin. Also, they are gall inducers on *Hypecoum* and *Fumaria* (Fumarioideae, Papaveraceae).

The new genus morphologically most resembles species of the *Isocolus*/*Aulacidea* clade (see Fig. 1), however, species of *Aulacidea* differ from those of *Fumariphilus* by having antennae with 11 flagellomeres and a closed radial cell. *Fumariphilus* can be well differentiated from *Isocolus* by having notauli that are weakly impressed anteriorly, antenna with 10 flagellomeres and a R1 vein that reaches the anterior margin of the forewing. From *Neaylax, Fumariphilus* can be distinguished by the trapezoidal shape of its clypeus, with the clypeo-pleurostomal lines diverging towards the ventral margin (subparallel or slightly diverging in *Neayla*x); the longitudinally striated sculpture of its mesopleuron (striate-reticulate in *Neaylax*) and the difference in host plant family association, Papaveraceae in *Fumariphilus* and Lamiaceae in *Neaylax*.

Fumariphilus **gen. nov.**, is also morphologically similar to *Aylax* Hartig, and to the other genera of the tribe Aylacini. However, members of this tribe differ from *Fumariphilus* by having antennae with 12 flagellomeres in females (10 flagellomeres in *Fumariphilus*); a pronotum that is short dorso-medially, less than 0.17X as long as the maximum length of the outer lateral margin, and with admedian depressions that are narrowly separated and strongly transverse (in *Fumariphilus*, the dorso-medial part of the pronotum is one-third as long as the maximum length of the outer lateral margin and the admedian depressions are distinct, spherical to oval and widely separated) and a mesopleuron sculpture that is striate-reticulate or reticulate (longitudinally striate in *Fumariphilus*). In addition, *Fumariphilus* differs from the genera of the tribe Aylacini by its host plant genera association: Aylacini genera only associate with species of *Papaver*, whereas *Fumariphilus* associates with plants of the genera *Fumaria* and *Hypecoum*.

Description. Body slightly pubescent. Head in anterior view generally oval or more or less triangular (Figs. 2A, 4C), weakly alutaceous or coriaceous on front and vertex, with some piliferous punctures; genae not expanded behind eyes. Facial striae radiating from clypeus laterally well marked, reaching ventral margin of compound eyes, faint or absent medially (Figs. 2A, 4C). Anterior tentorial pits, epistomal sulcus and, clypeo-pleurostomal lines visible. Clypeus trapezoidal with ventral margin weakly or moderately projecting over mandibles. Malar (subocular) sulcus absent. Head from posterior view moderately pubescent, without occipital carina but with some transversal rugae or ridges (Figs. 2B, 4B). Distance between occipital and oral foramina shorter or as long as occipital foramen.

Antenna (Figs. 2C, 4E) with 10 flagellomeres in female, 13 in male; flagellum not broadening towards apex. F1 as long as F2.

Pronotum medially long (high), in anterior view ratio of median distance between anterior and posterior margins to lateral distance between these margins about 0.4 (Fig. 3A). Submedian pronotal depressions oval transverse, deep, open laterally. Pronotal plate present but inconspicuous; lateral margins of pronotal plate only visible ventrally; pronotal plate medially almost smooth and sparsely pilose. Lateral surface of pronotum without sculpture, more densely pubescent.

Mesoscutum weakly coriaceous, sometimes with weak piliferous puctures (Figs 2D, 4D). Notauli narrow and convergent posteriorly, clearly impressed in posterior one half of mesoscutum, weakly impressed to almost absent

anteriorly. Median mesoscutal impression absent or visible in posterior one sixth of mesoscutum. Transscutal fissure present. Scutellar foveae from shallow, and smooth (Fig. 4D) to oval, with distinct margins and with some rugae (Fig. 2D). Meoscutellum with variable sculpture. Posterodorsal and posterior margins of axillula distinct. Mesopleuron entirely longitudinally costulate, the intervals smooth (Fig. 2E). Mesopleural triangle distinctly impressed, ventral margin clearly marked.

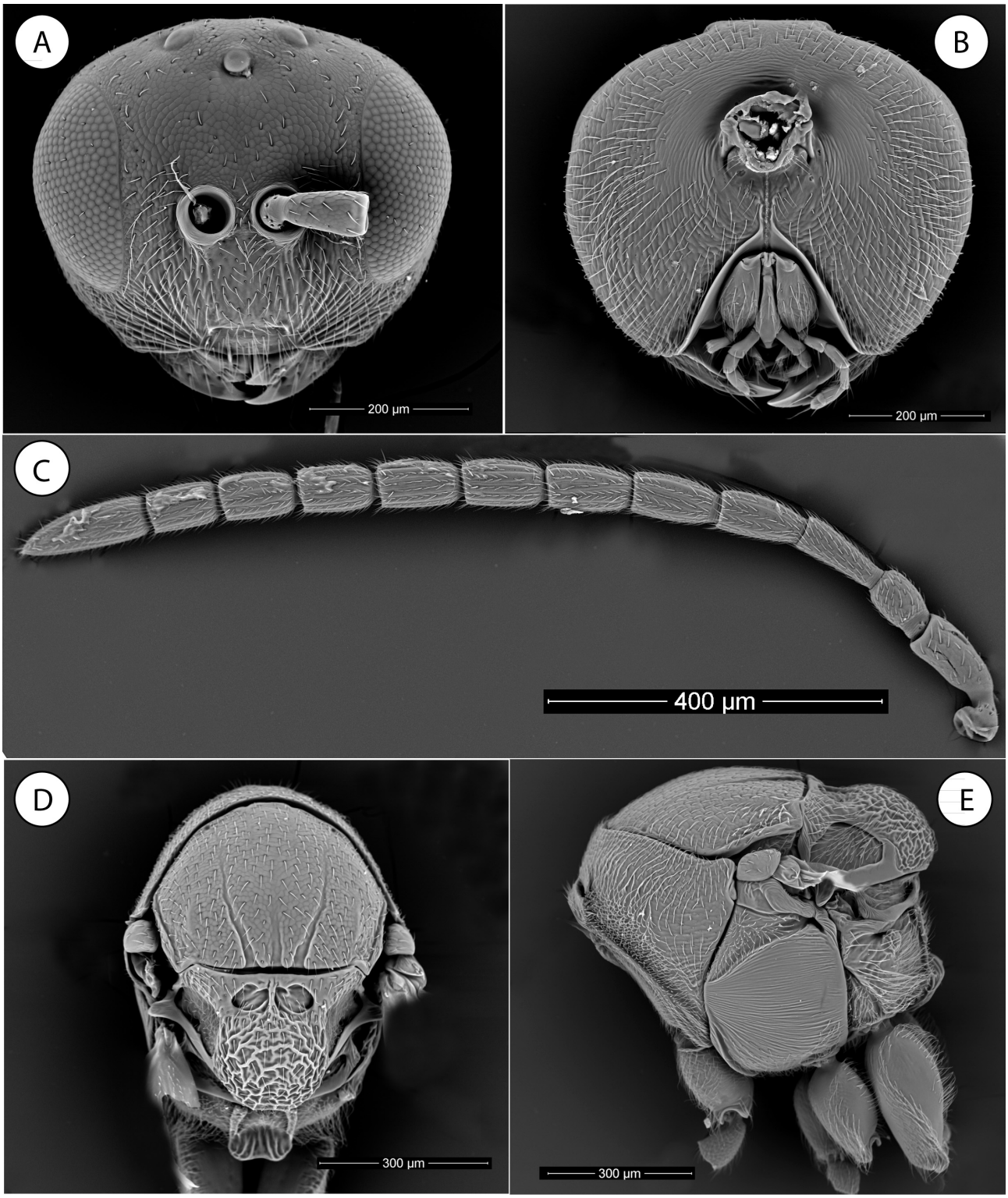

FIGURE 2. *Fumariphilus versicolor*, **n. comb.**, SEM photos of a female. (A) Head, anterior view. (B) Head, posterior view. (C) Antenna. (D) Mesosoma, dorsal view. (E) Mesosoma, lateral view.

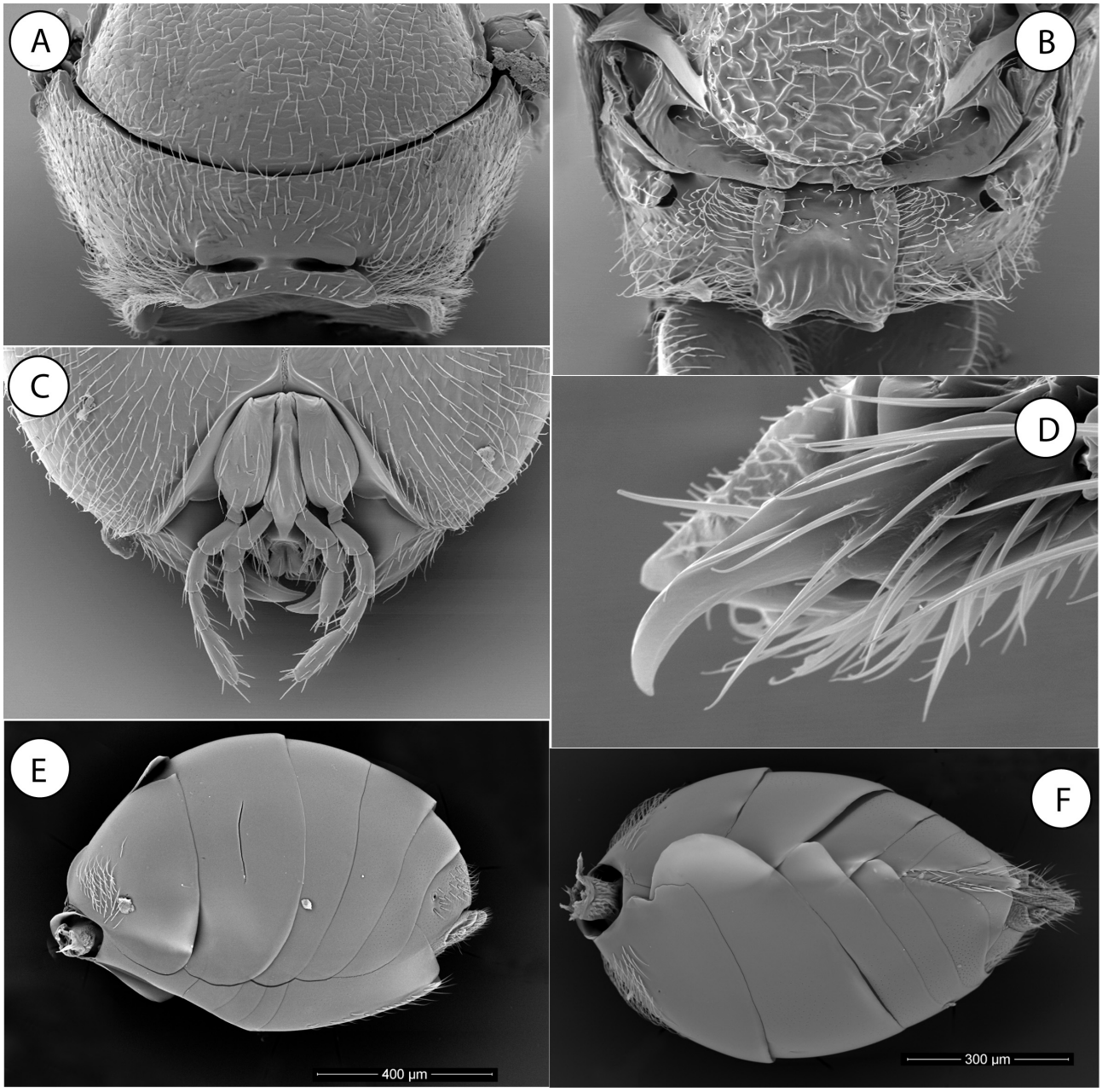

FIGURE 3. *Fumariphilus versicolor*, **n. comb.**, SEM photos of a female. (A) Pronotum, antero-dorsal view. (B) Propodeum. (C) Mouth parts, posterior view. (D) Metatarsal claw. (E) Metasoma, lateral view. (F) Metasoma, ventral view.

Metascutellum (Fig. 3B) conspicuously constricted medially. Metapleural sulcus meeting anterior margin of metapectal-propodeal complex slightly above mid-height of latter. Lateral propodeal carinae broad, subparallel (Fig. 3B). Lateral and median propodeal area smooth, laterally strongly pubescent. Nucha dorsally with some weak longitudinal rugae.

Metatarsal claws simple, without a basal lobe or tooth (Fig. 3D).

Forewing hyaline; radial cell open along anterior margin (Figs. 5C, 5D); R_1 ending slightly before or just reaching the anterior margin of wing. Areolet either present or absent. Hair fringe along apical present, moderately long.

Metasoma with third abdominal tergum (second gastral) covering less than one third of metasoma, with a conspicuous hair patch present antero-medially (Fig. 3E). Projecting part of hypopygial spine short, shorter than basal height of spine; the hypopygial spine bearing some long setae on each side, the apical ones surpassing the apex of the ventral spine. (Figs. 3E, 3F).

Terminal-instar larva (Figs. 7, 8 and 5E, 5F): is of type hymenopteriform; body composed of head and 13 segments almost bare and without appendages. Maxillae triangular and with two pairs of maxillary palps and two pairs of maxillary setae present. Labium rhomboidal; salivary opening surrounded by tuberculate sculpture. Labial palps and labial setae present. Mandibles almost symmetrical with three teeth each.

Gall structures: Galls of *Fumariphilus* species are unilocular and develop in fruits (Fig. 6).

Host plant association: *Fumariphilus* species associate with plants of the genera *Hypecoum* and *Fumaria* (Fumarioideae, Papaveraceae).

Biology: Life cycle is univoltine with bisexual reproduction. A single generation emerges in spring, after overwintering in galls that have fallen to the ground from the dried-out host plants.

Distribution: Circum-Mediterranean, extending east to Armenia, Iran and Central Asia (Nieves-Aldrey 2003).

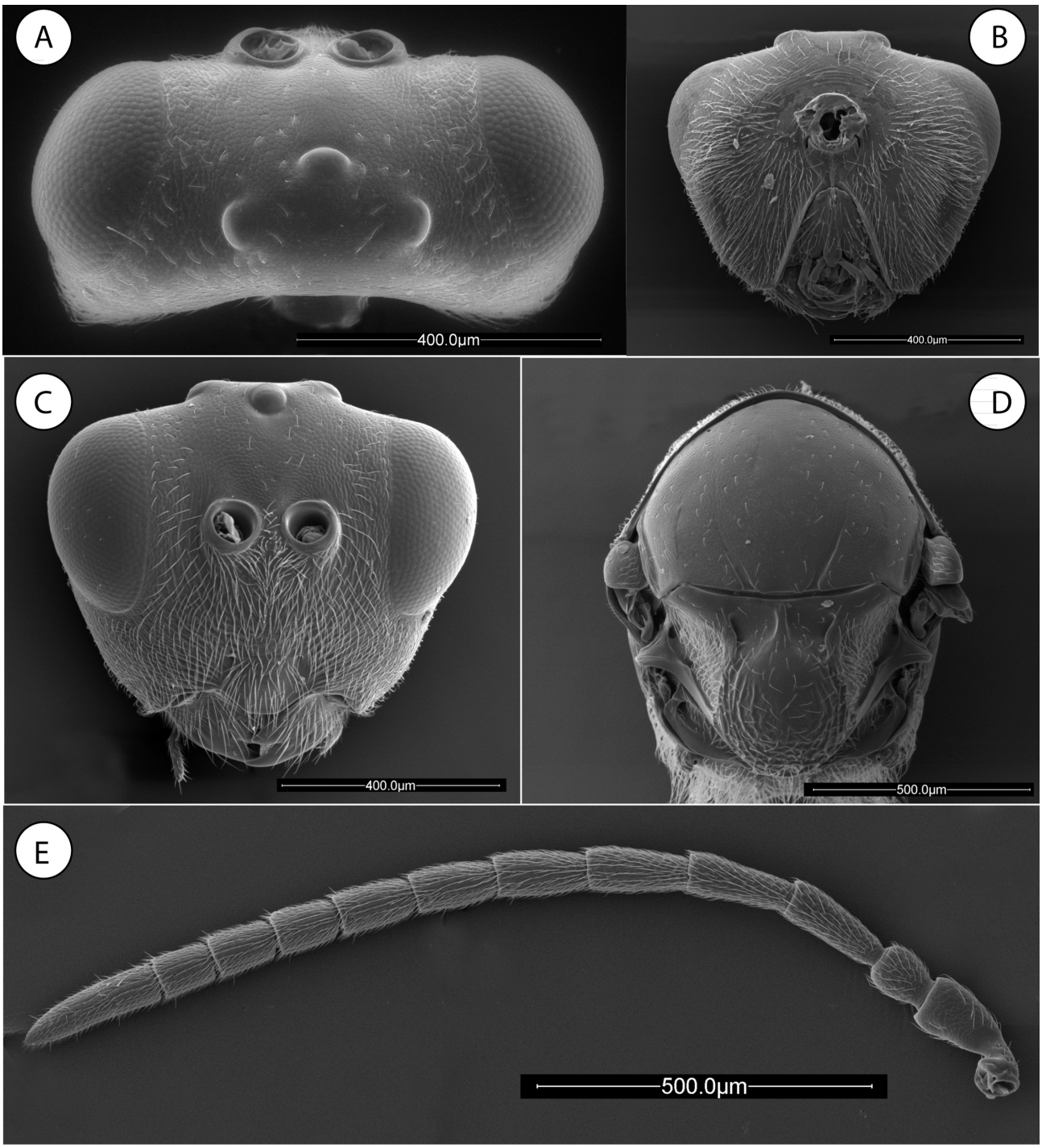

FIGURE 4. *Fumariphilus hypecoi*, **n. comb.**, SEM photos of a female. (A) Head, dorsal view. (B) Head, posterior view. (C) Head, anterior view. (E) Mesosoma, dorsal view. (E) Antenna.

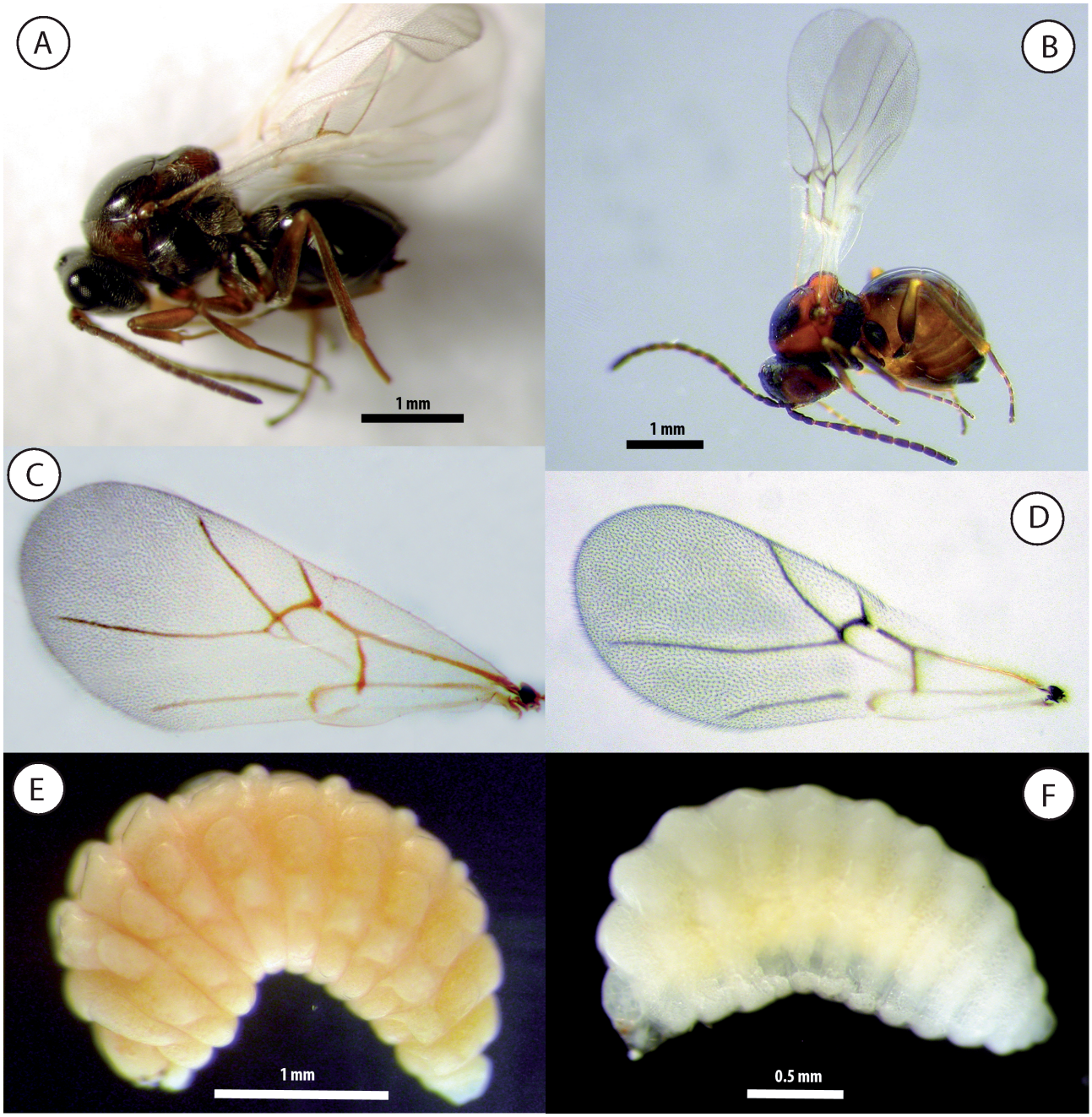

FIGURE 5. Habitus, forewing and terminal instar larvae of *Fumariphilus hypecoi,* **n. comb**. (A), (C), (E) and *Fumariphilus versicolor***, n. comb**. (B), (D) and (F). All in lateral view.

Key to species of *Fumariphilus* gen. nov.

1. Head rounded in anterior view; ventral margin of clypeus slightly projecting over mandibles (Fig. 2A). Notauli weekly impressed but visible in anterior one third of mesoscutum; median mesoscutal impression visible posteriorly (Fig. 2D). Scutellar foveae with some irregular rugae; mesoscutum with coriaceous, dull sculpture; mesoscutellum with rugose sculpture (Fig. 2D). Forewing with absent areolet; Rs vein reaching anterior margin of wing. Galls in fruits of species of *Fumaria* . . . . . ***F. versicolor*** **(Nieves-Aldrey)**

- Head trapezoid in anterior view; ventral margin of clypeus distinctly projecting over mandibles (Fig. 4C). Notauli narrow and shallow, clearly visible only in posterior one third of mesoscutum, faint anteriorly; median mesoscutal impression absent (Fig. 4D). Scutellar foveae shallow, smooth and shining. Mesoscutum delicately shining coriaceous; mesoscutellum delicately alutaceous medially, with concentric rugae laterally (Fig. 4D). Forewing with a visible triangle shaped areolet; Rs vein not quite reaching anterior margin of wing (Fig. 5C). Galls in fruits of *Hypecoum* species. . . . . ***F. hypecoi*** **(Trotter)**

***Fumariphilus versicolor* (Nieves-Aldrey, 1985) n. comb.**
(Figs. 2, 3, 5B, 5D, 5F, 6A–D, 7A–F)

Aylax versicolor Nieves-Aldrey, 1985. *Bol. Soc. Port. Entomol.,* suppl. 1(1): 122
Neaylax versicolor (Nieves-Aldrey): Nieves-Aldrey, 1994. *J. Hymenopt. Res.,* 3: 189

Material examined: Spain, Salamanca, Aldeadávila, I.2001, 1 male and 6 females emerged from galls collected IV.30.2000 on *Fumaria capreolata*; Spain, Tarragona, Marca, 2 females extracted alive X.10.2022 from galls collected V.01.2002 on *Fumaria officinalis*; Spain, Madrid, Valdemorillo 16 females emerged II.2002 from galls collected IV.15.2000 on *Fumaria officinalis*. All these materials J. L. Nieves-Aldrey leg. Held at the MNCN, Madrid, Spain.

Other material examined*:* Spain, Ciudad Real, Pozuelo de Calatrava, 1 female with missing date, La Fuente leg.; Spain, Guipúzcoa, Ormaiztegui, 1 female (missing date), La Fuente leg.; Spain, Zaracoza, Ambel, 3 males and 2 females, Dusmet leg.; Spain, Valladolid, Sardón, Dusmet leg.; Greece, Corfú, 1 female, Paganetti leg.; France, Avignon, 7 females with missing collector and date. All these materials from the Cabrera y Díaz collection housed in the MNCN.

Redescription: The original description of this species was written in Spanish and is incomplete because it was based on observations made using only light microscopy. Here, a more detailed re-description is provided in English and illustrated with additional diagnostic characters that were observed using SEM. Moreover, the terminal instar larva of the species is described here for the first time.

Female. Body 2.0–2.2 mm. Coloration of body variable, from mostly black to predominantly reddish; in some individuals the entire body, including legs and antennae are reddish or reddish-orange, with parts of frons, pronotum medially, ventral part of mesopleuron and two first antennomeres darker while other individuals have a predominantly black coloration with parts of body reddish. Forewing hyaline and veins yellowish.

Head. Head, in dorsal view about 2X as broad as long, as wide as mesosoma; genae not expanded behind eyes. POL slightly longer as OOL, posterior ocellus separated from inner orbit of eye by 3X its diameter. The sculpture is weakly coriaceous with some piliferous punctures.

In anterior view (Fig. 2A) head rounded or oval-rounded, 1.2X as broad as high; lower face moderately pubescent, with some piliferous punctures laterally; with facial striae radiating from clypeus absent medially but laterally reaching ventral margin of compound eyes and lower margin of antennal sockets. Upper face (frons) and vertex weakly coriaceous and, with only some sparse setae. Ocellar plate not raised. Lateral margin of gena rounded, not much convergent towards ventral margin of head; height of malar space 0.4X the height of compound eye. Clypeus sub-rectangular. Ventral margin of clypeus only slightly projecting over mandibles. Anterior tentorial pits hardly visible. Epistomal sulcus and clypeo-pleurostomal lines weakly marked. Antennal sockets situated at mid-height of compound eye; distance between antennal rim and compound eye as long as width of antennal socket including rim; distance between antennal sockets less than 0.5X the diameter of an antennal socket.

Head posterior view (Fig. 2B) with occiput densely pubescent; without occipital carina and with some weak transverse rugae present above occipital foramen. Gular sulci free, well separated at hypostomata. Oral foramen about 2X as long as occipital foramen; distance between oral and occipital foramina about 0.6X height of occipital foramen.

Mouthparts (Fig. 3C). Mandibles moderately large, right mandible with three teeth; left with two teeth. Maxillary stipes about two times as long as broad. Maxillary palp five-segmented. Labial palp three-segmented.

Female antenna (Fig. 2C) 0.6X as long as body, with 10 flagellomeres. Elongate placodeal sensilla inconspicuous but present from second flagellomere. Scape 2X as long as broad; 1.3X as long as pedicel. F1 slightly longer as F2. F3 to F9 similar in length. F10 from 2X to 2.4X as long as F9; rarely a weak division visible in the last flagellomere then the antenna appearing as 13 segmented.

Mesosoma. Pronotum medially long (high) (Fig. 3A); in anterior view ratio of median distance between anterior and posterior margins to lateral distance between these margins about 0.45. Submedian pronotal depressions oval transverse, deep, open laterally, separated by a distance equal to half of its breadth. Pronotal plate present but short and inconspicuous; lateral margins of pronotal plate only visible ventrally; pronotal plate medially almost smooth and sparsely pilose. Lateral surface of pronotum without sculpture, more densely pubescent.

Mesoscutum dull, weakly coriaceous and sparsely pubescent (Fig. 2D). Notauli narrow and convergent posteriorly, clearly impressed in posterior one half of mesoscutum, weakly impressed but visible anteriorly. Median mesos-

cutal impression present in posterior one sixth of mesoscutum. Scutellar foveae oval, with distinct margins, shining, with some rugae, separated medially by a septum and with a relatively broad separation from the transscutal fissure. Scutellum relatively large, as long as 0.9X as mesoscutum. Mesoscutellum with strong reticulate-rugose sculpture. Posterodorsal and posterior margins of axillula distinct. Mesopleuron entirely longitudinally costulate, the intervals smooth (Fig. 2E). Mesopleural triangle distinctly impressed, ventral margin clearly marked.

Metanotum. Metascutellum (Fig. 3B) conspicuously constricted medially. Bar ventral to metanotal trough almost smooth. Metanotal trough narrow, pubescent.

Metapectal-propodeal complex. Metapleural sulcus meeting anterior margin of metapectal-propodeal complex slightly above mid-height of latter. Lateral propodeal carinae broad, subparallel. Lateral and median propodeal area smooth, laterally strongly pubescent, medially more moderately (Fig. 3B). Nucha dorsally with some weak longitudinal rugae .

Legs. Claws simple, without a basal lobe or tooth (Fig. 3D).

Forewing (Fig. 5D). Slightly longer than body, hyaline and pubescent. Radial cell open along anterior margin; about 2.4X as long as broad. R_1 ending slightly before the anterior margin of wing; first abscissa of radius (2r) curved and radius (Rs) slightly bowed and reaching anterior margin of wing. Areolet absent. Hair fringe along apical present, moderately long.

Metasoma. Female metasoma (Figs. 3E, 3F). Slightly longer than head + mesosoma; third abdominal tergum (second gastral) covering less than one third of metasoma; about 1.4X as long as fourth tergum; a conspicuous hair patch is present antero-medially on the third abdominal tergum. Fourth to seventh terga bare, T6 and T7 with weak micropunctures on the postero-dorsal area. Ventral spine of hypopygium short, not projecting, united almost to apex with the lateral flaps. Rows of long setae are present on each side, the apical ones surpassing the apex of the ventral spine.

Male. Slightly smaller than female; body length 1.7–2.0 mm. Coloration more predominantly black, excepting clypeus, mandibles, legs excepting coxae, and metasoma ventrally which are reddish. Antennae relatively longer, with 14 segments. Otherwise similar to female.

Description of the terminal-instar larva. Material examined, Spain, Madrid, Valdemorillo, 15/iv/2000 ex galls in fruits of *Fumaria officinalis;* Salamanca, Aldeadávila ex gall on *Fumaria caprolata*, J.L. Nieves leg (n=4)

Description: Length 1.9 mm (range 1.7–2.1; n=4)

Body in ventral view more or less fusiform, segments of larval body widest approximately around the middle, tapering towards anterior and posterior end (Fig. 7A); curved ventrally in lateral view (Fig. 7B). Integument whitish and smooth, with a few short setae concentrated in the head region and the first thoracic segment. Body composed of head and 13 segments; three thoracic, nine abdominal and one anal segment. First thoracic segment, in ventral view appearing as divided into three parts, one dorsal and the other ventral, the later sub-divided into two lateral and one medial; first abdominal segment slightly constricted and narrowed than third thoracic segment; abdominal segments 2–5 of similar length and progressively narrower towards anal segment; anal segment short ,truncate at apex and wider than long.

Head (Fig. 7C) more or less triangular, medial area of vertex convex. Antennal areas and antennae not visible. Antennal setae absent. A pair of very short and inconspicuous genal setae present.

Mouthparts. Clypeus (Fig. 7D) well marked with its ventral margin straight and clearly prolonged ventrally into a sub-rectangular piece above the labrum; pair of supraclypeal setae present. Labrum sub-trapezoidal with straight subparallel sides; apical margin straight, pairs of ventrolateral and medioapical short setae present. Mandibles covered by the labrum. Maxillae triangular with its apex pointed and with two pairs of maxillary palps and two pairs of maxillary setae present. Labium large, rhomboidal, convex; salivary opening situated under a hand fan shaped depression; the area surrounding the salivary opening present a tuberculate sculpture. Labial palps and labial setae present.

Mandibles (Figs 7E, 7F) Smooth and bare. Both mandibles almost symmetrical, with two teeth and a third secondary smaller tooth, more long in the right mandible; the second middle tooth slightly blunt and being shorter than half of the large apical tooth.

Gall structures: Galled fruits (Figs. 6A, B), usually measuring 2 mm x 2.5 mm, are slightly inflated and bigger than those without galls (about 3 mm in diameter). Unilocular; each galled fruit contains a large larval chamber with a single larva (Figs. 6C, D). Mature galled fruits usually fall to the ground later than non-galled fruits.

Host plant association: Galls are formed in the fruits of *Fumaria* species. In Spain, they are more frequently

found on *Fumaria officinalis* and *Fumaria capreolata* than on other species of *Fumaria* (Nieves-Aldrey 2003). The galls, due to their small size, are not highly visible in the fruits, and some evidence suggests they may be locally abundant (Nieves-Aldrey 2003).

FIGURE 6. Galls of *Fumariphilus versicolor,* **n. comb** on *Fumaria officinalis* (A, B). (C) Section of a galled fruit showing a larva. (D) Section of a mature fruit with a fully developed adult inside. (E) Galls of *Fumariphilus hypecoi,* **n. comb.** on *Hypecoum procumbens*. (F) Section of a mature fruit with a fully developed adult inside.

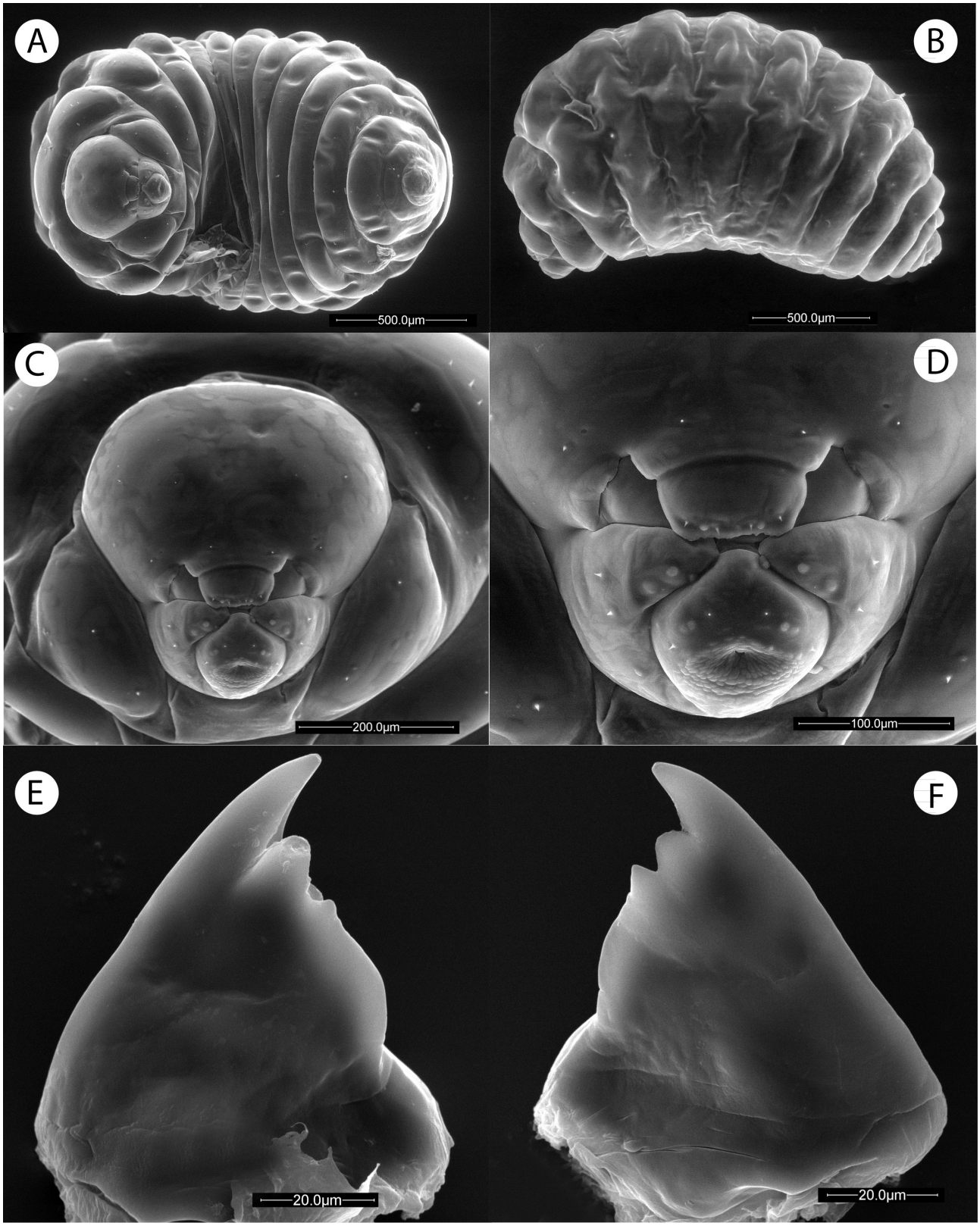

FIGURE 7. *Fumariphilus versicolor*, **n. comb.**, SEM photos of a terminal instar larva. (A) Body, ventral view. (B) Body, lateral view. (C) Head, anterior view. (D) Detail of mouth parts. (E) Left mandible. (F) Right mandible.

Biology: Life cycle is univoltine with, typically, bisexual reproduction, as in most herb gall wasps. Adults emerge in early spring, after overwintering in galls that have fallen to the ground when the host plants start to bloom again.

Distribution: Originally described and cited from Spain, Greece and France (Nieves-Aldrey 1985, 2003).

Remarks: The species is similar to *F. hypecoi* in coloration and morphology. However, besides gall structure and host plant association, the two species differ by the diagnostic characters provided in the identification key of the species of *Fumariphilus*.

Fumariphilus hypecoi (Trotter, 1913) n. comb.

(Figs. 4, 5A, 5C, 5E, 6E, 6F, 8)

Aulax Hypecoi Trotter, 1913. *Marcellia*, 11: 214
Aylax spirorhynchussi Diakontshuk, 1990. News of faunistics and systematics Kiew, p 126
Aylax hypecoi Trotter. Nieves-Aldrey & Melika, 2005. *Journ. Nat. Hist*., 39(27): 2526

Material examined: Bulgaria, Plovdic, Dzhendem tepe, 165 m, five females reared from galls collected V.19.2001 on *Hypecoum imberbe* (Papaveraceae), A. Stojanova leg. Held at the MNCN, Madrid, Spain.

Nieves-Aldrey & Melika (2005) thoroughly re-described and illustrated the adult wasps; therefore, they will not be further discussed here. With regard to the immature stages, Stojanova & Draganov (2008) previously provided notes on the life cycle of *A. hypecoi* Trotter, including data on the morphology and development of the egg, larva and pupa. Here, a more detailed morphological description of the terminal instar larva is provided, along with some SEM images.

Description of the terminal instar larva. Material examined: Bulgaria, Plovdiv, Dzhendem tepe, 165 m, larvae extracted from galls found in *Hypecoum imberbe*; galls collected 19 May 2001. A Sojanova leg. (n=4)

Description: length 2.7 mm (range 2.3 – 3 mm; n=4).

Body in ventral view fusiform, segments of larval body widest approximately around the middle, tapering towards the anterior and posterior ends (Fig. 8A); in lateral view more clearly tapering towards the posterior end (Fig. 8B). Integument smooth, almost bare and with a yellowish orange coloration (Fig. 5E). Body composed of head and 13 segments: three thoracic, nine abdominal and one anal. First thoracic segment appears, in ventral view, divided into three parts, one anterior and one posterior that is further sub-divided into two lateral and one medial; first abdominal segment slightly constricted and narrower than the third thoracic segment; abdominal segments 2–5 similar in length and progressively narrower towards the anal segment; anal segment short, truncated at the apex and wider than long.

Head (Fig. 8C) more or less triangular, medial area of vertex slightly sunken. Antennal areas and antennae not visible. Antennal setae absent. A pair of very short and inconspicuous genal setae present.

Mouthparts. Clypeus (Fig. 8D) well marked with its ventral margin straight and clearly prolonged ventrally into a sub-rectangular piece above the labrum; pair of supraclypeal setae present. Labrum sub-trapezoidal with slightly convergent sides; apical margin straight, pairs of ventrolateral and medioapical short setae present. Mandibles covered by the labrum but apex visible. Maxillae triangular with its apex pointed and with two pairs of maxillary palps and two pairs of maxillary setae present. Labium large, diamond shaped or rhomboidal; salivary opening situated under a rhomboidal depression; the area surrounding the salivary opening present a tuberculate sculpture. Labial palps and labial setae present.

Mandibles (Figs. 8E, 8F) Smooth and bare. Both mandibles with three teeth; the second middle tooth slightly blunt and being as long as half of the large apical tooth in the left mandible; the second tooth of the right mandible blunt and subdivided into two small teeth.

Gall structures: One or more seeded sections of the fruits are considerably inflated. Each galled fruit contains from one to three oval to globose, unilocular galls.

Host plant association: Galls are formed in the fruits of *Hypecoum* species (Figs. 6E, F). Galls in fruits of *Hypecoum imberbe* collected in Bulgaria form a conspicuous swelling on the fruit.

Biology: Life cycle is typically univoltine, as in most herb gall wasps. In the studied material, all reared individuals were females, except for one male. Adults emerge from the galls from the end of winter to early spring, around the time the host plant starts flowering. The larvae overwinter inside the galls and pupate a little before emergence.

Distribution: Originally described from Tripoli (North Africa) by Trotter (1913), its distribution extends from the Eastern Mediterranean (Algeria, Bulgaria, Greece) to Transcaucasia (Armenia) and Central Asia (Turkmenistan)

(Nieves-Aldrey & Melika 2005). More recently, it was cited from Turkey (Katilmis & Kiyak 2008, 2011) and Iran (Melika & Karimpour 2012).

Remarks*:* *F. hypecoi* morphologically resembles *F. versicolor* in its general appearance and variable coloration. However, the two species can be easily distinguished by the diagnostic characters given in the identification key of the species of *Fumariphilus.*

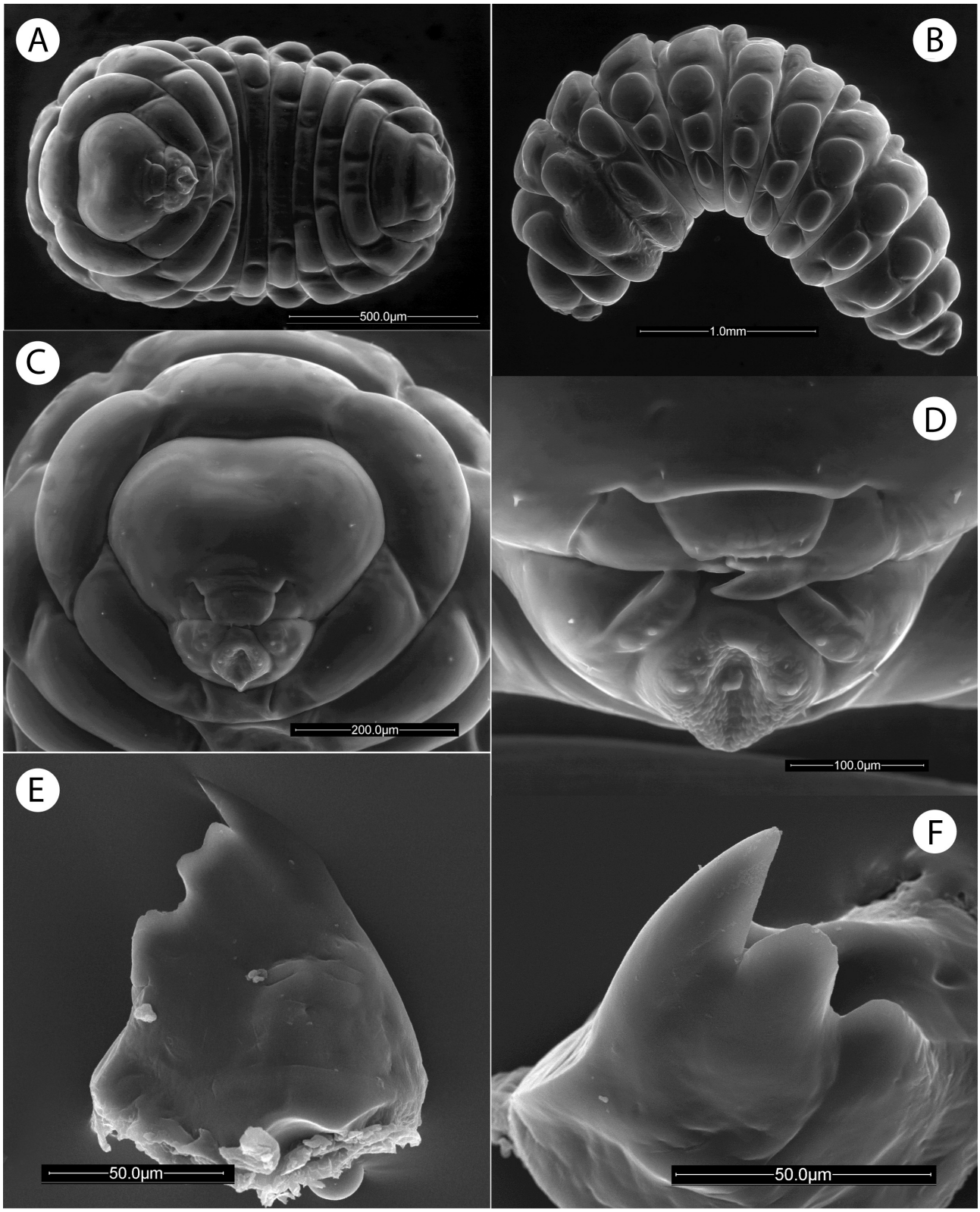

FIGURE 8. *Fumariphilus hypecoi*, **n. comb.**, SEM photos of a terminal instar larva. (A) Body, ventral view. (B) Body, lateral view. (C) Head, anterior view. (D) Detail of mouth parts. (E) Right mandible. (F) Left mandible.

Key to the genera of the Aulacideini tribe

The re-classification of the different tribes of herb gall wasps, and the recognition of the tribe Aulacideini as a monophyletic entity (Ronquist *et al.* 2015), necessitate updating the identification keys of the genera included in this new tribe. A thorough revision of this tribe's genera, particularly of those that form galls on Lamiaceae, i.e., *Rhodus* Quinlan, 1968, *Neaylax* Nieves-Aldrey, 1994 and *Hedickiana* Nieves-Aldrey, 1994, whose current taxonomic arrangement is unsatisfactory, is currently being carried out (unpublished data). However, in the meanwhile, a provisional updated identification key for the Aulacideini genera is provided here.

1. Dorsal part of pronotal plate distinct, with lateral margins marked, close reaching anterior margin of mesoscutum (Figs 9A, 9B). Facial strigae radiating from clypeus either weak and short, not reaching compound eye, or irregular and indistinct (Figs 9E, 9F). Clypeus strongly trapezoid with ventral part broadly projecting over mandibles (Figs 9E, 9F). Gall inducers associated with Lamiaceae of the genera *Nepeta*, *Glechoma* and *Phlomis*. **2**

-- Dorsal part of pronotal plate usually less distinct and with lateral margins only marked ventrally (Figs 9C, 9D). Facial strigae radiating from clypeus regular and distinct, usually reaching compound eye (Figs 9G, 9H) Clypeus trapezoid or subquadrate, with ventral part usually not or only slightly projecting over mandibles (Fig. 9G). Gall inducers associated with *Valerianella, Salvia, Hypecoum, Fumaria* and several Asteraceae genera,. **3**

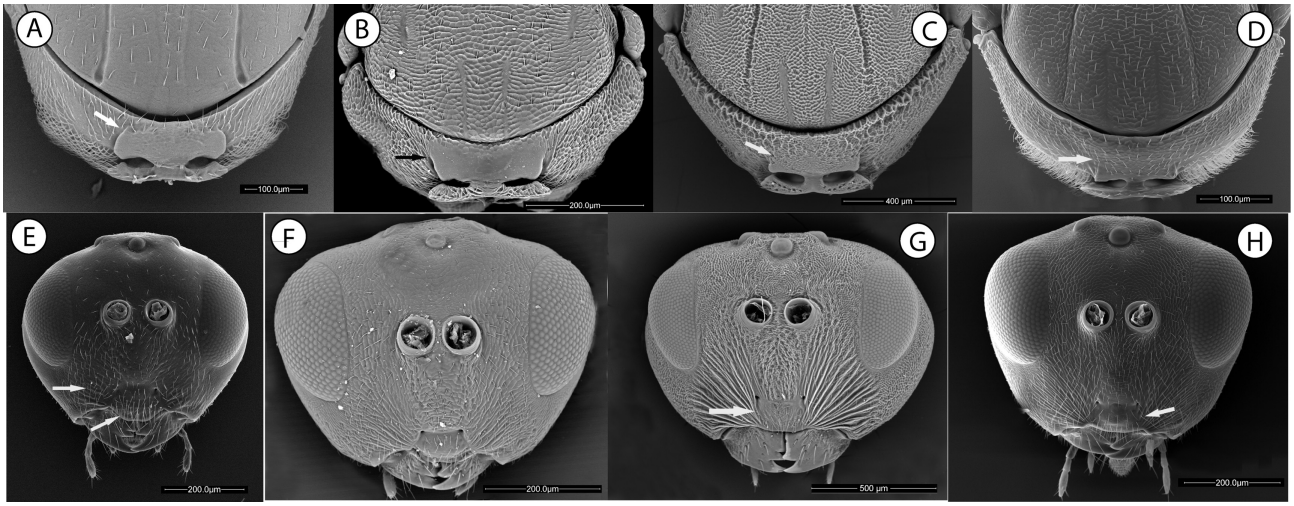

FIGURE 9. Pronotum in antero-dorsal view and head in anterior view of (A, E) *Liposthenes kerneri* (Wachtl). (B, F) *Panteliella fedtschenkoi* (Rübsaamen). (C, G) *Antistrophus silphii* Gillette. (D, H) *Aulacidea martae* Nieves-Aldrey.

2. Female antenna with 11 flagellomeres (Fig. 10D). Lateral margins of dorsal part of pronotal plate converging dorsally (Fig. 9A). Notauli conspicuous, marked entirely (Fig. 10A). Mesoscutum with almost smooth to weak coriaceous sculpture. Propodeum without a median propodeal carina; lateral propodeal carinae well marked, subparallel (Fig. 10B). Third abdominal tergum with a dense hair patch anterolaterally (Fig. 10C). Gall inducers on *Nepeta* and *Glechoma* (Lamiaceae). . . . . ***Liposthenes***

-- Female antenna with 12 flagellomeres (Fig. 10H). Lateral margins of dorsal part of pronotal plate subparallell or slightly divergent dorsally (Fig. 9B). Notauli faint anteriorly, indistinct posteriorly (Fig. 10E). Mesoscutum with conspicuous alutaceous-reticulate sculpture. Propodeum with a median propodeal carina; lateral propodeal carinae not well marked and divergent (Fig. 10F). Third abdominal tergum without a dense hair patch anterolaterally (Fig. 10G). Gall inducer on *Phlomis* (Lamiaceae). . . . . ***Panteliella***

3. Clypeus subquadrangular; clypeo-pleurostomal lines subparallell or slightly converging towards ventral margin of clypeus; ventral margin not or only slightly projecting over mandibles (Figs 11A, 11B, 11C, 11E). Gall inducers on *Valerianella*, *Salvia*, and some genera of Nearctic Asteraceae, mainly *Silphium* **4**

-- Clypeus trapezoidal; clypeo-pleurostomal lines diverging towards ventral margin of clypeus and ventral margin of clypeus usually more or less projecting over mandibles (Figs 11D, 11F). Gall inducers on Fumarioideae (Papaveraceae) and Lactuceae (Asteraceae) 6

4. Head female in anterior view as high as wide, slightly higher than wide in male (Fig. 11B); Genae long; malar space more of ½ as long as height of an eye in female, longer (about 0.7) in male. Female antenna with 11 flagellomeres; third antennal segment longer than A4 in male antenna; with dense placodeal sensilla (Figs. 12A, 12B). Facial strigae radiating from clypeus strong, reaching compound eyes and extended to ventral margin of antennal sockets (Fig. 11B). Gall inducers on *Valerianella*, (Valerianaceae). . . . . ***Cecconia***

-- Head in anterior view wider than high in both sexes (Figs 11A, 11C, 11D); malar space shorter than 1/2 of height of an eye. Female antenna with 11 or 12 flagellomeres. Third antennal segment as long as or shorter than A4 in male antenna; with few and sparse placodeal sensilla (Figs 12C, 12D, 12E, 12F). Gall inducers on *Salvia* (Lamiaceae) and some Nearctic genera of Asteraceae. 5

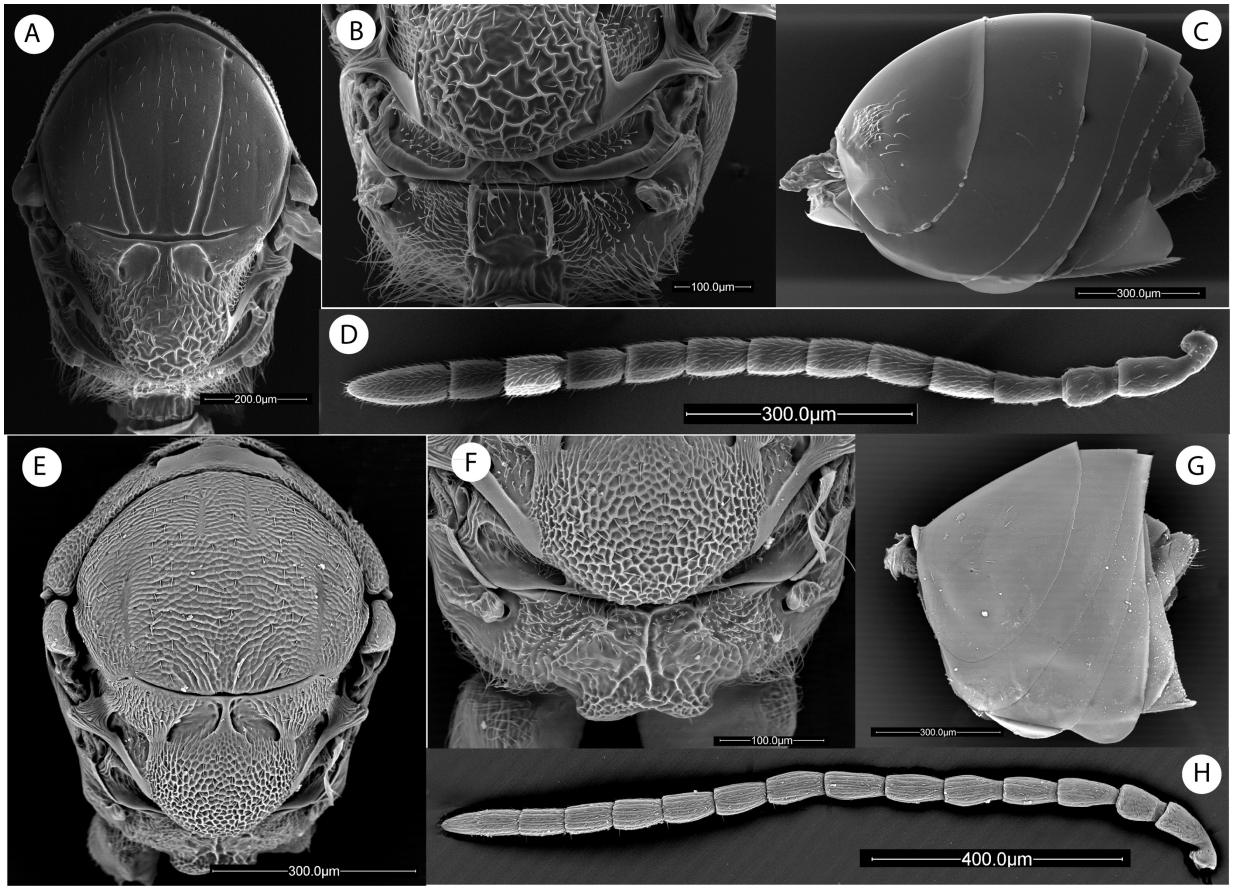

FIGURE 10. *Liposthenes kerneri* (Wachtl) (A–D). (A) Mesosoma, dorsal view. (B) Propodeum. (C) Metasoma, lateral view. (D) Female antenna. *Panteliella fedtschenkoi* (Rübsaamen) (E–H). (E). (E) Mesosoma, dorsal view. (F) Propodeum. (G) Metasoma, lateral view. (H) Female antenna

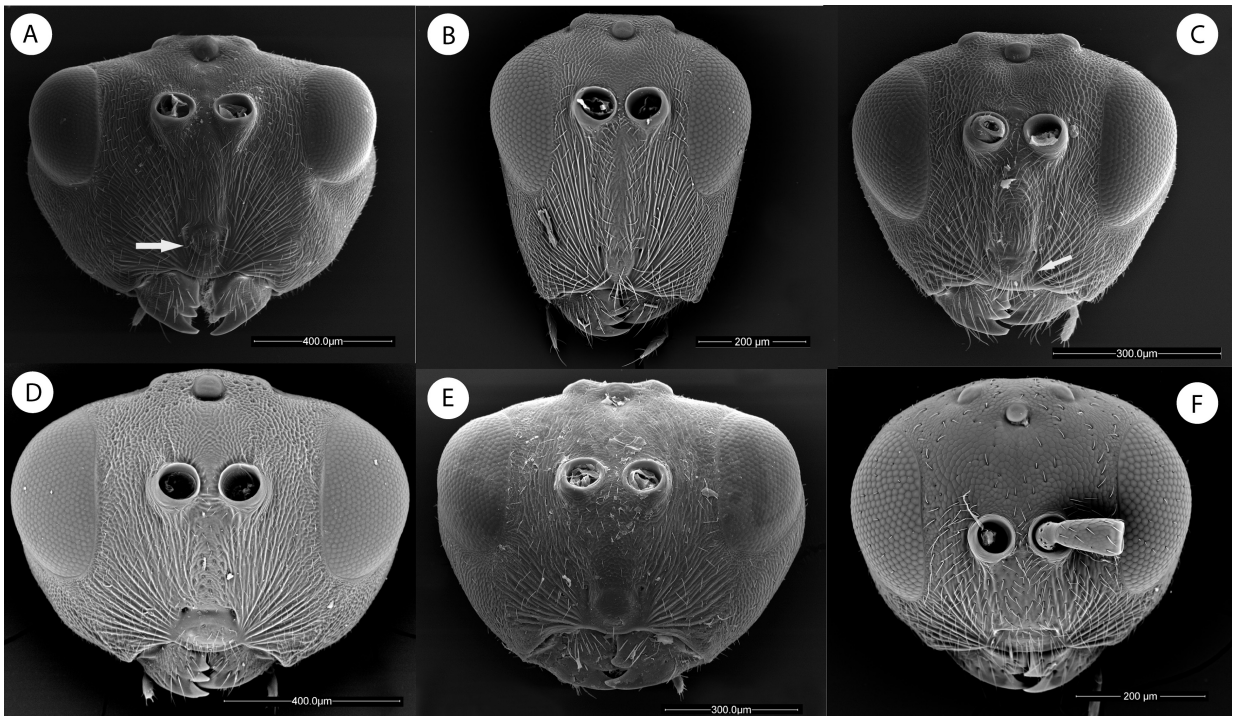

FIGURE 11. Head, anterior view. A female specimen shown in all panels except (B). (A) *Hedickiana levantina* (Hedicke). (B) *Cecconia valerianellae* (Thomson). (C) *Neaylax verbenaca* (Nieves-Aldrey). (D) *Isocolus leuzeae* Nieves-Aldrey. (E) *Rhodus oriundus* Quinlan. (F) *Fumariphilus versicolor* (Nieves-Aldrey).

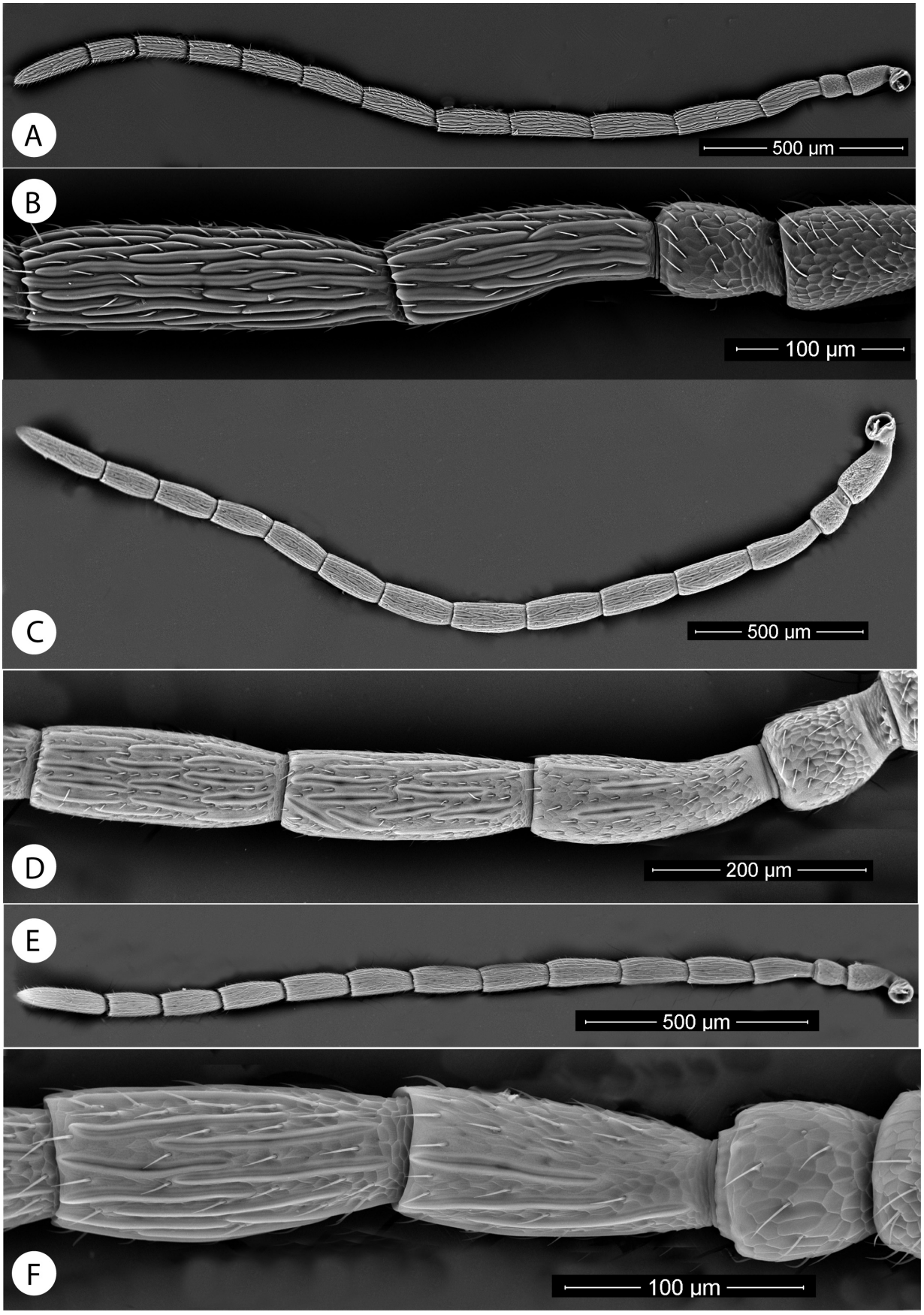

FIGURE 12. Male antenna and detail of the first antennomeres. (A, B) *Cecconia valerianellae* (Thomson). (C, D) *Antistrophus silphii* Gillette. (E, F) *Neaylax verbenaca* (Nieves-Aldrey).

5. Mesoscutum, pronotum and mesopleuron with strong reticulate rugose sculpture. Notauli deeply impressed, medial mesoscutal impression marked (Fig. 13A). Distal margin of forewing without hair fringe (Fig. 13E). Gall inducers on *Silphium* and other Nearctic genera of Asteraceae. . . . . ***Antistrophus***

-- Mesoscutum usually with coriaceous or coriaceous-punctate sculpture (Figs 13B, 13C, 13D); mesopleuron striate-reticulate. Notauli usually faint in anterior half; medial mesoscutal impression short and weakly marked. Distal margin of forewing with or without hair fringe (Figs 13F, 13G). Gall inducers on *Salvia* (Lamiaceae). . . . . *Neaylax*, *Rhodus* and *Hedickiana* *

*These three genera together form a monophyletic clade; they are closely related and could eventually be considered synonymous. A revision of the genera and species of this clade is necessary and will be treated elsewhere.

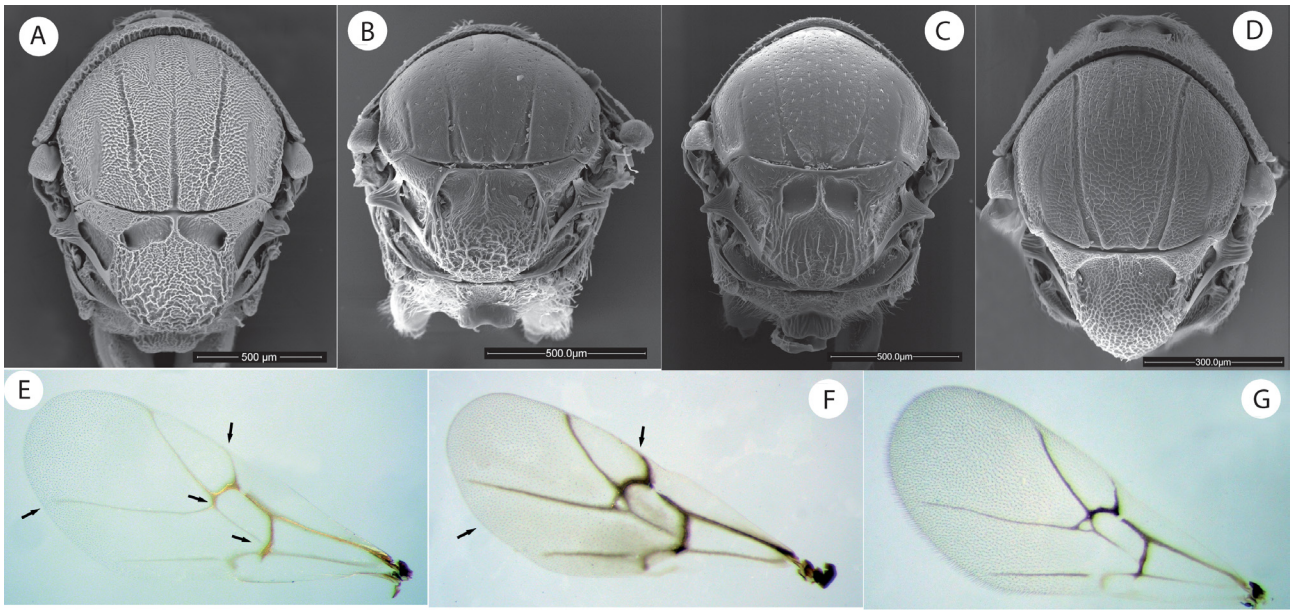

FIGURE 13. Mesosoma in dorsal view and forewing of (A, E) *Antistrophus silphii* Gillette. (B) *Rhodus oriundus* Quinlan. (C, F) *Hedickiana levantina* (Hedicke). (D, G) *Neaylax verbenaca* (Nieves-Aldrey).

6. Female antenna with 10 flagellomeres (Figs. 2C, 4E). Notauli weakly impressed in anterior one third of mesoscutum; vertex and mesoscutum weakly coriaceous with scattered piliferous punctures (Figs. 2D, 4D). Radial cell open on anterior margin of forewing; R1 reaching anterior margin (Figs 5C, 5D). Gall inducers on *Hypecoum* and *Fumaria* (Fumaroideae) Papaveraceae)). . . . . ***Fumariphilus* gen. nov.**

-- Female antenna with 11 flagellomeres (Fig. 14A). Notauli usually impressed throughout (Figs 14B, 14C, 14D); vertex and mesoscutum without piliferous punctures (Fig. 14B). Radial cell either open or closed on anterior margin (Fig. 14E); if open, then R1 not reaching anterior margin of forewing (Fig. 14F). Gall inducers on Asteraceae 7

7. Radial cell open on anterior margin of forewing; R1 not quite reaching anterior margin (Fig. 14F). Distal margin without hair fringe. Gall inducers mainly on *Centaurea* . . . . . ***Isocolus***

-- Radial cell closed on anterior margin of forewing (Fig. 14E). Distal margin with hair fringe present, more or less long. Gall inducers on several genera of Asteraceae, mainly *Hieracium* . . . . . ***Aulacidea***

Discussion

With the description of the new genus *Fumariphilus*, *Aylax* Hartig, *sensu* Nieves-Aldrey, 1994, is now sufficiently delimited within the tribe Aylacini *sensu stricto* Ashmead, together with the genera *Barbotinia* Nieves-Aldrey, 1994 and *Iraella* Nieves-Aldrey, 1994. These three genera are formed by species that only associate with plants of the genus *Papaver* (Papaveraceae). Furthermore, *Neaylax* Nieves-Aldrey is now sufficiently delimited within the tribe Aulacideini Nieves-Aldrey, Nylander & Ronquist, 2015 and specifically belongs to the group formed by species inducing galls on Lamiaceae. Based on current knowledge, the known diversity of the tribe Aulacideini, including the new genus described here, now comprises 10 genera and about 80 valid species (Liljeblad 2002, Ronquist *et al*. 2015, Nastasi & Deans 2021).

Although this work contributes to a more natural classification of the Aulacideini, in which monophyletic lineages are delimited as genera, much work remains to be completed. As indicated in the identification key of the genera of this tribe, the group of genera that induce galls in the plants of Lamiaceae (i.e., *Neaylax* Nieves-Aldrey,

Rhodus Quinlan and *Hedickiana* Nieves-Aldrey), is in particular need of revision. This is also evidenced by previous molecular phylogenetic analyses (Ronquist *et al*. 2015) and by newly revised morphological data (Nieves-Aldrey, unpublished data). The taxonomic revision of these three genera is a priority and will be addressed in a forthcoming study.

Two other Aulacideini genera are also in need of taxonomic revision: *Aulacidea* Ashmead, 1897 and *Antistrophus* Walsh, 1869. *Aulacidea*, with around 40 species described worldwide, is the most diverse genus of Aulacideini. In contrast to the other genera of herb gall wasps, species of this genus have been recorded on host plant genera from different botanical families, mainly Asteraceae but also Lamiaceae and Rosaceae, a feature that challenges the paradigm of the strict conservatism in host plant family choice in cynipids (Ronquist & Liljeblad 2001). However, I have some reasonable doubts about the reliability of some of these records and suggest they may represent host plant misidentifications (Nieves-Aldrey, personal observations and unpublished data). Moreover, published phylogenetic evidence (Ronquist *et al*. 2015) indicates that *Aulacidea*, as currently conceived, is not monophyletic as the species of this genus not associated with Asteraceae may represent different phylogenetic lineages and thus are likely erroneously placed within *Aulacidea*. This possibility is reinforced by the fact that, currently, *Aulacidea* is supported by only a single morphological character state, namely a radial cell that is closed along the forewing margin. Besides its intrinsic ambiguity, many studies have outlined this trait as a potential homoplasy (Liljeblad *et al* 2008). Regarding the Nearctic genus *Antistrophus*, the taxonomic limits of this genus also need be re-defined according to preliminary data from an ongoing study (Nastasi, personal communication).

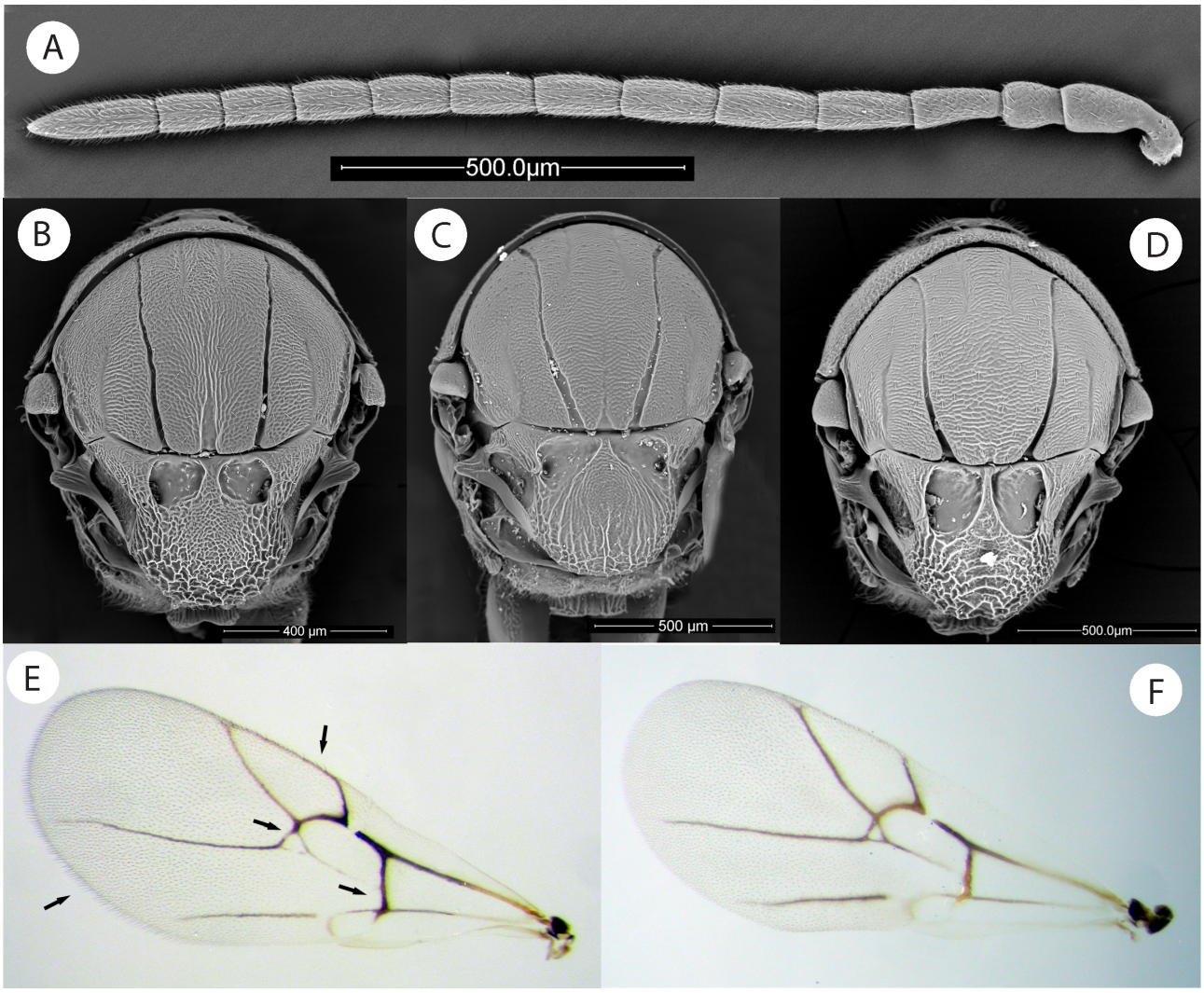

FIGURE 14. (A) Female antenna of *Aulacidea hieracii* (Bouche). Mesosoma in dorsal view of (B) *Aulacidea hieracii* (Bouche), (C) *Aulacidea acroptilonica* Tyurebaev and (D) *Isocolus lichtensteini* (Mayr). Forewing of (E) *Aulacidea hieracii* (Bouche) and (F) *Isocolus leuzeae* Nieves-Aldrey.

Herb gall wasps are less well studied than tree and bush gall wasps because their host plants are generally more difficult to identify and to sample in the field. For this reason, and because these gall wasps also constitute a less rich fauna, descriptions of new taxa of cynipid herb gallers have been scarce compared with the increase seen in the number of oak gall wasp descriptions in recent years (Melika *et al*. 2021). Despite this, there is still ground for new discoveries, particularly if target host plants are carefully sampled and examined for the presence of galls, including cryptic ones, which are relatively frequent in this group of gall wasps. The possibility of finding new species of *Fumariphilus*, or taxa related to this new genus, cannot be discarded. In fact, besides *Fumaria*, the tribe Fumarieae Dumort has 18 other genera that may be potential hosts for new species of *Fumariphilus* or for species of related undescribed genera. A hint of this possibility is the record of an unidentified gall in a species of *Corydalis* DC. from the region of Tibet (Ronquist, personal communication). In Spain, I have looked for galled fruits in species of *Platycapnos* DC. and *Sarcocapnos* DC., genera related to *Fumaria*, but, to date, have been unsuccessful in finding any.

Acknowledgments

I thank Anelia Stojanova and George Melika for sharing study materials of *Aylax hypecoi* collected in Bulgaria. I am also indebted to Fredrik Ronquist for allowing me to reproduce part of the results related to the herb gall wasp lineages from their cynipid molecular phylogenetic studies. Laura Tormo and Marta Furio provided technical assistance in the production of the SEM images, and Louis Nastasi made useful comments on the identification key of the genera of Aulacideini.

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