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Taxonomy of inquilines of oak gall wasps of Panama, with description of eight new species of *Synergus* Hartig (Hymenoptera, Cynipidae, Synergini)

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Abstract

This paper reports the first study of the inquiline oak gall wasp fauna of Panama. Samples were collected at 19 sites in Panama, and inquiline specimens were reared from 63 gall morphotypes, including six species of *Quercus*, mainly *Q. salicifolia* and *Q. bumelioides*. Two genera were found: *Synergus*, represented by 10 species, and the recently described genus *Agastoroxenia* Nieves-Aldrey & Medianero, with a single species, *A. panamensis* Nieves-Aldrey & Medianero. S*ynergus* was recorded for the first time in Panama*; Synergus mesoamericanus* and *Synergus nicaraguensis*, which were formerly recorded from Guatemala and Nicaragua, have now been recorded in Panama, and eight new species of *Synergus* are described here: *Synergus elegans, S. laticephalus, S. ramoni, S. rufinotaulis, S. luteus, S. gabrieli, S. baruensis and S. chiricanus*. A key for the identification of the studied fauna is provided. An overall similarity cluster analysis of the inquilines of oak gall wasps of Panama, including one Neotropical and two Palaearctic species as outgroups, is included.

Key words: Gall wasps, inquilines, neotropic, Quercus, identification key, taxonomy, biology

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Introduction

The inquilines (Hymenoptera, Cynipidae, Synergini) develop commensally inside the galls of other cynipids, which are a group of wasps that induce complex galls in plants, mainly in *Quercus* species (Fagaceae) (Ronquist 1994; Nieves-Aldrey 2001). Nine genera and one hundred and seventy-one species of inquilines are known, distributed mainly in the Holarctic region (Csóka *et al*. 2005; Melika *et al*. 2005; van Noort *et al*. 2006; Ács *et al.* 2010; Nieves-Aldrey & Medianero 2010). In the Nearctic region, eighty-nine species have been recorded (Ritchie 1984), and closer to the Centroamerican region, the fauna of Mexico is thought to be rich in inquiline species, though only two species have been actually recorded from that country (Ritchie 1984; Pujade-Villar & Melika 2005; Pujade-Villar *et al.* 2009).

The most species-rich inquiline genus is *Synergus* Hartig, with ninety-three species, which represents approximately 56% of the group's world diversity. Most *Synergus* species are distributed in the Holarctic, with forty in the Palaearctic and fifty-three species in the Nearctic (Ritchie 1984; Abe *et al*. 2007). *Synergus filicornis*, a species described from Guatemala (Cameron 1883), was for a long time the only extant *Synergus* species recorded from Central and South America. In recent years, five species have been added to this list. Three of these species are from Guatemala: *S. cultratus* Ritchie & Shorthouse, *S. mesoamericanus* Ritchie & Shorthouse and *S. kinseyi* Ritchie & Shorthouse (Ritchie & Shorthouse 1987). One is from Nicaragua, *S. nicaraguensis* Díaz & Gallardo, 1998 and one species is from Colombia, *Synergus colombianus* Nieves-Aldrey, 2005 (Díaz & Gallardo 1998; Nieves-Aldrey 2005).

The gall wasp fauna of Panama, which is a small country in Central America, was almost entirely unknown with the single exception of the species *Andricus championi*, recorded from Chiriqui region (Cameron 1883). The presence of gall wasps in Panama is linked to the distribution of their host plants of the *Quercus* species, which are represented in Panama by nine species inhabiting high altitude areas in the mountains from Chiriqui to the Darien region and extending as far south as Colombia (Correa *et al*. 2004). For this reason, it has been assumed that unknown gall wasp and inquiline fauna should exist in Costa Rica, Panama and Colombia (Nieves-Aldrey 2005; Pujade-Villar & Hansson 2006). This presumption has been confirmed in recent years by the first gall wasps and inquilines being recorded from Colombia (Nieves-Aldrey 2005) and the discovery of a rich gall wasp fauna in Panama (Medianero & Nieves-Aldrey 2010; Nieves-Aldrey & Medianero 2010).

A study of the Cynipidae associated with *Quercus* species in Panama was conducted within the scope of a collaborative project of the University of Panama and the Museo Nacional de Ciencias Naturales (CSIC) (Spain). The first results of this study, including a revision of the Neotropical cynipini genus *Amphibolips*, with the description of three new species from Panama, and the description of the first inquiline from Panama, corresponding to the new genus *Agastoroxenia* Nieves-Aldrey & Medianero, have already been published (Medianero & Nieves-Aldrey 2010; Nieves-Aldrey & Medianero 2010). Further reports on gall-inducing cynipid genera of Panama are in preparation, and we present the results concerning the inquilines here.

The objectives of the work reported here were to study the inquiline oak gall wasps of Panama taxonomically, to describe new species, to perform a cluster analysis based on the morphology of the adults and to provide freshly collected specimens of the inquiline genera and species of Panama for ongoing molecular phylogenetic studies of the Synergini.

As has been revealed by recent DNA barcoding results, the present taxonomy of the inquilines of oak gall wasps is usually based on only a few diagnostic characters and a relatively poor set of morphological characters, resulting in disagreements between classifications or groupings supported by morphology and sequence data. A morphological analysis based on SEM images and focused on a significative group of Synergini was performed for the first time with the aim of finding a more reliable set of diagnostic characters for the Synergini.

MATERIALS AND METHODS

Selected taxa and specimens.

We studied two genera and 11 species of Synergini from Panama. All studied species were reared from cynipid galls collected from *Quercus* species at several collecting sites in Panama. The identification of the *Quercus* spe-

cies was based on several key references (Burger 1977; D'Arcy 1987; Breedlove 2001), as well as on comparison with materials from the collection of the University of Panama and the Smithsonian Tropical Research Institute.

One European species of the genus *Saphonecrus* Dalla Torre & Kieffer and one European and one Neotropical species of *Synergus* Hartig were included as outgroups for comparative purposes in a cluster analysis of the inquilines from Panama (Table 1).

Sampling and rearing.

Field data were taken from samplings conducted between December 2007 and May 2009 at nineteen sites in Panama. Fifteen sites in the west of Panama were sampled monthly. Intensive samplings were carried out with durations of between four to six hours per site.

Voucher specimens of all species were deposited in the entomology collections of the *Museo Nacional de Ciencias Naturales*, Madrid (Spain) and Maestría en Entomología, Universidad de Panamá (MEUP).

Unless otherwise stated, the samples were collected by the junior author of this report.

Preparation for morphological study

For observation under a scanning electron microscope (SEM), adult cynipids were dissected in 70% ethanol, air-dried, mounted on a stub and coated with gold, and micrographs were acquired with an EVO 40 ZEISS and a FEI QUANTA 200 (high vacuum technique) for several standardized views. Forewings were mounted in euparal on slides and later examined under a Wild MZ8 stereomicroscope. Images of the adult habitus were taken with a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereomicroscope. Measurements were made with a calibrated micrometer attached to an ocular of the light microscope. The terminology used for the morphological structures and abbreviations followed Ronquist and Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001) and Liljeblad *et al*. (2008).

Cluster analysis

A cluster analysis was performed. The ingroup (inquilines of Panama) in the analysis was composed of *Agastoroxenia* Nieves-Aldrey & Medianero, the eight new species of *Synergus* and *S. nicaraguensis* Diaz & Gallardo and *S. mesoamericanus* Ritchie & Shorthouse while the outgroup included *Saphonecrus lusitanicus* Tavares, 1902, *Synergus colombianus* Nieves-Aldrey and *S. ibericus* Tavares, 1920. Morphological variation between all of the studied inquilines was coded in an observation matrix of character states, which included coding of 65 characters, 62 of which were related to external morphology based on SEM images and three of which were based on the biology of the studied species (Table 1, Appendix I). Cluster analyses, UPGMA (unweighted pair group method analysis), was performed in PAUP* 4.0b10b (Swofford 2002) to obtain an overall similarity phenogram.

Results

The inquilines of Panama

Agastoroxenia Nieves-Aldrey & Medianero, 2010

Diagnosis. This recently described genus is readily distinguished from other genera of Synergini by the presence of 13-segmented antenna in both females and males. Additional diagnostic antennal characteristics are the pedicel being relatively long, 2.5 times as long as wide and longer than the scape and F2, and the F1 of the male antenna is strongly curved dorsally, excavated medially and expanded apically and basally. Other distinctive morphological features are the small basal tooth of the metatarsal claw, measuring less than 1/3 as long as the apical tooth and the irradiating facial striae, which are strong, broad and blunt.

Monotypic. A single species known, *Agastoroxenia panamensis* Nieves-Aldrey & Medianero, 2010, described as an inquiline in unidentified *Andricus* galls on *Quercus lancifolia* SchIedl. & Cham. In Chiriquí, Piedra Candela (Panama) (Nieves-Aldrey & Medianero 2010)

Synergus Hartig, 1840

Diagnosis. Female antenna 14 segmented, male antenna with 15 or, rarely, 16 segments. Facial striae irradiating from the clypeus reaching the toruli and the compound eyes. Frontal carinae usually present, sometimes weak or even completely absent. Lateral pronotal carine present in most Palaearctic species, usually absent in Neotropical species. Sculpture of the mesoscutum, shape of the notauli and the scutellar foveae quite variable; lateral propodeal carinae subparallel. Radial cell of the forewing usually closed, sometimes obsoletely closed, rarely open. Metatarsal claws with a strong basal tooth, rarely simple. Metasomal terguites 2+3 usually with micropunctures on the posterior margin: sometimes inconspicuous or completely absent.

Synergus is closely related to *Saphonecrus* and S*ynophrus*, and doubts remain about the relationship between these three genera. Some basal *Synergus* species appear to be closely related to *Saphonecrus* (Acs *et al*. 2010).

Mayr (1872) divided the European *Synergus* species into sections I and II, a classification that has been followed by most subsequent authors (Tavares 1920; Eady & Quinlan 1963; Nieves-Aldrey 2001; Pujade-Villar *et al.* 2003; Melika 2006). However, recent molecular phylogenetic studies strongly indicated that this division was artificial and should not be followed.

Diversity and Distribution. The world fauna of *Synergus* species were catalogued by Ritchie (1984), who listed 104 species throughout the Holarctic region. Gillette (1896) revised the 24 Nearctic *Synergus* species known at that time, and an additional 29 species have been described since (Burks 1979). Ritchie & Shorthouse (1987) revised the species from Guatemala, and new species were described from Nicaragua (Diaz & Gallardo 1998) and Colombia (Nieves-Aldrey 2005) The current estimate of the world fauna includes approximately 100 valid species.

Biology. *Synergus* species attack galls on *Quercus* spp., with the exceptions of *S. castanopsidis* (Beutenmueller), which is known to attack galls of *Dryocosmus castanopsidis* on *Castanopsis* spp. in Oregon and California (Burks 1979; Pujade-Villar & Melika 2005), and an unnamed *Synergus* species from Japan that has been reared from galls of *Dryocosmus kuriphilus* Yasumatsu on the chestnut *Castanea* (Otake *et al.* 1982).

First recorded from Panama.

List of species from Panama

Synergus elegans Nieves-Aldrey & Medianero sp. nov.

(Figs. 1A, 3B, 5J, 6B, 8A,10F, 13A, 15A, 16A, 17B, 18A–B)

Type material. Holotype ♀ (Fig. 18A) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2095). PANAMA, Chiriquí, Boquete, El Salto, 8º 47' 32.08" N, 82º 27' 37.09" W, 1,431 m; ex gall *Amphibolips castroviejoi* Medianero & Nieves-Aldrey, 2010 on twigs of *Quercus salicifolia* Née (Fagaceae), gall collected 07.v.2008, E. Medianero leg. Paratypes: 3♂, 7♀, same data as holotype; 1♂, 1♀, same data as holotype, except for being collected at the road to Volcancito, 1,404 m, 31.i.2008. Ten paratypes in the MNCN, one male and one female paratype in Maestría en Entomología, Universidad de Panamá (MEUP). 1♀ paratype of the type series was dissected for SEM observation (in the MNCN).

Additional non-type material: 4♂, 8♀, ex gall *Amphibolips aliciae* Medianero & Nieves-Aldrey, 2010 on *Q. salicifolia*, Boquete, road to Volcancito, 25.i.2009; 1♀, same data, collected 12.i.2008. 1♂,7♀, ex gall *Amphibolips salicifoliae* Medianero & Nieves-Aldrey, 2010 on *Q. salicifolia*, Volcan Baru, 2,070 m, 28.i.2009; ex gall *Cynips sp*., on *Q. bumelioides*, Volcán Barú, 3,079 m, 23.x.2008. 2♂, 4♀, ex gall unidentified genus on *Q. bumelioides*, Volcán Barú, 3,079 m, 23.x.2008. 2♂, 4♀, ex gall *Disholcaspis sp.* on *Q. lancifolia*, Renacimiento, 1,270 m, 22.i.2009. 5♀, ex gall unidentified genus on *Q. bumelioides*, Volcán Barú, 1,800–2,000 m, 23.x.2008. 3♂,4♀, ex gall *Disholcaspis sp*., Volcán Barú, 1,800–2,000 m, 30.i.2008. 1♂, 4♀, ex gall of an unidentified genus on *Q. lancifolia*, Boquete, Palmira, 19.vii.2008.

Etymology. Named after the elegant, polished aspect of this wasp.

Diagnosis and comments. Together with *Synergus laticephalus* sp. n., *S. elegans* forms a distinctive group that is readily distinguished from the remaining *Synergus* species from Panama. Their main distinguishing morphological features are as follows: head transverse-trapezoid, frontal carinae absent, horizontal sculpture of the mesopleuron not extended into the speculum, scutellum margined laterally and posterodorsally, coriarious sculpture on the mesoscutum, notauli narrow and widely separated posteriorly, scutellar foveae quadrangular and shal-

low; basal tooth of the metatarsal claws short, radial cell short and wide, ambiguously closed, and apical setae of the hypopigial spine extending far beyond the apex. Of the known Nearctic species, *S. elegans* resembles *S. castanopsidis* (Beutenmüller) in some characters, such as the smaller extension of the horizontal sculpture of mesopleuron (Pujade-Villar & Melika 2005), but differs in many other characters, such as the total absence of frontal carinae and the radial cell being ambiguously closed. We have also seen undescribed materials from Mexico belonging to this distinctive group.

Synergus elegans is a species that is common, highly generalist with regard to host gall preferences, and displays a high degree of morphological variability. Variation is related to its coloration, the visibility of the median mesoscutal impression, the ratio of F1/F2, and characters of the forewing venation. It remains possible that more than one cryptic species could be involved under the name *S. elegans* as here defined.

Description. Body length (measured from the anterior margin of the head to the posterior margin of the metasoma) 1.96 mm (range 1.66–2.22; N = 9) for females; 1.76 mm (range 1.34–1.90; N = 4) for males. Head predominantly yellowish or orange, frons and vertex medially, the entire occiput, clypeus medially and teeth of mandibles black; lateral areas of face and genae yellow-red. Mesosoma and metasoma of female shining black, except for a rufous coloration on the lateral and basal areas of the metasoma; tegulae yellow. Antenna and legs entirely yellowish, excepting metacoxae with brownish or blackish coloration more or less extended. Forewing hyaline, with yellow pale veins. Male with similar coloration to female but black coloration on face extended only on the ocelar triangle, and is also less extended on the metacoxae.

Female. Head in dorsal view (Fig. 3B) 2.1 times wider than long. Gena not expanded behind compound eye. POL 1.5 times longer than OOL, posterior ocellus separated from inner orbit of eye by about 2 times its diameter. Head in anterior view (Fig. 1A) wide, trapezoid, 1.4 times wider than high, genae straight, not expanded. Face weakly pubescent. Face with marked, regular, irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; the carinae are present laterally but lacking dorsomedially on the face. Clypeus indistinct, ventral margin straight, slightly sinuate, not projecting over mandibles (Fig. 1A). Anterior tentorial pits visible; epistomal sulcus and clypeo-pleurostomal lines indistinct. Malar space 0.6 times height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye 1.1 times width of antennal socket including rim. Frons delicately coriarious, not punctuate, without visible frontal carinae (Figs. 1A, 3B). Vertex and occiput, dorsally and laterally coriarious, without rugae or punctures. Gula relatively long; distance between occipital foramen and oral foramen slightly longer than the height of the occipital foramen. Hypostomal sulci meeting at dorsal part of gula, close to the occipital foramen.

Mouthparts (Fig. 1A). Mandibles strong, exposed; right mandible with three teeth; left with two teeth. Cardo of maxilla visible, maxillary stipes about 1.5 times longer than wide. Maxillary palp five-segmented. Labial palp three-segmented.

Antenna with 14 segments (Fig. 5J); flagellum not broadening towards apex; with relatively long, erect setae and placodeal sensilla visible on flagellar segments F6–F12. Relative lengths of antennal segments: 26:17.5:33.5:26:25:23:20.5:18:16:15.5:15:15:14:23; Pedicel 1.7 as long as wide; F1 1.3 times as long as F2. Ultimate flagellomere 2.5 times longer than wide, 1.6 times as long as F11. Placodeal sensillae on F8–F11 disposed in one single row of 2–4 visible sensillae in each flagellomere.

Mesosoma. Pronotum with sparse short pubescence. Ratio of length of pronotum medially/laterally = 0.25. Pronotal plate (Fig. 8A) indistinct dorsally; lateral margins of pronotum rounded, without a lateral pronotal carina. Lateral surface of pronotum with coriarious sculpture. Mesoscutum (Fig. 8A) with weak alutaceous-imbricate sculpture. Notauli shallowly impressed and narrow, posteriorly not wider than transscutal fissure; faint in anterior one third, not strongly converging posteriorly, widely separated at meeting with the trasscutal fissure. Median mesoscutal impression very faint or completely absent, sometimes indicated as a shallow median depression. Anteroadmedian signa virtually invisible. Scutellar foveae superficial, shallowly impressed, the shape is more or less quadrangular, their anterior margins straight and laterally forming and angle about 90° contra the transscutal fissure; posterior margins indistinct. Scutellum with alutaceous-imbricate sculpture; dorsal surface with a distinct sharp margin posteriorly and posterolaterally (Fig. 8A, 10F). Mesopleuron (Fig. 10F) with longitudinal, regular striae relatively weak, the interspaces smooth, the sculpture not extended into the speculum (Fig. 10F).

Metapectal-propodeal complex. Metapleural sulcus meeting posterior margin of mesopectus at about 2/3 of height of metapectal-propodeal complex. Lateral propodeal carinae distinct, broad, subparallel. Median propodeal areas smooth and pubescent. Nucha dorsally sulcate.

Legs. Tarsal claw (Fig. 16A) with base produced into a secondary acute tooth relatively short, measuring less than 1/2 of length of apical tooth.

Forewing (Fig. 17B). Slightly longer than body. Radial cell 2.4 times longer than wide. R1 depigmented along marginal cell, the radial cell appearing ambiguously closed (Fig. 17B); areolet indistinct; vein Rs+M invisible. Basal cell with dense, closely spaced setae. Apical margin of wing with a moderately long fringe of setae.

Metasoma (Fig. 13A). As long as head plus mesosoma. First metasomal tergum longitudinally sulcate dorsally and laterally. Metasomal tergum T2+3 fused, smooth and shining, without micropunctures, covering almost the entire metasoma; anteromedian area only with a row of 5-7 setae. Projecting part of hypopygial spine clearly extended beyond attachment of lateral flap (Fig. 15A); lateral setae of hypopigial spine long and sparse spaced; apical setae projected beyond apex spine.

Male (Fig. 18B). Similar to female except as follows: Antenna 15-segmented; F1 weakly curvate and excavate medially, slightly expanded apically (Fig. 6B). Placodeal sensillae present on flagellomeres 2-13, arranged in one row of 2-5 sensillae. Relative length of antennomeres: 25:20:36:27:25:24:21:20:20:19:17:17:16:16:22.

Distribution. Chiriquí region of Panama, near Costa Rica, from an altitude of 1,200 m near Boquete to 3,000 m in Volcan Barú.

Biology. This new species is a generalist inquiline attacking a wide array of cynipid galls from different genera. Our data indicated that it is very common in galls of the three Panamanian species of *Amphibolips*, and it is also a frequent inquiline in galls of species of *Disholcaspis*, *Cynips* and other Panamanian cynipid genera. The host galls are detachable. The host plants of the *Quercus* section attacked by the host gall inductor belong to both the *Quercus* and *Lobata* sections.

Synergus laticephalus Nieves-Aldrey & Medianero sp. nov.

(Figs. 1B, 3C, 5B, 7E, 8B, 10E, 13B, 15B, 17A, 18C)

Type material. Holotype ♀ (Fig. 18C) (in MNCN, Madrid, Spain), card-mounted. Cat. nº 2096). PANAMA, Chiriquí, Boquete, El Salto, 8º 47' 32.08" N, 82º 27' 37.09" W, 1,431 m; ex gall of an unidentified cynipid genus on twigs of *Quercus salicifolia* Née (Fagaceae) (Fig. 22G), gall collected 19.vii.2008, E. Medianero leg. Paratypes: 4♀, same data as holotype.

Additionally, 1♀ paratype of the type series was dissected for SEM observations (in the MNCN).

Etymology. Named after the short, wide shape of its head.

Diagnosis and comments. This species is closely related to *S. elegans*, being similar in color, habitus and a majority of its morphological characters. It differs with respect to a more transverse head in dorsal view, which is more than 2.5 times as wide as long; POL about 1.2 as long as OOL and OOL more than two times the diameter of a lateral ocellus. Notauli are percurrent in *S. laticephalus*. Furthermore, F1 is as long as F2, while it is longer than F2 in *S. elegans*, and the malar distance is as long as the eye (0.6 times as long as eye in *S. elegans*).

Description. Body length 2.64 mm (range 2.53–2.77; N = 5) for females. Male unknown.

Head yellow-red with frons and vertex medially and occiput black. Mesosoma black; metasoma dorsally black, and reddish ventrally; tegulae yellow. Antenna dirty yellowish; legs entirely yellowish, excepting metacoxae with reddish coloration basally. Forewing hyaline, with dirty yellow veins.

Female. Head in dorsal view (Fig. 3C) 2.7 times wider than long. Gena not expanded behind compound eye. POL 1.2 times longer than OOL, posterior ocellus separated from inner orbit of eye by 2.3 times its diameter. Head in anterior view (Fig. 1B) wide, trapezoid, 1.4 times wider than high, genae straight, not expanded. Face weakly pubescent. Face with marked, regular, irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; laterally to the toruli some rugae extended dorsally towards frons; the carinae are present laterally and medially on the face. Ventral margin of clypeus sinuate, slightly not projecting over mandibles (Fig. 1B). Malar space as long as height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye as wide as antennal socket including rim. Frons alutaceous, not punctuate, without visible frontal carinae (Figs. 1B, 3C). Vertex and occiput without rugae or punctures. Head posterior view and mouthparts as *S. elegans.*

Antenna with 14 segments (Fig. 5B); flagellum filiform. Relative lengths of antennal segments: 23:13:26:26:22:20:17:16:14:14:12:12:12:20; Pedicel 1.8 as long as wide; F1 as long as F2. Ultimate flagellomere

2.8 times longer than wide, 1.6 times as long as F11. Placodeal sensillae on F8–F11 disposed in one single row of 2–4 visible sensillae in each flagellomere.

Mesosoma. Pronotum with lateral margins rounded, without a lateral pronotal carina. Lateral surface of pronotum with coriarious sculpture. Mesoscutum (Fig. 8B) with weak coriarious-alutaceous-sculpture. Notauli percurrent, well impressed but narrow, posteriorly not wider than transscutal fissure; not strongly converging posteriorly, widely separated at meeting with the trasscutal fissure. Median mesoscutal impression invisible, at most indicated as an obsolete median depression. Anteroadmedian signa scarcely visible. Scutellar foveae superficial, smooth, quadrangular, posterior margins indistinct. Scutellum with coriarious sculpture and some transversal rugae visible; dorsal surface with a distinct sharp margin posteriorly and posterolaterally (Figs. 8B, 10E). Mesopleuron (Fig. 10E) with weak longitudinal, regular striae, the interspaces smooth, not extended ventrally and dorsolaterally, at the speculum (Fig. 10F).

Metapectal-propodeal complex as in *S. elegans*. Lateral propodeal carinae distinct, broad, subparallel, slightly curved.

Legs. Tarsal claw with base produced into a secondary acute tooth measuring about 1/3 of length of apical tooth.

Forewing (Fig. 17A). Slightly longer than body. Radial cell 2.4 times longer than wide. R1 depigmented along margin of radial cell, the radial cell appearing ambiguously closed (Fig. 17A); radius more heavily pigmented; areolet indistinct; vein Rs+M invisible. Basal cell with dense, closely spaced setae. Apical margin of wing with a moderately long fringe of setae.

Metasoma (Fig. 13B). As long as head plus mesosoma. First metasomal tergum longitudinally sulcate dorsally and laterally. Metasomal tergum T2+3 fused, smooth and shining, without micropunctures, covering almost the entire metasoma; anteromedian area only with a row of 5–7 setae. Projecting part of hypopygial spine not quite extended beyond attachment of lateral flap (Fig. 15B); apical setae projected beyond apex spine.

Distribution. Found at a single site near Boquete (Panama, Chiriqui), altitude 1,400 m.

Biology. This new species was reared from unidentified galls on *Quercus salicifolia* (Quercus, Lobata section). The host gall is irregularly spherical on twigs, falling to the ground when mature (Fig. 22G). Unfortunately the gall inducer host cynipid was not reared and could not been identified, even to the generic level.

Synergus mesoamericanus Ritchie & Shorthouse, 1987

New record from Panama

Studied material. 3♂, 6♀, Chiriquí, Boquete, road to Volcancito, 1,450 m, ex gall *Andricus championi* (Cameron) on *Quercus bumelioides*, 31.xii.2008. E. Medianero leg. 2♀ Volcán Barú, 2,500–3,000 m ex gall *Andricus championi* (Cameron) on *Quercus bumelioides*, 16-vi.2008.

Diagnosis and comments. As in the case of the group composed of *S. elegans* and *S. laticephalus*, this species, together with the new species *S. ramoni*, forms a clearly differentiated group, easily distinguished from the remaining *Synergus* species from Panama. Distinguishing characters include frontal carinae being indistinct, obscured by very irregular and branched interrupted rugae; facial striae irregularly sinuate, branched near the ventral margin eyes; antennae with F1 1.5 times as long as F2 in both sexes and F1 in males strongly expanded apically; basal cell of the forewing densely setose with veins being darkly pigmented and metasomal T2+3 not punctate posteriorly. The body coloration is predominantly red, red-black or black.

S. mesoamericanus was described from materials reared from large tuberose galls collected in Guatemala by Kinsey (assigned the name "*brelandi*" in their manuscript). Type material of the gall inducer insect was examined by us and corresponds to a species of *Andricus* (Nieves-Aldrey, unpublished). The galls of "*brelandi*" are, however, similar to the galls of *Andricus championi* (Cameron) from which the Panamanian material was reared.

The type material of *S. mesoamericanus* was examined by the first author (see also Nieves-Aldrey 2005). The Panamanian specimens differ from the Guatemalan specimens in their relatively larger size, longer radial cell and the R1 vein being more pigmented along the margin of the forewing, the radial cell appearing unambiguously closed, differently than previously stated in the diagnosis of the species (Ritchie & Shorthouse 1987). For this reason, we do not discard the possibility that our Panamanian specimen materials could correspond to a different closely related species. We prefer not to describe the material as new until further comparisons are made with

freshly collected materials from the type locality in Guatemala, which could elucidate this question in the future.
Additional descriptive data

Female (habitus, Fig. 18D). Head in dorsal view (Fig. 3E) 2 times as wide as long; genae not expanded behind compound eye. POL 0.9 as OOL, posterior ocellus separated from inner orbit of eye by 1.9 times its diameter. Head in anterior view (Fig. 1D) 1.2 times wider than high. Facial carinae reaching ventral margin of eye and ventral margin of toruli; dorsally extended to frons and branched near margin compound eye. Ventral margin of clypeus straight. Frons with irregular branched frontal carinae reaching ocelli, grosere piliferous punctures present (Figs 1D, 3E). Vertex and occiput without some rugae.

Female antenna with 14 segments (Fig. 5H). Pedicel 1.3 as long as wide; F1 1.5 times as long as F2. Ultimate flagellomere 1.8 times as long as F11. F1 of male curved in de middle and moderately expanded apically.

Pronotum without a lateral pronotal carina. Lateral surface of pronotum with rugose sculpture. Mesoscutum (Fig. 8E) with transverse, undulate, interrupted rugae. Notauli percurrent, convergent posteriorly and wider than transscutal fissure; narrowly separated at meeting with the trasscutal fissure. Median mesoscutal impression present, extending anteriorly about 2/3 of length of mesoscutum. Scutellar foveae ellipsoidal, anterior margins widely divergent from the trasscutal fissure, posterior margins indistinct. Scutellum not margined laterally, with rugose sculpture. Mesopleuron (Fig. 10D) with strong longitudinal, irregular striae, the striated sculpture extended into the speculum; coriarious sculpture visible in the interspaces, anterodorsally and ventrally. Lateral propodeal carinae distinct, broad, slightly convergent posteriorly.

Tarsal claw (Fig. 16D) with base produced into a secondary acute tooth measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17D). Veins of radial cell well pigmented, the radial cell appearing unambiguously closed areolet distinct; vein Rs+M visible. Basal cell with dense, closely spaced setae. Apical margin of wing with a short fringe of setae.

Metasoma (Fig. 13D). Metasomal tergum T2+3 fused, smooth and shining, without micropunctures, covering almost 2/3 of metasoma; anteromedian area with a group of setae extending towards dorsal region of targeted. Projecting part of hypopygial spine quite extended beyond attachment of lateral flap (Fig. 15F); apical setae not projected beyond apex spine.

Distribution. Recorded previously from Guatemala and now from Panama (Volcán Barú).

Biology. The available biological data indicate that this species is a specialist inquiline associated with large tuberose galls induced by *Andricus* species in Panama and Guatemala (Fig. 21B).

Synergus ramoni Nieves-Aldrey & Medianero sp. nov.

(Figs. 1C, 3F, 5C, 6G, 7B, 8C, 10C, 12D, 13F, 16B, 17C, 18E–F)

Type material. Holotype ♀ (Fig. 18F) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2097). PANAMA, Chiriquí, Boquete, El Salto, 8º 47' 32.08" N, 82º 27' 37.09" W, 1,431 m; ex gall of an unidentified cynipid genus on twigs of *Quercus salicifolia* Née (Fagaceae) (Fig. 22A), gall collected 27.xi.2008, E. Medianero leg. Paratypes: 1♂, 1♀, same data as holotype; 1♂,1♀, Boquete, Road to Volcancito, 1,404 m, 22.x.2008. E. Medianero leg. In the MNCN. Additionally, 1♀ paratype of the type series was dissected for SEM observation (in the MNCN).

Etymology. Named after Ramón Hernández, dear friend of the first author, in acknowledgment of his invaluable help in the first collecting trip of oak gall wasps of Panama, which led to this study.

Diagnosis and comments. This species is closely related to *S. mesoamericanus*, being similar in a majority of their diagnostic morphological characters. It differs from that species with respect to its black coloration, narrower head, larger ocellar triangle and the posterior ocelli being closest to the margin of eyes. Furthermore, the frons is more closely punctate, and the frontal carinae are less marked in *S. ramoni*; the sculpture of mesopleuron is weaker; the speculum is partially smooth; and the radial cell is 2.8 times as long as wide (less than 2.5 in *S. mesoamericanus*).

Description. Body length 2.75 mm (range 2.69–2.77; N = 3) for females; 2.41 (range 2.21–2.61; N = 2) for males.

Head, mesosoma and metasoma predominantly black; mouthparts and sides of frons near the toruli yellowish; metasoma ventrally red brown; antennae blackish yellow; distal half less dark. Legs mainly black, apex of femora

and tibiae and tarsi dark yellowish. Forewing hyaline, slightly darkened; veins brown. The male differ in having entirely the face, genae, and the antennal flagellum yellowish.

Female. Head in dorsal view (Fig. 3F) 1.9 times as wide as long. Gena not expanded behind compound eye. POL 1.6 times longer than OOL, posterior ocellus separated from inner orbit of eye by 1.3 times its diameter. Head in anterior view (Fig. 1C) narrow, only 1.1 times wider than high, genae very slightly expanded, strongly punctate. Face moderately pubescent, with marked, irregular, irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; branched near compound eyes. Ventral margin of clypeus straight not projected over mandibles. Malar space 0.6 as long as height of compound eye. Toruli situated slightly below mid-height of compound eye; distance between toruli short, shorter than diameter of a torulus; distance between mesal margin of compound eye and lateral margin of a torulus shorter than diameter of a torulus, including rim. Frons closely and conspicuously punctate, frontal carinae present but obscured by the punctate sculpture (Figs. 1C, 3F). Vertex and occiput rugose-punctate.

Female antenna with 14 segments (Fig. 5C); flagellum filiform. Relative lengths of antennal segments: 19:11:27:18:19:19:19:17:15:15:14:13:13:22; Pedicel 1.4 as long as wide; F1 1.5 as long as F2. Ultimate flagellomere 1.7 times longer as long as F11. Placodeal sensillae on F8–F11 disposed in one single row of 2–4 visible sensillae in each flagellomere. Male antenna with 15 segments; F1 excaved medially and moderately expanded apically (Fig. 6G).

Mesosoma. Pronotum without a lateral pronotal carina (Fig. 7B). Lateral surface of pronotum with rugose-punctate sculpture. Mesoscutum (Fig. 8C) with marked, undulate transverse rugae, the interspaces with coriarious sculpture. Notauli percurrent, well impressed, wider posteriorly, wider than transscutal fissure; moderately converging posteriorly. Median mesoscutal impression visible but shallowly impressed. Anteroadmedian signa well marked. Scutellar foveae ellipsoidal, with some rugose sculpture, anterior margins widely divergent from the fissure transscutal, posterior margins indistinct. Scutellum with rugose sculpture; not margined laterally and posterodorsally (Figs. 8C, 10C). Mesopleuron (Fig. 10C) medially with weak longitudinal striae, the interspaces with coriarious sculpture, the striae being weak and hardly visible dorsolaterally in the speculum (Fig. 10C).

Lateral propodeal carinae distinct, broad, subparallel. Median propodeal area pubescent, with some vertical rugae prolonged into the nucha. Nucha strongly sulcate, dorsally and laterally.

Legs. Tarsal claw (Fig. 16B) with base produced into a small secondary acute tooth measuring about 1/4 of length of apical tooth.

Forewing (Fig. 17C). Radial cell 2.8 times longer than wide. All the veins well pigmented, R1 well visible along margin of radial cell, the radial cell appearing unambiguously closed (Fig. 17C; areolet distinct; vein Rs+M visible. Basal cell with dense, closely spaced setae. Apical margin of wing with a short fringe of setae.

Metasoma (Fig. 13F). As long as head plus mesosoma. First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, smooth and shining, covering almost the entire metasoma; without micropunctures; anteromedian area only with a group of about 14 setae. Projecting part of hypopygial spine slightly extended beyond attachment of lateral flap; apical setae not projected beyond apex spine.

Distribution. Known only from the type locality near Boquete and Volcán Barú (Chiriqui, Panama).

Biology. *Synergus ramoni* inhabits twig galls on *Quercus salicifolia* (*Quercus*, Lobata section). The host gall is irregularly spherical and develops on twigs (Fig. 22A). The host cynipid was not reared, and it is unknown.

Synergus nicaraguensis Diaz & Gallardo, 1998

New record from Panama

Studied material. 1 ♂, 5♀, Chiriquí, Renacimiento, 1,270 m, ex gall *Disholcaspis sp.* on *Quercus lancifolia*, 24.xi.2008. E. Medianero leg.

Diagnosis and comments. This species is easily recognizable and can be distinguished from all of the remaining Neotropical *Synergus* species by having a forewing with a shaded infuscate area over the radial cell extended beyond the Rs vein. Other diagnostic features of this species are: radial cell short and wide, less than 2.5 times as long as wide. F1 3 as long as the pedicel. Metasomal T2+3 posteriorly closely and distinctly punctate, with the punctures extended over about 1/3 of the total length of the segment.

Until now, knowledge of this species was limited to the materials of the type locality (Jinotega, Nicaragua) (Diaz & Gallardo 1998). Our record from Panama is the second for this species in Central America, considerably increasing the size of its known distribution area. We examined the type material of *S. nicaraguensis* and compared it with our materials from Panama. The Panamanian insects differ slightly from the type material in their coloration, especially with respect to their almost entirely yellow legs, which are darker in the type specimens.

Additional descriptive data. Some descriptive date and illustrations of morphological characters which were omitted in the original description are here given.

Female (habitus, Fig. 19A). Head in dorsal view (Fig. 4B) 2 times as wide as long; genae not expanded behind compound eye. POL 1.5 as OOL, posterior ocellus separated from inner orbit of eye by about its diameter. Head in anterior view (Fig. 2E) 1.3 times wider than high. Facial carinae regular, deep, reaching ventral margin of eye and ventral margin of toruli; not branched near margin compound eyes. Ventral margin of clypeus straight. Frons with wide, slightly branched frontal carinae, reaching ocelli, weak piliferous punctures present.

Female antenna with 14 segments (Fig. 5E). Pedicel 1. 2 as long as wide; F1 as long as F2. Ultimate flagellomere 1.8 times as long as F11. F1 of male curved in de middle and moderately expanded apically.

Pronotum without a lateral pronotal carina. Lateral surface of pronotum with rugose sculpture. Mesoscutum (Fig. 8F) with wide, transverse, undulate, interrupted rugae, the interspaces with coriarious sculpture. Notauli percurrent, convergent posteriorly, wider than transscutal fissure; narrowly separated at meeting with the transscutal fissure. Median mesoscutal impression visible in posterior three quarts of mesoscutum but shallow. Scutellar foveae large, ellipsoidal, smooth, anterior margins widely divergent from the trasscutal fissure, posterior margins distinct. Scutellum not margined laterally, with strongly rugose sculpture. Mesopleuron (Fig. 11A) with strong, irregular, longitudinal striae, extended into the entire surface of mesopleuron; coriarious sculpture visible in the interspaces. Lateral propodeal carinae distinct, broad, subparallel (Fig. 12C).

Tarsal claw (Fig. 16C) with base produced into a large secondary acute tooth measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17E). Present a shaded infuscate area over the radial cell and extended beyond the Rs vein; radial cell short and wide, less than 2.5 as long as wide; vein Rs+M visible. Basal cell with dense, closely spaced setae. Apical margin of wing with a short fringe of setae.

Metasoma (Fig. 13E). Metasomal tergum T2+3 fused, smooth and shining, with close and distinct micropunctures in posterior half of metasoma; anteromedian area with a small group of 3–4 setae. Projecting part of hypopygial spine quite extended beyond attachment of lateral flap (Fig. 15E); hypopigial setae arranged in two rows; apical setae not projected beyond apex spine.

Distribution. Recorded from Nicaragua and now from Panama (Chiriquí, Renacimiento).

Biology. The species was originally recorded as an inquiline in an unidentified stem gall on *Quercus oleoides* that was similar to galls of *Xanthoteras quercusforticorne* (Diaz & Gallardo 1998). We have reared this inquiline from galls of an undescribed *Disholcaspis* species (Medianero & Nieves-Aldrey, unpublished). The host galls are gregarious and are formed in stems of *Quercus lancifolia* (Fig. 21H).

Synergus rufinotaulis Nieves-Aldrey & Medianero sp. nov.

(Figs. 2D, 4G, 4H, 5K, 6K, 8D, 11D, 13C, 17F, 19E–F)

Type material. Holotype ♀ (Fig. 19E) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2098). PANAMA, Chiriquí, Volcán Barú, 8º 46' 36 08" N, 82º 31' 39 03" W, 3079 m; ex gall *Cynips sp*. on twigs of *Quercus bumelioides* (Fagaceae), gall collected 23.x.2008, E. Medianero leg. Paratypes: 1♂, same data as holotype, but gall collected 22.vii.2008; 1♀, same data as holotype, reared from an unidentified gall (*Cynips* sp.?) 27.ii.2009. One paratype in the MNCN, another paratype in Maestría en Entomología, Universidad de Panamá (MEUP).

Etymology. Named after the reddish coloration of the notauli contrasting with the black mesoscutum.

Diagnosis and comments. This pretty, distinctive species differs from other Panamanian species by its long filiform antennae and long radial cell; the scutellum being subpentagonal, strongly reticulate-rugose dorsally, the large, quadrangular or irregularly rounded scutellar foveae, the wide well impressed notauli, reddish posteriorly in females, the mesopleuron with mixed striate and coriarious-rugose sculpture and the metasomal T2+3 with punc-

tures extended about 1/3 of metasoma length. With respect to its general aspect, the micropunctate metasoma, the shape of mesoscutal sculpture and the long radial cell resembles *S. colombianus*, but these two species are well distinguished by many other characters, such as the antennal F1 of males, which is more strongly expanded in *S. colombianus*, the wider notauli of *S. rufinotaulis*, the different mesoscutal coloration, the shape of the scutellar foveae and other features.

Description. Body length 3.36 mm (range 3.16–3.56; N = 2) for females; 2.77 (N = 1) for males. Female. Head black excepting a narrow band along internal margin of eyes, the entire genae, the sides of the face and the bases of the mandibles which are yellowish-red or orange. Antenae brown, last flagellar segments lighter. Mesosoma black, with dorsolateral margins of pronotum, posterior one third of notauli, tegulae and dorsal margin of metascutellum orange. Metasoma black dorsally and yellowish ventrally. Legs yellow, with basal half of metacoxae black; distal half of posterior tibiae and tarsi of all legs more or less brown. Forewing hyaline, veins brown. Male differs in having the orange coloration much reduced or absent; the mesosoma being entirely black, and the metasoma almost entirely black.

Female. (Fig. 19E). Head in dorsal view (Fig. 4H) 2.2 times as wide as long. Gena not expanded behind compound eye. POL 1.2 times longer than OOL, posterior ocellus separated from inner orbit of eye by 1.5 times its diameter. Head in anterior view (Fig. 2D) trapezoid, 1.3 times wider than high, genae not expanded. Face weakly pubescent, with marked, high, strong irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; the carinae widely spaced, especially medially, the interspaces smooth. Ventral margin of clypeus straight not projected over mandibles. Malar space 0.6 as long as height of compound eye. Toruli situated at midheight of compound eye; distance between toruli short, shorter than diameter of a torulus; distance between mesal margin of compound eye and lateral margin of a torulus shorter than diameter of a torulus, including rim. Frons with reticulate rugae, frontal carinae narrow, branched near lateral ocelli (Fig 2D). Vertex and occiput reticulate rugose, with piliferous punctures (Figs. 4G, 4H).

Female antenna with 14 segments (Fig. 5K); flagellum slender. Relative lengths of antennal segments: 18:8:27:27:25:24:20:15:14:12:11:10:9:15; pedicel slightly longer than wide; F1 as long as F2. Male antenna with 15 segments; F1 excaved medially and slightly expanded apically (Fig. 6K).

Mesosoma. Pronotum without lateral pronotal carina (Fig. 7B). Lateral surface of pronotum with reticulate-rugose sculpture. Mesoscutum (Fig. 8D) with, undulate transverse rugae, the interspaces with coriarious sculpture. Notauli percurrent, deep and wide thorough, crossed regularly by transversal mesoscutal sculpture; notauli moderately converging posteriorly. Median mesoscutal impression visible but shallowly impressed. Anteroadmedian signa visible. Scutellar foveae rounded, smooth, anterior margins straight and not quite diverging abruptly from the fissure transscutal, posterior margins distinct. Scutellum subpentagonal, not margined, with reticulate rugose sculpture (Fig. 8D). Mesopleuron (Fig. 11D) with the horizontal striae obscured by reticulate rugae, the interspaces with coriarious sculpture.

Lateral propodeal carinae distinct, broad, slightly convergent posteriorly. Median propodeal area pubescent, not sculptured. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17F). As long as body. Radial cell long, 3 times longer than wide. All the veins well pigmented, R1 well visible along margin of radial cell although narrowed and less pigmented, radial cell closed (Fig. 17F; areolet indistinct; vein Rs+M visible. Basal cell with sparse spaced setae. Apical margin of wing with a moderately long fringe of setae.

Metasoma (Fig. 13C). As long as head plus mesosoma. First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering almost the entire metasoma, smooth and shining, with well visible micropunctures, extended in posterior one third of tergite. Projecting part of hypopygial spine slightly extended beyond attachment of lateral flap; apical setae not projected beyond apex spine.

Distribution. Confined to the type locality Volcán Barú (Chiriqui, Panama).

Biology. *Synergus rufinotaulis* is present as inquiline in galls of an undescribed *Cynips* species (Fig. 22D), as well as in other detachable galls induced by an unknown cynipid species, presumably a *Cynips* species as well (Fig. 22F). In both cases, the host galls are spherical in shape, detachable and fall to the ground when mature. They grow on *Quercus bumelioides* (*Quercus*, Quercus section).

***Synergus gabrieli* Nieves-Aldrey & Medianero sp. nov.**
(Figs. 2A, 4D, 5L, 6F, 7F, 9A, 11C, 12B, 14A, 15C, 16F, 17G, 20A–B)

Type material. Holotype ♀ (Fig. 20A) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2099). PANAMA, Chiriquí, Volcán Barú, 8º 46' 36 08" N, 82º 31' 39 03" W, 1,800–2,070 m; ex gall *Neuroterus sp*. on leaves of *Quercus bumelioides* (Fagaceae), gall collected 26.iii.2009, E. Medianero leg. Paratypes: 6 ♂, 1♀, same data as holotype; 1 ♂, 2♀, same data but gall collected 30.i.2008. Six paratypes in the MNCN, four paratypes in Maestría en Entomología, Universidad de Panamá (MEUP).

Non-type material: 4♂, 2♀, Chiriquí, Renacimiento, 1,270 m, ex gall *Andricus guatemalensis* (Cameron) on *Quercus lancifolia*, 26.x.2008; 1♂, 1♀, same date, but gall collected at Piedra Candela, 18.vi.2008. 1♂, 2♀, Volcan Barú, ex gall *Andricus guatemalensis* on *Quercus bumelioides*, 30.i.2008. 3♂, 2♀, Boquete, Alto Quiel, 1,600 m, ex gall *Andricus guatemalensis* on *Quercus insignis*, 19.xii.2008.

Etymology. Named after Gabriel, son of the junior author.

Diagnosis and comments. A polyphagous, quite variable species; closely related to *Synergus chiricanus*, *S. baruensis* and *S. luteus*. Diagnostic characters of this species are the frontal carina being narrow and branched, faint before reaching the lateral ocelli; F1 of the female antenna 1.3 as long as F2, mesoscutum weakly coriarious with some minute closely spaced transverse rugae, metasomal T2+3 with punctures very weak, forming a narrow band.

Description. Body length 1.6 mm (range 1.50–1.66; N = 4) for females; 1.5 (range 1.19–1.58; N = 7) for males

Female. Head yellow red, ocellar triangle, vertex medially and occiput black. Antenae yellow. Mesosoma black, excepting dorsolateral margin of pronotum yellow red and tegulae yellow. Metasoma black dorsally to brownish red posteriorly. Legs pale yellow. Forewing hyaline, veins pale yellow. Male similar coloration of female. Metasoma and forewing venation darker.

Female. (Fig. 20A). Head in dorsal view (Fig. 4D) 2.1 times as wide as long. Genae not expanded behind compound eye. POL 1.6 times longer than OOL, posterior ocellus separated from inner orbit of eye by 1.4 times its diameter. Head in anterior view (Fig. 2A) trapezoid, 1.2 times wider than high, genae not expanded behind eyes. Face weakly pubescent, with marked, high, strong irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli, excepting the medial carina; the carinae are widely spaced, especially medially, the interspaces smooth. Ventral margin of clypeus weakly projected over mandibles. Malar space 0.6 as long as height of compound eye. Toruli size and relative separation as in the precedent species. Frons coriarious, weakly punctuate dorsally, frontal carinae narrow, faint before reaching lateral ocelli (Fig 4D). Vertex and occiput coriarious, with weak rugae and moderately punctate (Figs. 2A, 4D).

Female antenna with 14 segments (Fig. 5L); flagellum slightly broadened towards apex. Relative lengths of antennal segments: 19:12:30:23:23:22:20:17:15:15:14:13:12:21; pedicel 1.5 longer than wide; F1 1.3 as long as F2. Male antenna with 15 segments; F1 slightly excaved medially and very weakly expanded basally and apically (Fig. 6F).

Mesosoma. Pronotum without lateral pronotal carina (Fig. 7B). Lateral surface of pronotum with weakly-rugose sculpture. Mesoscutum (Fig. 9A) with, very weak interrupted transverse rugae, the interspaces with coriarious sculpture. Notauli percurrent, narrow and moderately converging posteriorly, with of a notaulus posteriorly not as wide as transscutal fissure. Median mesoscutal impression not visible. Scutellar foveae ellipsoidal, smooth, anterior margins moderately diverging from the fissure transscutal, posterior margins discernible. Scutellum not margined, with moderate rugose sculpture, weaker medially (Fig. 9A). Mesopleuron (Fig. 11C) with regular horizontal striae extended on the speculum, the interspaces smooth, coriarious sculpture not apparent.

Lateral propodeal carinae distinct, broad, slightly convergent posteriorly (Fig. 12B). Median propodeal area smooth, with short pubescence. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth measuring about 1/3 of length of apical tooth (Fig. 16F).

Forewing (Fig. 17G) longer than body. Radial cell long, 3.4 times longer than wide. R1 not well visible along margin of radial cell, narrowed and less pigmented, radial cell ambiguously closed; areolet indistinct; vein Rs+M invisible. Basal cell with widely spaced sparse setae. Apical margin of wing with a long fringe of setae.

Metasoma (Fig. 14A). First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering 4/5 parts of metasoma, smooth and shining, with minute, obsolete, micropunctures forming a narrow band posterodorsal to tergite. Anterolateral pubescence composed of a group of 4–5 setae. Projecting part of hypopygial spine slightly extended beyond attachment of lateral flap; apical setae not projected beyond apex spine (Fig. 15C).

Variation. *S. gabrieli* is a relatively common species that inhabits a moderately wide array of host cynipid galls. The variability of this species is accordingly high. Its variability is related not only to its coloration but also to the sculpture of the frons, vertex and mesoscutum, the relative average of antennal F1 and F2 and the shape of F1 of the male antennae. It is possibile that that this variability may obscure the existence the some closely related cryptic species. Ongoing molecular DNA studies may answer this question in the future.

Distribution. Chiriqui region, Panama.

Biology. This new species is a polyphagous inquiline that shows a preference for attacking the leaf galls induced by *Andricus guatemalensis* (Fig. 21D) and an undescribed species of *Neuroterus* (Fig. 21E) on *Quercus* species of both the *Quercus* and *Lobatae* sections.

Synergus chiricanus **Nieves-Aldrey & Medianero sp. nov.**
(Figs. 2B, 4C, 5I, 6D, 7D, 9D, 11B, 12A, 14B, 17H, 20C)

Type material. Holotype ♀ (Fig. 20C) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2100). PANAMA, Chiriquí, Boquete, Bajo Mono 8º 49' 44 06" N, 82º 28' 37 01" W, 1,547 m; ex gall *Andricus* sp. on buds of *Quercus insignis* (Fagaceae), gall collected 26.i.2009, E. Medianero leg. Paratypes: 1♂, 2♀, same data as holotype. Two paratypes in the MNCN, one paratype in Maestría en Entomología, Universidad de Panamá (MEUP).

1♀ paratype of the type series was dissected for SEM observations (in the MNCN).

Etymology. Named after the region of the collecting site.

Diagnosis and comments. This species is morphologically similar to the closely related species S. *gabrieli*, S. *baruensis* and *S. luteus*. It differs from these species, in addition to its smaller size, with respect to the mesoscutal sculpture, which is strong, with the interrupted transverse rugae widely spaced; F1 of female antenna 1.9 as long as pedicel; 1.1 as long as F2, septum separating the scutellar foveae being broad and the lateral propodeal carinae strongly convergent. The radial cell is less than three times as long as wide.

Description. Body length 1.86 mm (range 1.82–1.90; N = 2) for females; 1.98 (N = 1) for males.
Female. Head yellow red, excepting the frons and the occiput medially black. Antenae dirty yellow, brownish apically. Mesosoma black, excepting dorsolateral margin of pronotum reddish and tegulae yellow. Metasoma black dorsally to brownish red posteriorly. Legs yellow. Forewing hyaline, veins pale yellow. Male similar coloration of female but lateral surface of pronotum yellow, dorsal areas of mesopleuron reddish, distal areas of metasoma yellow reddish.

Female. (Fig. 20C). Head in dorsal view (Fig. 4C) about 2 times as wide as long. Genae slightly expanded behind compound eye. POL 1.4 times OOL, posterior ocellus separated from inner orbit of eye by 1.2 times its diameter. Head in anterior view (Fig. 2B) rounded, 1.2 times wider than high, genae slightly expanded behind eyes. Sculpture on face similar to *S. gabrieli*. Malar space 0.5 as long as height of compound eye. Toruli size and relative separation as in the precedent species. Sculpture on frons and vertex similar as *S. gabrieli*. (Figs. 2B,4C).
Female antenna with 14 segments (Fig. 5I); flagellum slightly broadened towards apex; pedicel 1.2 as long as wide; F1 1.2 as long as F2. Male antenna with 15 segments; distal half widened. F1 excaved medially and slightly expanded apically (Fig. 6D).

Mesosoma. Pronotum without lateral pronotal carina (Fig. 7D). Lateral surface of pronotum with coriarious-striated sculpture. Mesoscutum (Fig. 9D) with, strong, interrupted transverse carinae, the interspaces with coriarious sculpture. Notauli percurrent, narrow and moderately converging posteriorly, width of a notaulus posteriorly as wide as transscutal fissure. Median mesoscutal impression not visible. Scutellar foveae ellipsoidal, smooth, widely separated anteriorly by a septum; anterior margins diverging from the fissure transscutal, posterior margins visible. Scutellum not margined, with moderate rugose carinate sculpture, (Fig. 9D). Mesopleuron (Fig. 11B) with wide, blunt, close spaced horizontal striae, extended on the speculum, the interspaces without visible coriarious sculpture.

Lateral propodeal carinae distinct, broad, strongly convergent posteriorly (Fig. 12A). Median propodeal area smooth and pubescenct. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth large, measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17H). Radial cell 3 times as long as wide. R1 depigmented along margin of radial cell, radial cell ambiguously closed; areolet indistinct; vein Rs+M invisible. Basal cell with widely spaced sparse setae. Apical margin of wing with a long fringe of setae.

Metasoma (Fig. 14B). First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering 4/5 parts of metasoma, smooth and shining, micropunctures absent. Anterolateral pubescence composed of a group of 4–5 setae. Hypopygial spine as in *S. gabrieli*.

Distribution. Chiriqui region, Panama.

Biology. Reared only from small galls within buds of *Quercus insignis*. The cynipid host is an unidentified *Andricus* species that is likely undescribed.

***Synergus baruensis* Nieves-Aldrey & Medianero sp. nov.**
(Figs. 2C, 4F, 5F, 6J, 9C, 11F, 14C, 17J, 20D–E)

Type material. Holotype ♀ (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. (Cat. nº 2101). PANAMA, Chiriquí, Boquete, Alto Chiquero 8º 50' 49 01" N, 82º 29' 18 04" W, 1869 m; ex gall of an undescribed *Callirhytis*? species on *Quercus salicifolia* (Fagaceae), gall collected 10.v.2008, Medianero & Nieves leg. Paratypes: 6♂, 6♀, same data as holotype; 1♂, road to Volcancito, 1,400 m, 25.i.2009, E. Medianero leg. Eight paratypes in the MNCN, four paratypes in Maestría en Entomología, Universidad de Panamá (MEUP). 1♀ paratype of the type series was dissected for SEM observations (in the MNCN).

Etymology. Named after the Volcan Barú, the best collecting site for cynipids in Panama.

Diagnosis and comments. This new species resembles *S. luteus*, *S. gabrieli* and *S. colombianus* in its general aspect and in most morphological characters. The distinguishing characters for these species are mentioned in the identification key. The diagnostic characters of *S. baruensis* can be summarized as follows: coloration predominantly yellowish in the two sexes; frontal carinae strong, high, not branched, reaching close to the lateral ocelli; F1 of female antenna 2.8 as long as pedicel; 1.2 as long as F2; sculpture of mesoscutum weakly coriarious with some weak transverse rugae; lateral propodeal carinae moderately convergent; radial cell three times as long as wide, venation well pigmented, in males the distal end of the radial cell is extended by a pigmented small triangle; extension of micropunctures on the posterior metasomal 2+3 terguites forming a narrow band, punctures quite weak

Description. Body length 2.4 mm (range 2.14–2.77; N = 6) for females; 2.4 (range 1.82–2.85; N = 7) for males.

Female (Fig. 20D). Head yellow red, the frons (inside frontal carinae), ocelar triangle and occiput, around the occipital foramen, black. Antennae brown dorsally and yellowish ventrally. Mesosoma black, but sides of pronotum and scutellum, lateral margins of mesoscutum and speculum are yellow red; tegulae yellow. Metasoma black dorsally and anterolaterally, the half ventral and the posterolateral areas yellow. Legs yellow, excepting all tarsi slightly darkened. Forewing hyaline, veins dirty yellow. Male (Fig. 20E) similar to female but yellow coloration much more extended, only small areas black in pronotum medially, sides of ocelli, posterior half of mesoscutum (among notauli), propodeum and metasoma dorsally. Coxae of legs more pale yellow.

Female. (Fig. 20D). Head in dorsal view (Fig. 4F) 2 times as wide as long. Genae not expanded behind compound eye. POL 1.8 times OOL, posterior ocellus separated from inner orbit of eye by about its diameter. Head in anterior view (Fig. 2C) more or less trapezoid, 1.2 times as wide as high, genae slightly expanded behind eyes. Facial carinae strong, regular, reaching toruli and internal margin of eyes, not branched near compound eyes. Malar space 0.5 as long as height of compound eye. Toruli size and relative separation as in their closely allied species. Frontal carinae strong, high, not branched, close arriving lateral ocelli. Frons coriarious, with some punctures and very weak rugae; vertex and dorsal area of occiput coriarious punctuate; some rugae close to internal margins of eyes (Figs. 2C, 4F).

Female antenna with 14 segments (Fig. 5F); flagellum filiform not broadened towards apex; relative lengths of antennal segments: 18:9.5:28:23:21:21:18.5:16:13:12:11:10:10:18.5; pedicel 1.3 as long as wide; F1 1.2 as long as F2. Male antenna with 15 segments; distal half slighty broadened; F1 excaved medially and slightly expanded apically (Fig. 6J).

Mesosoma. Pronotum without lateral pronotal carina. Mesoscutum moderately pubescent (Fig. 9C); with weak, coriarious striate sculpture. Notauli percurrent, narrow and moderately converging posteriorly; notauli not

broadened posteriorly, as wide as transscutal fissure. Median mesoscutal impression virtually invisible. Scutellar foveae ellipsoidal, shallow, smooth, narrowly separated anteriorly by a septum. Scutellum not margined, with rugose sculpture. Mesopleuron (Fig. 11F) with close spaced horizontal striae, extended on the speculum, the interspaces without visible coriarious sculpture.

Lateral propodeal carinae distinct, broad, moderately convergent posteriorly (Fig. 12A). Median propodeal area smooth and pubescenct. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth large, measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17J). Radial cell 2.9 times as long as wide. R1 slightly narrower along margin of radial cell, but radial cell closed; areolet indistinct; vein Rs+M incomplete. Basal cell with few sparse setae. Apical margin of wing with a long fringe of setae.

Metasoma (Fig. 14C). First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering 4/5 parts of metasoma, smooth and shining, weak micropunctures visible forming a narrow band on posterodorsal area of terguite. Anterolateral pubescence forming a patch of about 14 setae. Projection of the hypopygial spine short; apical setae not projected beyond apex spine.

Distribution. Chiriqui region, Panama.

Biology. *Synergus baruensis* is an inquiline inhabiting galls of an undescribed cynipid species that are provisionally attributed here to the genus *Callirhytis.* The galls are grown on the leaves and buds of *Quercus salicifolia*, being integral and plurilocular (Fig. 21G). Both the host galls and the inquiline cynipid seem to be common in the Chiriquí region of Panama.

Synergus luteus Nieves-Aldrey & Medianero sp. nov.

(Figs. 2F, 4E, 5G, 6E, 9B, 11E, 14D, 15D, 16E, 17I, 20F–G)

Type material. Holotype ♀ (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2102). PANAMA, Chiriquí, Volcan Barú , Rio Seco 8º 47' 54 05" N, 82º 30' 32 05" W, 2447 m; ex gall of *Loxaulus sp* on *Quercus bumelioides* (Fagaceae), gall collected 26.xi.2008, E. Medianero leg. Paratypes: 2♂, 5♀, same data as holotype; 1♂, 1♀, same data as holotype, but collected at 2,870 m, 22.xii.2008. Seven paratypes in the MNCN, two paratypes in Maestría en Entomología, Universidad de Panamá (MEUP).
1♀ paratype of the type series was dissected for SEM observations (in the MNCN).

Etymology. Named after the predominantly yellow coloration of this species.

Diagnosis and comments. Closely related to *Synergus colombianus* and *Synergus baruensis*; can be distinguished from *S. colombianus* by the F1 being longer than F2 in the female antenna and not strongly expanded dorsally in male antenna, in addition to its predominantly yellow coloration. Compared to *S. baruensis*, *S. luteus* differs in its coloration, in the weaker and more branched frontal carinae, the stronger transverse sculpture of the mesoscutum, the expanded genae and the metasomal 2+3 terguites being visibly punctate posteriorly.

Description. Body 2.7 mm (range 2.45–3; N = 5) for females; 2.05 (range 1.9–2.2; N = 2) for males.

Female (Fig. 20F). Head yellow red, the ocelar triangle, the occiput, around the occipital foramen, and tip of mandibles black. Antennae yellow. Mesosoma predominantly yellow red; the margin anterolateral of pronotum, anterior part of anteromedial signa, ventral area of mesopleuron, metanotum and propodeum black. Metasoma yellowish red, dorsally black. Legs yellow, excepting the metatarsomeres slightly darkened. Forewing hyaline, veins pale yellow. Male (Fig. 20G) similar to female but black coloration more extended on frons and vertex medially, the entire mesonotum and the metasoma, excepting its apical area.

Female. (Fig. 20F). Head in dorsal view (Fig. 4E) 2 times as wide as long. POL 1.3 times OOL, posterior ocellus separated from inner orbit of eye by 1.3 times its diameter. Head in anterior view (Fig. 2F) more or less rounded, 1.2 times as wide as high, genae slightly expanded behind eyes. Facial carinae strong, regular, reaching toruli and internal margin of eyes, slightly branched near compound eyes, medially in face the carinae arriving close to ventral margin of toruli. Ventral margin of clypeus slightly projected over mandibles. Malar space 0.6 as long as height of compound eye. Toruli size and relative separation as in their closely allied species. Frontal carinae branched and diffuse close lateral ocelli. Frons coriarious-punctate; vertex and dorsal area of occiput coriarious-punctate (Figs. 2F, 4E).

Female antenna with 14 segments (Fig. 5G); flagellum filiform not broadened towards apex; relative lengths of antennal segments: 20:11:29:22:23:24:21:20:16:15:15:12:12:24; pedicel 1.3 as long as wide; F1 1.3 as long as F2.

Male antenna with 15 segments; distal half slighty broadened; F1 curvated medially and slightly expanded apically; F1 2 times as long as F2 (Fig. 6E).

Mesosoma. Pronotum without lateral pronotal carina, laterally with coriarious-striate sculpture. Mesoscutum moderately pubescent, with strong horizontal, closely spaced, striate sculpture (Fig. 9B). Notauli percurrent, slightly converging posteriorly; notauli slightly broadened posteriorly, being wider than width of transscutal fissure. Median mesoscutal impression not impressed. Scutellar foveae ellipsoidal, shallow, slightly rugose, separated anteriorly by a narrow septum. Scutellum not margined, with horizontal, irregular, rugose sculpture. Mesopleuron (Fig. 11E) with close spaced, regular, horizontal striae, extended also on the speculum, the interspaces without visible coriarious sculpture.

Lateral propodeal carinae distinct, broad, rather convergent posteriorly. Median propodeal area smooth and pubescenct. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth large, measuring 1/2 of length of apical tooth (Fig. 16E).

Forewing (Fig. 17I). Radial cell long, about 3.2 times as long as wide. R1 slightly depigmented along margin of radial cell, the radial cell appearing ambiguously closed; areolet inconspicuous but visible; vein Rs+M quite pale, but visible. Basal cell sparsely pubescent. Apical margin of wing with a long fringe of setae.

Metasoma (Fig. 14D). First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering almost all the metasoma, smooth and shining, micropunctures present, forming a band on posterior one third of metasomal terguite. Anterolateral pubescence forming a group of about 7 setae. Projecting part of the hypopygial spine clearly expanded beyond attachment with sternite (Figs. 14D, 15D); lateral pubescence of hipopigial spine conspicuous and closely spaced; apical setae of hypopigial spine not projecting beyond apex spine.

Distribution. Known from the Volcán Barú area, Chiriqui region, Panama.

Biology. This new species inhabits galls of an undescribed species of the *Loxaulus* or *Bassettia* genera (Medianero & Nieves-Aldrey in prep.). The host galls consist of small swellings, which are sometimes inconspicuous, on twigs or small branches of *Quercus bumelioides.* The host galls are, thus, integral non-detachable, plurilocular and often cryptic (Fig. 22B).

Key to inquiline species of Panama

1 Female and male antenna with 13 segments. Pedicel long, 2.5 as long as wide and longer than the scape and F2 (Fig. 5A); F1 of male antenna strongly curved dorsally, excavated medially, and expanded apically and basally (Fig. 6A). Basal tooth of the metatarsal claw small, less than 1/3 as long as the apical tooth. Frontal carinae present (Fig. 1F) . . . . . ***Agastoroxenia***

• Female antenna with 14 segments, rarely 15; male antenna 15 segmented. Pedicel not as long; being shorter than the scape and F2 (Figs 5B–L); F1 of males less strongly curved dorsally, sometimes moderately to strongly expanded dorsally, or only slightly expanded basally and apically (Figs. 6B–K). Basal tooth of the metatarsal claw usually more than 1/3 as long as apical tooth. Frontal carinae present or absent (Figs 1A, 2C) . . . . . 2 (**Synergus)**

2 Mesopleuron with longitudinal, horizontal striate sculpture extended only medially and basally, speculum of mesopleuron smooth and shining; the striae weak (Figs. 10E, 10F). Scutellum with a clear and projected posterior margin, also margined laterally (Figs. 8B, 10F). Scutellar foveae shallow, sometimes indistinct (Fig. 8A). Notauli narrow, widely separated posteriorly (Fig. 8A). Subapical setae of the ventral spine of the hypopygium long, projected beyond the apex spine (Fig. 15A). Frontal carina absent; front and vertex with coriarious sculpture, not punctuate (Fig. 1A). Metasomal tergum T2+3 without micropunctures posteriorly (Fig. 13A) **3**

• Mesopleuron entirely striate, the striae usually stronger and extended on the speculum (Figs 10D, 11D). Scutellum not margined, sometimes a weak, non-projected posterior margin visible (Figs 8C, 8D, 10C, 11C). Notauli more widely separated and usually broader (Figs 8D, 8E). Scutellar foveae oval or rounded, deeper. Supapical setae of ventral spine of hypopygium short, not projected beyond the apex of the spine (Figs 15C, 15E). Frontal carina usually present; front and vertex punctate, usually with a coriarious-rugose sculpture (Figs 1C, 1D, 2B). Metasomal tergum T2+3 with or without micropunctures posteriorly. **4**

3 Head from the dorsal view less than 2.5 as wide as long (Fig. 3B). POL 1.5 to 1.8 as long as OOL; OOL less than two times the diameter of a lateral ocellus. F1 slighter longer than F2 (Fig. 5J). Scutellum coriarious. . . . . ***Synergus elegans* sp. n.**

• Head strongly transverse in dorsal view, more than 2.5 times as wide as long (Fig. 3C). POL about 1.2 as long as OOL; OOL more than two times the diameter of a lateral ocellus. F1 as long as F2 (Fig. 5B). Scutellum with some transverse rugae . . . . . ***Synergus laticephalus* sp. n.**

4. F1 1.5 times as long as F2 (Figs 5C, 5H). F1 in males strongly expanded apically (Figs 6G, 6H). Frontal carinae indistinct, obscured by very irregular and branched interrupted rugae (Figs 1C, 1D). Facial striae irregularly sinuate, branched near the ventral margin of the eyes. Basal cell of forewing densely setose; veins darkly pigmented (Figs 17C, 17D). Metasomal T2+3 not punctate posteriorly. Body coloration predominantly reddish to black (Figs 18D, 18F) **5**

- F1 as long as F2, or at most 1.2 longer than F2 (Figs 5D, 5E, 5L). F1 of males usually only slightly expanded apically, or slightly expanded basally and apically (Figs 6D, 6E, 6J). Frontal carinae usually distinct, sometimes branched before reaching the lateral ocelli (Figs 2A–F). Facial striae regular, sharp, not branched near the ventral margin of the eyes. Basal cell of forewing much less densely setose; veins usually paler (Figs 17G–J). Metasomal T2+3 punctate or not. Body coloration predominantly yellowish to yellow red (Figs 19A, 20F) **6**

5 POL shorter than OOL (Fig. 3E). Frons with strong irregular rugae, with the intervals punctate (Fig. 1D). Sculpture of mesopleuron strong; the longitudinal carina dense and extended over the speculum (Fig. 10D). Radial cell less than 2.4 as long as wide (Fig. 17D). Face yellow, metasoma red, legs black (Fig. 18D) **. . . .** ***Synergus mesoamericanus*** **Ritchie & Shorthouse**

- POL longer than OOL (Fig. 3F). Frons without irregular rugae and more closely punctuate (Fig. 1C). Sculpture of mesopleuron weak; with only a few longitudinal carinae medially with coriarious sculpture in the intervals and speculum partially smooth (fog. 10C). Radial cell 2.8 as long as wide (Fig. 17C). Predominantly black coloration (Fig. 18F) . . . . . **. . . . . .** ***Synergus ramoni*** **sp. n.**

6 Forewing with a shaded infuscate area over the radial cell and extended beyond the Rs vein (Fig. 17E); radial cell short and wide, less than 2.5 as long as wide. F1 three times as long as pedicel (Fig. 5E). Metasomal T2+3 punctate posteriorly with the punctures extended over about 1/3 of the total length of the segment (Fig. 13E) **. .** ***Synergus nicaraguensis*** **Díaz & Gallardo.**

- Forewing hyaline, without shaded infuscate areas; radial cell relatively longer, 2.6 to 3 times as long as wide (Figs 17G–J). F1 usually less than 2.6 times as long as the pedicel (Figs 5F, 5G, 5L), if close to three times as long, then forewing hyaline. Metasomal T2+3 posteriorly punctate or not, if present, punctures usually extended over a narrower area **7**

7 Scutellar foveae large, quadrangular or irregularly rounded (Fig. 8D). Notauli deep, broad, broadening and converging posteriorly. Scutellum subpentagonal, strongly reticulate-rugose dorsally. Frons and vertex with a reticulate-rugose sculpture (Figs. 2D, 4G). Mesopleuron with a mixed striate-rugose sculpture, the intervals with coriarious sculpture (Fig. 11D). Facial carina sharp, widely spaced (Fig. 2D). Metasoma black dorsally with the notauli posteriorly reddish. Metasomal T2+3 with punctures extended about 1/3 of the metasomal length (Fig. 13C) **. . . . . .** ***Synergus rufinotaulis*** **sp. n.**

- Scutellar foveae usually smaller, oval or ellipsoidal (Figs. 9A–D). Notauli not as deep, narrower and less convergent posteriorly. Scutellum rounded with a weaker rugose sculpture. Frons and vertex less strongly sculptured, punctate or rugose punctuate (Figs 2A–C). Mesopleuron usually with a striated, regular sculpture (Figs. 11A–C). Facial carina more closely spaced. Metasomal T2+3 with punctures usually forming a band, extended about 1/4 of metasomal length. Mesosoma dorsally with a different coloration **8**

8 Metasomal T2+3 conspicuously punctate posteriorly, with the fine punctures extending about one third of the total length of the tergum (Fig. 14D). Mesoscutum with strong, closely spaced, interrupted, sinuate, transverse rugae (Fig. 9B). Frontal carinae narrow, branched close the lateral ocelli (Fig. 2F). Reared from stem, integral, no detachable galls **9**

- Metasomal T2+3 with punctures less visible, with the punctures forming a narrow band or only a dorsal patch (Figs. 14A, 14C). Mesoscutum coriarious with weak interrupted transverse rugae (Fig. 9A), or with stronger rugae, but then more widely spaced (Fig. 9D). Frontal carinae either narrow, branched, or wide and not branched (Fig. 2C). Reared from integral or detachable galls.. . . . . **10**

9 F1 of female antenna as long as F2 (Fig. 5D); F2 of male strongly expanded apically (Fig. 6I). Ventral margin of clypeus not projected over mandibles. Genae not expanded behind eyes. Radial cell 2.8 as long as wide; venation darkly pigmented. Body reddish and black; basal half of metacoxae black in both sexes (Figs. 19C, 19D) . . . . . ***Synergus colombianus*** **Nieves-Aldrey**

- F1 1.2 as long as F2 (Fig. 5G); F2 of male slightly expanded apically (Fig. 6E). Ventral margin of clypeus slightly projected over mandibles. Genae expanded behind eyes. Radial cell ~~l~~ slightly more than three times as long as wide, venation pale. Body yellowish with basal half of metacoxae entirely yellow in both sexes (Figs. 20F, 20G) . . . . . ***Synergus luteus*** **sp. n.**

10. Frontal carina broad, not branched, or only branched close to the lateral ocelli. F1 1.1 to 1.2 as long as F2 . . . . . **11**

- Frontal carina narrow and branched (Fig. 2A, 4D). F1 1.3 as long as F2 (Fig. 5L). (Fig. 9A) . . . . . .***Synergus gabrieli*** **sp. n.**

11 Sculpture of mesoscutum weakly coriarious with some weak transverse rugae (Fig. 9C). F1 of female antenna 2.8 as long as pedicel (Fig. 5F). Lateral propodeal carinae moderately convergent. Radial cell three times as long as wide, venation well pigmented (Fig. 17J). . . . . .***Synergus baruensis*** **sp. n.**

- Mesoscutum sculpture with strong, widely spaced, interrupted transverse rugae (Fig. 9D). F1 of female antenna 1.9 as long as pedicel (Fig. 5I). Lateral propodeal carinae strongly convergent (Fig. 12A). Radial cell less than three times as long as wide, venation pale (Fig. 17H) . . . . . .***Synergus chiricanus*** **sp. n.**

Cluster analysis

Results. The phenogram resulting of the overall similarity, cluster analysis (UPGMA) (Fig. 23) recovered some main groupings; one cluster more similar to the Palaearctic outgroup *Saphonecrus lusitanicus* formed by *Synergus elegans* and *S. laticephalus*; another distinctive cluster composed by *S. mesoamericanus* and the new species *S. ramoni*, and a third diffuse grouping of the core Panamanian *Synergus* species, including the Colombian *S. colombianus*, which are more closely similar to the palaearctic species *Synergus ibericus*.

Discussion

The expected and observed diversity of inquilines of oak gall wasps from Panama.

It is generally assumed that there is a positive correlation between the number of *Quercus* species and their associated host gall-inducing and inquiline fauna. The richness of the Panamanian flora, with 9 *Quercus* species present, led us to believe that a richer, previously unsampled, fauna of inquilines of oak gall wasps awaited discovery in this country. This hypothesis has been confirmed by the results of this study. In comparative terms, the total of nine species of *Quercus* in Panama is close to the number of 10 species present in the Iberian peninsula (Nieves-Aldrey 2001). The number of inquilines of oak gall species found in Panama is eleven, which are from two genera, while thirty species from four genera have been recorded from Iberia, which is a geographic area that is much larger in size. Furthermore, it must be emphasized that the sampling effort has been considerably smaller in the case of the single study made in Panama, and more inquiline species will surely be found and added to the list of cynipid inquilines in Panama after further sampling. In this respect, our results indicated that more undescribed species could be present in our studied materials, although they have not been formally described here because of the low number of individuals available or due to their poor condition or their poor associated biological data. Therefore, even more cryptic *Synergus* diversity might be uncovered if sequence data of the studied samples were examined. According to our results, the richness of the Neotropical fauna is clearly much greater than expected, being close to the richness observed in the Oriental region (Abe *et al.* 2007) and much closer to the cynipid richness of the western Palaearctic and Nearctic faunas than was previously assumed (Nieves-Aldrey 2001; Ritchie & Shorthouse 1987; Csoka *et al.* 2005; Melika *et al.* 2005).

Relationships of the Holarctic and the Neotropical Synergus species

All the neotropical species studied share an important morphological character namely the absence of a lateral pronotal carina. While the core or main group of Palaearctic *Synergus* species, the species associated to white oaks Quercus sect Quercus, have a distinct lateral pronotal carina, it is weak, indistinct or absent in *Synergus plagiotrochi* Nieves-Aldrey & Pujade-Villar, *S. variabilis* Mayr, *S. flavipes* Hartig, *S. acsi* Melika & Pujade-Villar and *S. consobrinus* Giraud in Houard. Interestingly all these later species are associated to Quercus of the sections Cerris or Ilex and, according the molecular results of Acs et al (2010), form the more basal clades within the Palaearctic *Synergus*, close to the genera *Saphonecrus* and *Synophrus*. The absence of a lateral pronotal carina thus appears to be a plesiomorphic character state in the Palaearctic *Synergus* shared with the Neotropical species. Whether or not this implies the taxonomic separation of the genus into different genera will be a matter of discussion in further studies after sequence data are analyzed.

Biology. Quercus section associations

Our analysis of the host plant associations of the west Palaearctic fauna of inquilines shows a strong specificity within different sections of *Quercus*, subgenus *Quercus* (Nieves-Aldrey et al, unpublished information).] The species associated with *Quercus* of the sections *Cerris* and *Ilex* are quite distinctive and more basal than the species linked to *Quercus* species of the section *Quercus*. One remarkable observation is that no inquilines species share *Quercus* hosts belonging different *Quercus* sections. For the studied Panamanian species, the specificity with respect to the different *Quercus* sections can be traced in our data matrix (character 63, Appendix 1). It is striking that the specificity for host plant is not as strong as for the Palaearctic species, and at least one species, *S. elegans*, is associated with *Quercus* hosts belonging to two sections: *Quercus* and *Lobatae*, while six species are associated only with galls on plants of the *Quercus* section: *S. mesoamericanus, S. nicaraguensis, S. luteus, S. gabrieli, S. chiricanus* and *S. rufinotaulis*; and four species, *S. laticephalus, S. ramoni, S. baruensis* and *S. colombianus*, are linked to *Quercus* of the *Lobata* section.

Reliability and use of morphological characters in the taxonomy of Synergus

A number of weaknesses and flaws have been found in the current taxonomy and classification of *Synergus* based on morphological characters, as the failure of barcodes to discriminate among recognized morphological species has recently been shown, and the existence of cryptic lineages within several morphologically determined *Synergus* species was not recognized by morphological taxonomy. We believe that such mistakes have been caused in part by the limited set of morphological characters traditionally used in the taxonomy of this group or by errors in the identification of these species by different taxonomists.

In this study, we found some useful additional characters in the diagnosis and identification of inquilines genera and *Synergus* species, that have been ignored or rarely used in classical studies. Among these useful characters are the following: the relative size and shape of the basal tooth of metatarsal claw; the shape of the lateral carinae of the propodeum; the shape of the anterolateral pubescence on TA3; the shape and pilosity of the hipopygium and the pubescence on the basal cell of forewing. It is also crutial acquire good SEM images of the surface sculpturing of the frons, vertex, mesoscutum and mesopleuron because some interpretations based on artists' line drawings are weakly reliable and difficult to use for comparisons and descriptions.

It is important however to emphasize that the complication in *Synergus* taxonomy and the difficulty to establish a sound classification of this genus, comes not only from the point of view of morphology but also from molecular analysis, as recent results revealed (Acs et al, 2010).

Future work

This study found evidence that the rich fauna of previously undescribed inquiline species of oak gall wasps found in this study in Panama might represent only a fraction of the actual diversity that exists. Much more sampling will be required to achieve a deeper understanding of this fauna, especially with regard to the previously unsampled community of subterranean oak gall species and the cryptic galls in twigs, which usually host specific inquiline faunas. Until now, very little was known about the life cycles, immature stages, food webs, parasitoids, community structure and other aspects of the biology and ecology of the Panamanian species here studied, and much more field work will be needed in the future to fill these scientific gaps. Obtaining sequence data for the studied species and performing molecular phylogenetic studies of this fauna is also an obvious priority for future research in this group of species. Hopefully, these type of studies are s taking place as part of ongoing international projects.

Acknowledgements

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Appendix 1. List of characters and character states used for cluster analysis

Explanation of abbreviations used in the character descriptions (*x* refers to an integer): A*x* = antennomere *x*; F*x* = flagellomere *x*; *x*T = abdominal tergum *x*.

Head, anterior view, female

1. Ratio of width /height of the head (0) oval o rounded; as wide as high (ratio 1–1.1) (1) slightly trapezoid, slightly wider than high (ratio 1.22–1.25) (2) transverse; clearly wider than high (ratio 1.34–1.41).
2. Shape of genae, (0) not expanded behind compound eyes (Figs. 1E, 3B) (1) slightly expanded behind compound eyes (2) strongly expanded (Figs. 1F, 3D)
3. Shape of ventral margin of clypeus: (0) straight or slightly sinuate, not projecting over mandibles (Fig. 2E) (1) slightly projecting over mandibles (Fig. 1B).
4. Facial
5. striae radiating from lateral clypeus: (0) long, reaching eye margins, toruli and laterally extending into genal area (1) short, not reaching toruli and not extending over genal area.
6. Distinctness of facial
7. striae (0) iregular, low, weak, not widely spaced (Fig. 1A) (1) regular, higher, stronger, more widely spaced (Fig. 2D). (2) strong and deep but closely spaced.
8. Shape of apical end of facial
9. striae (0) regular, not branched close compound eyes (Fig. 2D) (1) irregular, sinuate or undulate, branching close margin compound eyes (Fig. 1C).
10. Frontal carinae: (0) absent (Fig. 3A) (1) present (Fig. 3D).
11. Distinctness and shape of frontal carinae (0) narrow and incomplete, faint or branched before reaching lateral ocelli (Fig. 3E) (1) narrow, somewhat branched but reaching lateral ocelli (2) complete, wide and not branched (Fig. 2C).
12. Distance between toruli, compared to diameter of a torulus, including rim: (0) short, subequal or shorter than half diameter (0,35–0,5) (Fig. 1C) (1) long; more than 0,6 diameter of a torulus (Fig. 1A).
13. Distance between mesal margin of compound eye and lateral margin of a torulus: (0) shorter than diameter of a torulus included rim (0,5–0,85) (Fig. 2D) (1) as long as or a little longer than diameter of a torulus (Fig. 1A).
14. Relative position of toruli on face; distance of ventral margin of toruli to ventral margin of compound eye: (0) high, distance 1.6–2 times diameter of a torulus; (1) intermediate, 1– 1,5 times diameter (2) low, subequal to shorter than diameter.
15. Length of malar space: (0); short 0,3–0,6 veces as long as length of compound eye (1) long, 0,8 as long as compound eye (Fig. 1B).
16. Sculpture on frons: (0) weakly coriarious (1) coriarious rugose, with some rugae dorsally.
17. Punctures on frons: (0) absent (Fig. 1A) (1) present (Fig. 3F).

Head dorsal view

18. Sculpture on vertex: (0) weakly coriarius (1) slightly rugose (2) strongly rugose
19. Punctures on vertex: (0) absent (1) present, weak (2) present, strong.
20. Ocellar triangle (POL/OOL): (0) POL shorter tan OOL (Fig. 3E) (1) 1.4 a 1.8 longer tan OOL (Fig. 3F) (2) more than 2 times OOL (2–2.4).
21. Size of ocelli (OOL/diameter of lateral ocelli: (0) OOL shorter than diameter (Fig. 3F) (1) 1–1.4 times as long as diameter (2) 1.7–1.9 veces (3) more than 2 times (2.2) (Fig. 3C).

Head posterior view

22. Sculpture on dorsal region of occiput (0) coriarious (1) rugose.
23. Punctures on dorsal region of occiput (0) absent (1) present.

Antennae, female

24. Number of completely separated flagellomeres: (0) 11 (1) 12 (2) 13
25. Length scape (0) 1–1,5 times as long as pedicel (1) 1,6–1,8 (2) 2 times as long as pedicel.
26. Ratio length/width of pedicel (0)
27. short, 1–1,5 as long as wide (Fig. 5C) (1) 1.6–1.8 times as long as wide (2) more than 2 times as long as wide (2.2–2.6) (Fig. 5A).
28. Ratio A3/A2 (0) 1.5–1.7 (1) 1.9–2.3 (2) 2.5–2.7 (3) 2.9–3.
29. Length of F1 (0) short, about as long as F2 (Fig. 5D) (1) 1.2–1.3 as long as F2 (2) about one and a half as long as F2 (1.42–1.47) (3) about two times as long as F2 (Fig. 5A).

Antennae, male

30. Shape of F1 (0) weakly curvate and excavate medially, slightly expanded basally and apically (1) weakly curvate and excavate medially, slightly expanded apically (Fig. 6B) (2) weakly curvate and excavate medially, strongly expanded apically (Fig. 6I) (3) strongly curvate and excavate medially, the ventral margin strongly convex, strongly expanded basally and apically (Fig. 6A).
31. Number of completely separated flagellomeres (0) 13 (1) 12 (2) 11

Pronotum, female

32. Lateral pronotal carina (0) absent (Fig. 7B) (1) present (Fig. 7A).
33. Sculpture on lateral pronotal surface (0) coriarious (1) coriarious-rugose, the rugae more or less conspicuous.
34. Shape of pronotum, lateral view (0) short, about as long as high (1) long, much more longer than high

Mesoscutum

35. Sculpture of mesoscutum (0) coriarious (Fig. 8A) (1) coriarious-rugose, with transverse rugae more or less marked (Fig. 8C).
36. Shape of the transversal rugae of mesoscutum (0) closely spaced (1) widely spaced, the interspaces more broad.
37. Shape of the notauli (0) percurrent and distinct (Fig. 8C) (1) almost percurrent, but anterior half indistinct or faint (Fig. 8A)
38. Median mesoscutal impression (0) entirely absent or invisible (1) present, indicated at least as a slight impression at posterior margin of mesoscutum (Fig. 8F).
39. Extension of median mesoscutal impression (0) short and superficial, indicated only as a slight impression at posterior margin of mesoscutum (1) longer and more deeply impressed, reaching or surpassing mid region of mesoscutum.
40. Width of notauli (0) shallowly impressed and narrow; posteriorly not wider than trasscutal fissure (Fig. 8B) (1) wider and deeply impressed, posteriorly wider than transscutal fissure (Fig. 8D).
41. Separation of notauli at the meeting with transscutal fissure (relative convergence of notauli posteriorly). (0) notauli weekly convergent posteriorly, widely separated at meeting with transscutal fissure; the distance between notauli margins 8.4 to 11.5 as breadth of a notaulus. (1) notauli more strongly convergent posteriorly, less widely separated at meeting with transscutal fissure, the distance between notauli as 3.3 to 6.5 the breadth of a notaulus.
42. Shape of scutellar foveae (0) elipsoidal (Fig. 8E) (1) quadrangular (Fig. 8B) (2) rounded (Fig. 8D).
43. Anterior margin of the scutellar foveae (0) curved, widely divergent of the transscutal fissure, from the joining point of the foveae (1) more or less straight and then laterally divergent (2) straight along the entire anterior margin, and then forming an angle about 90º with the trasscutal fissure.
44. Posterior margin of the scutellar foveae (0) distinct (1) indistinct.
45. Distinctiness of the scutellar foveae (0) well impressed, deep and distinct (1) shallow, somewhat indistinct.
46. Dorsal surface of scutellum (0) not margined posteriorly and posterolaterally (Fig. 8E) (1) with a distinct flange, with distinct sharp margin posteriorly and posterolaterally (Fig. 8B).

Mesopleuron

47. Sculpture on speculum (0) horizontal carinae present (Fig. 10D) (1) smooth, not carinate (Fig. 10E).
48. Shape of the carinate sculpture of mesopleuron (0) regular, carinae sharp and narrow, the interspaces smooth (Fig. 11C) (1) irregular, carinae wider and blunt, the interspaces with coriarious sculpture (Fig. 11B) (2) mesopleuron with a mixed coriarious-reticulate and horizontally carinate sculpture (Fig. 11D) (3) horizontal carinae weak and reduced, the interspaces smooth (Fig. 10E).

Metapectal-propodeal complex

49. Lateral propodeal carinae (0) subparallel (Fig. 12C) (1) slightly convergent posteriorly anterior distance between carinae 1. 4 times as posterior distance between them (Fig. 12B) (2) strongly convergent posteriorly, anterior distance between carinae 1.7 times as posterior distance between them (Fig. 12A).

Legs

50. Basal tooth of the metatarsal claw (0)
51. long, reaching more than 0.5 length of apical tooth (Fig. 16E) (1) short, not reaching half of length of apical tooth (Fig. 16B).

Metasoma, female

52. Anterolateral pubescence on TA3 (0) with a compact patch of setae ventro-laterad to abdominal petiole, extending towards dorsal region of tergite (1) group of the setae less compact, at least composed by 12

setae, and not extending towards dorsal region of tergite. (2) a group of few setae present extended also to dorsal region of tergite (3) only 2–3 setae visible (4) about 7 setae arranged on a vertical row.

53. Size of tergite TA3 (0) Almost covering entirely metasoma, remaining tergites almost invisible (Fig. 13A) (1) Not covering entirely metasoma, remaining tergites visible at least in part (Fig. 13D).
54. Shape of posterior margin of TA3 in lateral view (0) oblique, more or less straigth, forming a near 90° angle with dorsal margin of tergite (Fig. 13B) (1) rounded or curved, forming an obtuse angle with dorsal margin of tergite (Fig. 13E).
55. Ratio length/height of TA3 (0) short and high, about as long as high or slightly longer tan high (1) elongate, 1.2–1.4 times as long as high.
56. Micropunctures on posterior margin of TA3 + 4, (0) absent (1) present.
57. Extension of the micropunctures on posterior margin of TA3 + 4: (0) extended only on a small posterodorsal patch of tergite (1) forming a narrow band along the posterior margin (Fig. 14A) (2) Micropunctures extended at least to one-third of total length of tergite (Fig. 13E).
58. Length of projecting part of hypopigial spine (beyond attachment of lateral flap): (0) not projected behind attachment with sternite (Fig. 15B) (1) slightly projected (2) clearly projected (Fig. 15F).
59. Lateral pubescence of hypopigial spine (0) sparse, spaced, rows with 6–7 setae only (1) pubescence more dense and closely spaced, rows with 10 or more setae.
60. Apical setae of hypopigial spine (0) short, not projecting or only slightly projecting beyond apex of spine (Fig. 15E) (1) long, far projecting apex spine (Fig. 15A).

Forewing, female

61. Anterior margin of radial cell: (0) open; R1 ending at wing margin (1) ambiguous state, R1 depigmented, paler along wing margin, the radial cell appearing virtually open (Fig. 17B) (2) unambiguous closed, the R1 vein well pigmented, continuing along wing margin until reaching Rs. (Fig. 17C).
62. Wing coloration: (0) hyaline, without smoky or infuscate areas (1) with a heavily infuscate area on the radial cell.
63. Length of radial cell: (0) short and wide ; less than 2.5 times as long as wide (2.2–2.3) (1) intermediate length, 2.5–2.8 times as long as wide (2) long, about 3 times as long as wide.
64. Areolet: (0) inconspicuous (Fig. 17E) (1) conspicuous, clearly visible (Fig. 17D).
65. Definition of Rs+M: (0) invisible (1) visible at least in part (2) clearly visible.
66. Pubescence of basal cell (0) dense, closely spaced setae covering the basal cell (Fig. 17C) (1) scarce, few setae and more widely spaced (Fig. 17J).
67. Length of fringe of setae on apical margin: (0) short (Fig. 17D) (1) long (Fig. 17H).

Biology

63 Host plant section within *Quercus* subgenus attacked by the host gall wasp inductor: (0) *Quercus* (1) *Lobata* (2) *Quercus* and *Lobata* (3) *Ilex* and *Cerris*

64 Host plant gall attachment: (0) integral, fused with plant (1) detachable

65 inquiline specificity (0) monophagous (1) oligophagous (2) poliphagous

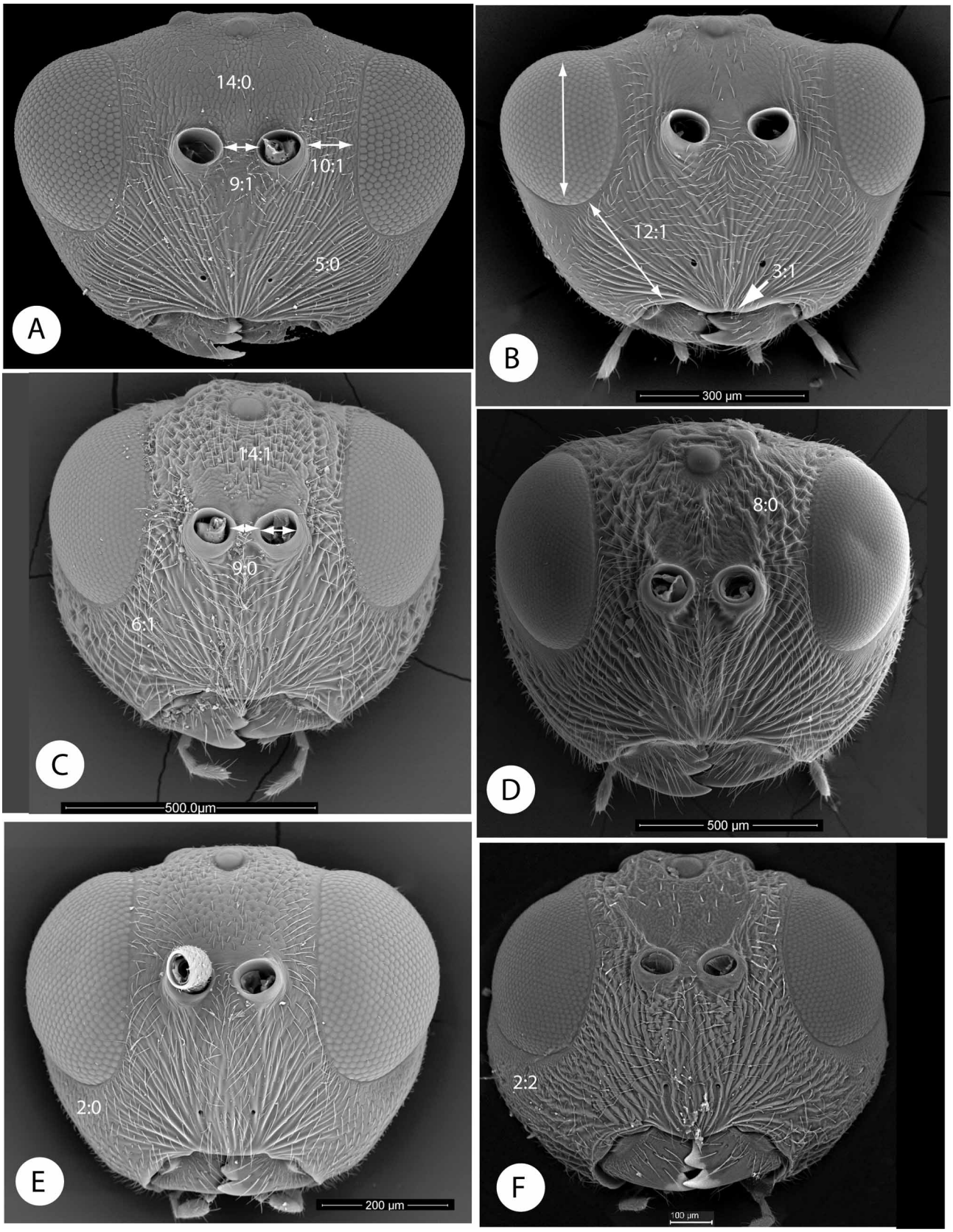

FIGURE 1. Head anterior view of inquilines of oak gall wasps: (A) *Synergus elegans*. (B) *Synergus laticephalus*. (C) *Synergus ramoni*. (D) *Synergus mesoamericanus*. (E) *Saphonecrus lusitanicus*. (F) *Agastoroxenia panamensis*.

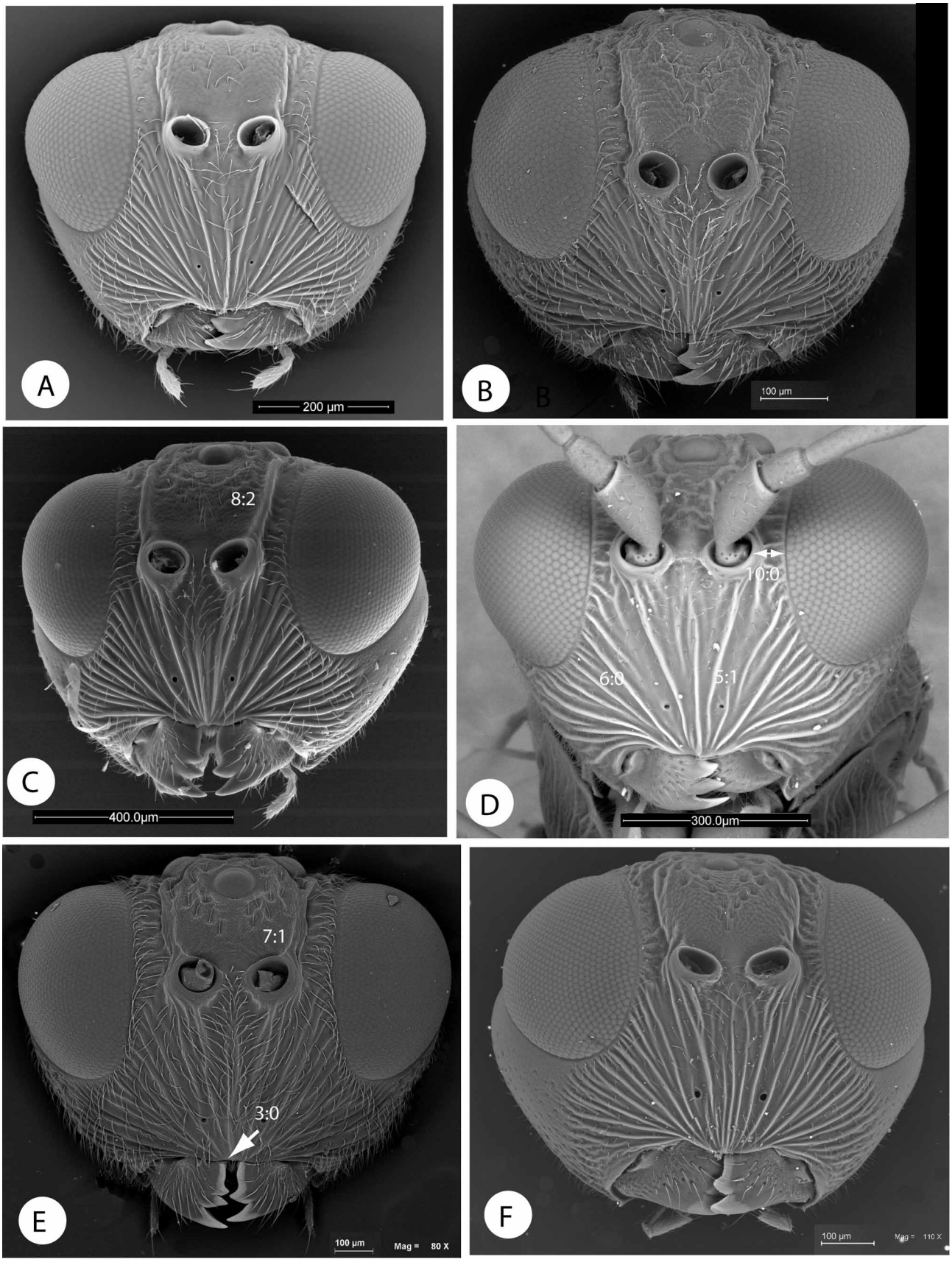

FIGURE 2. Head anterior view of *Synergus* species: (A) *Synergus gabrieli.* (B) *Synergus chiricanus.* (C) *Synergus baruensis.* (D) *Synergus rufinotaulis.* (E) *Synergus nicaraguensis.* (F) *Synergus luteus.*

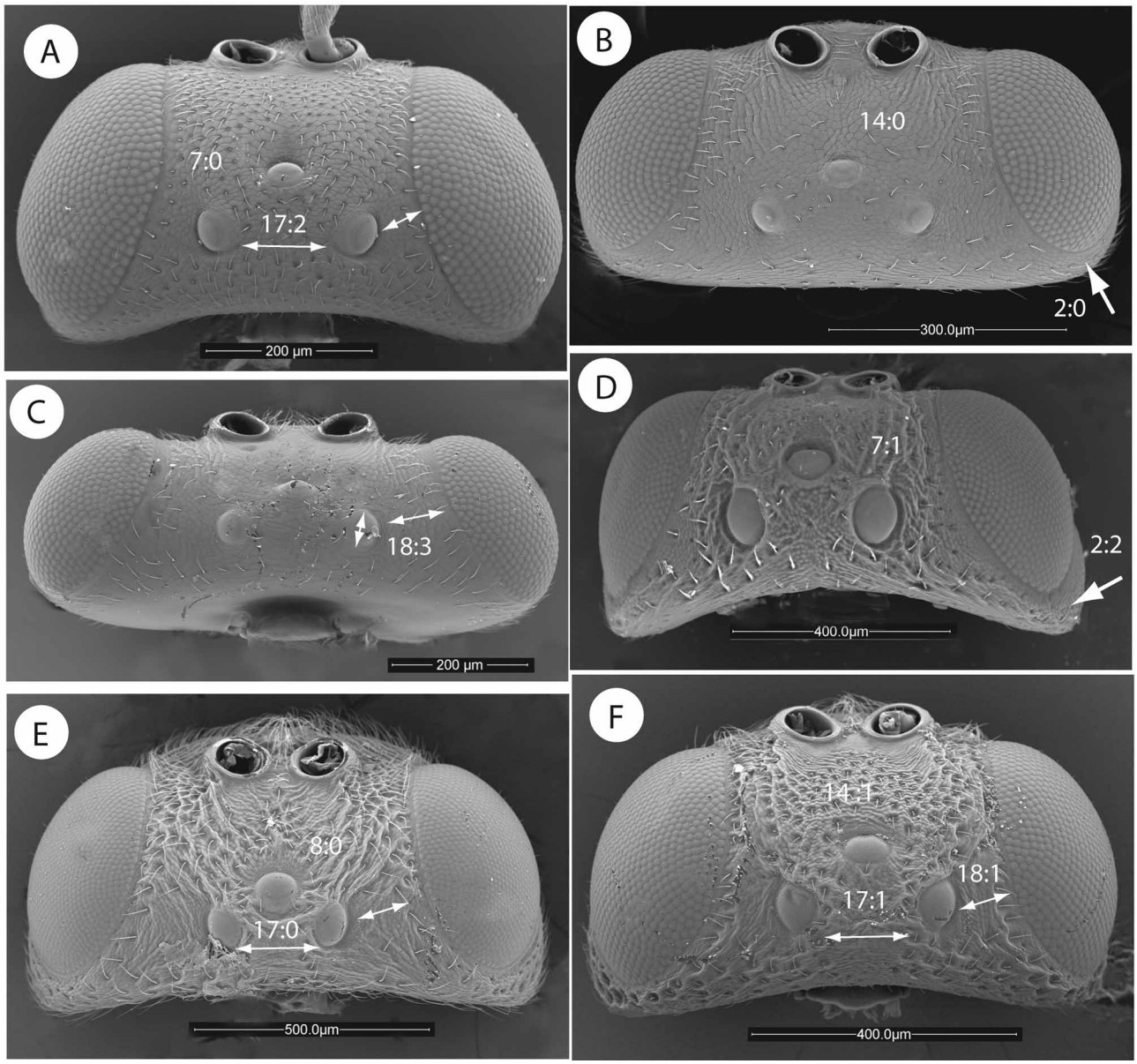

FIGURE 3. Head dorsal view of inquilines of oak gall wasps: (A) *Saphonecrus lusitanicus.* (B) *Synergus elegans.* (C) *Synergus laticephalus.* (D) *Agastoroxenia panamensis.* (E) *Synergus mesoamericanus.* (F) *Synergus ramoni.*

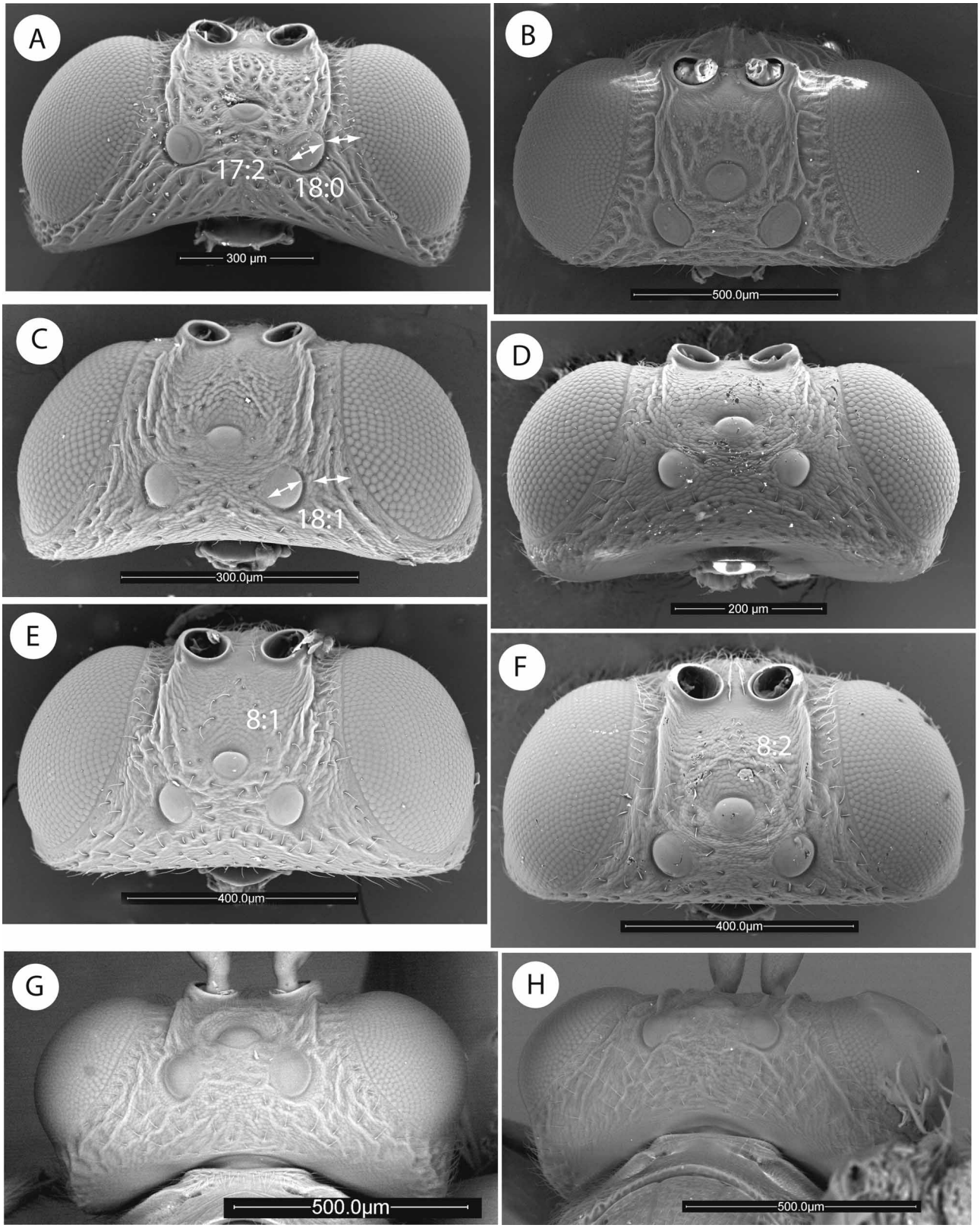

FIGURE 4. Head dorsal view of *Synergus* species: (A) *Synergus ibericus*. (B) *Synergus nicaraguensis.* (C) *Synergus chiricanus.* (D) *Synergus gabrieli.* (E) *Synergus luteus.* (F) *Synergus baruensis.* (G) *Synergus rufinotaulis*, male. (H) *Synergus rufinotaulis*, female.

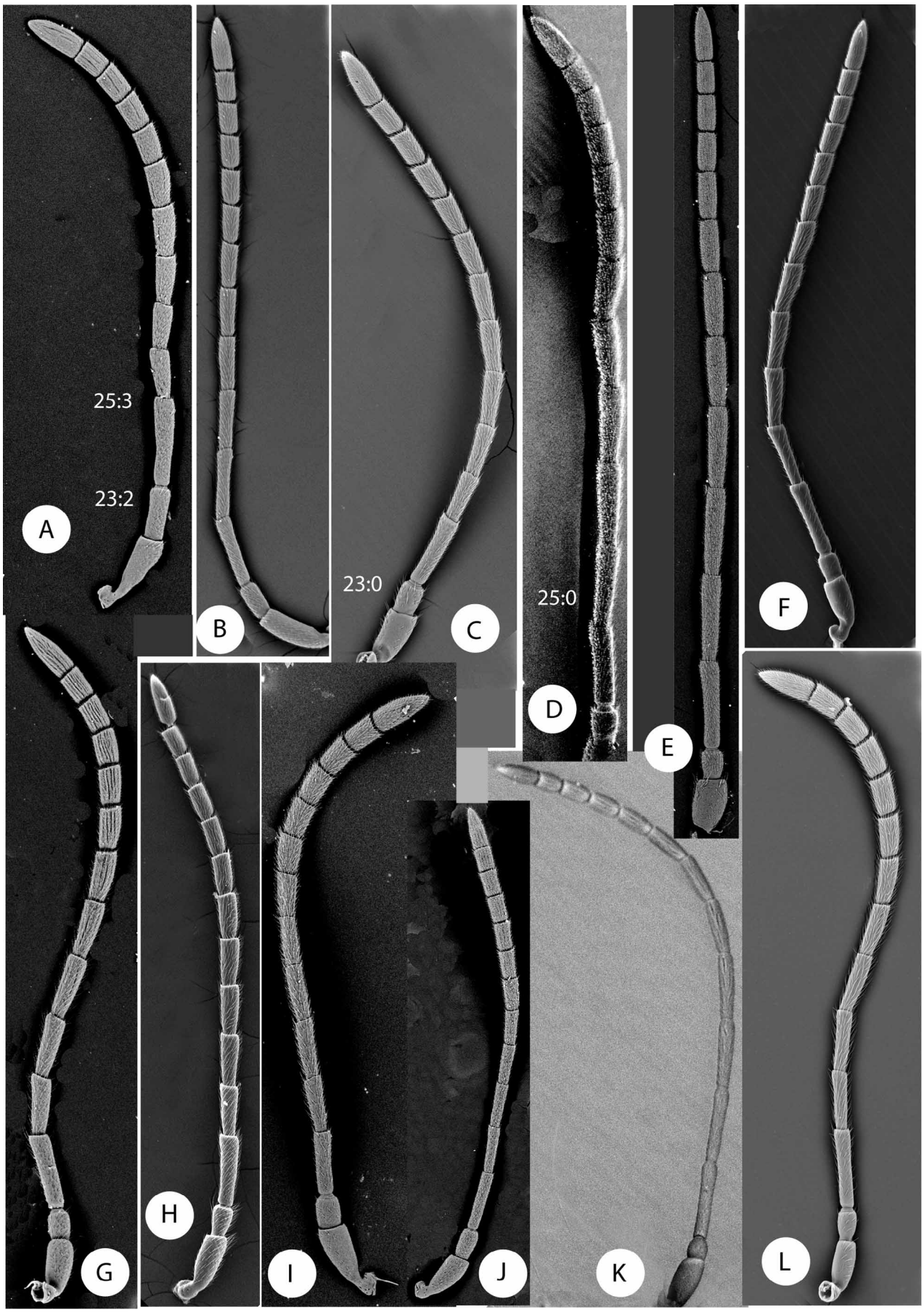

FIGURE 5. Female antennae of inquilines of oak gall wasps: (A) *Agastoroxenia panamensis.* (B) *Synergus laticephalus.* (C) *Synergus ramoni.* (D) *Synergus colombianus.* (E) *Synergus nicaraguensis.* (F) *Synergus baruensis*. (G) *Synergus luteus.* (H) *Synergus mesoamericanus.* (I) *Synergus chiricanus* (J) *Synergus elegans*. (K) *Synergus rufinotaulis*. (L) *Synergus gabrieli.*

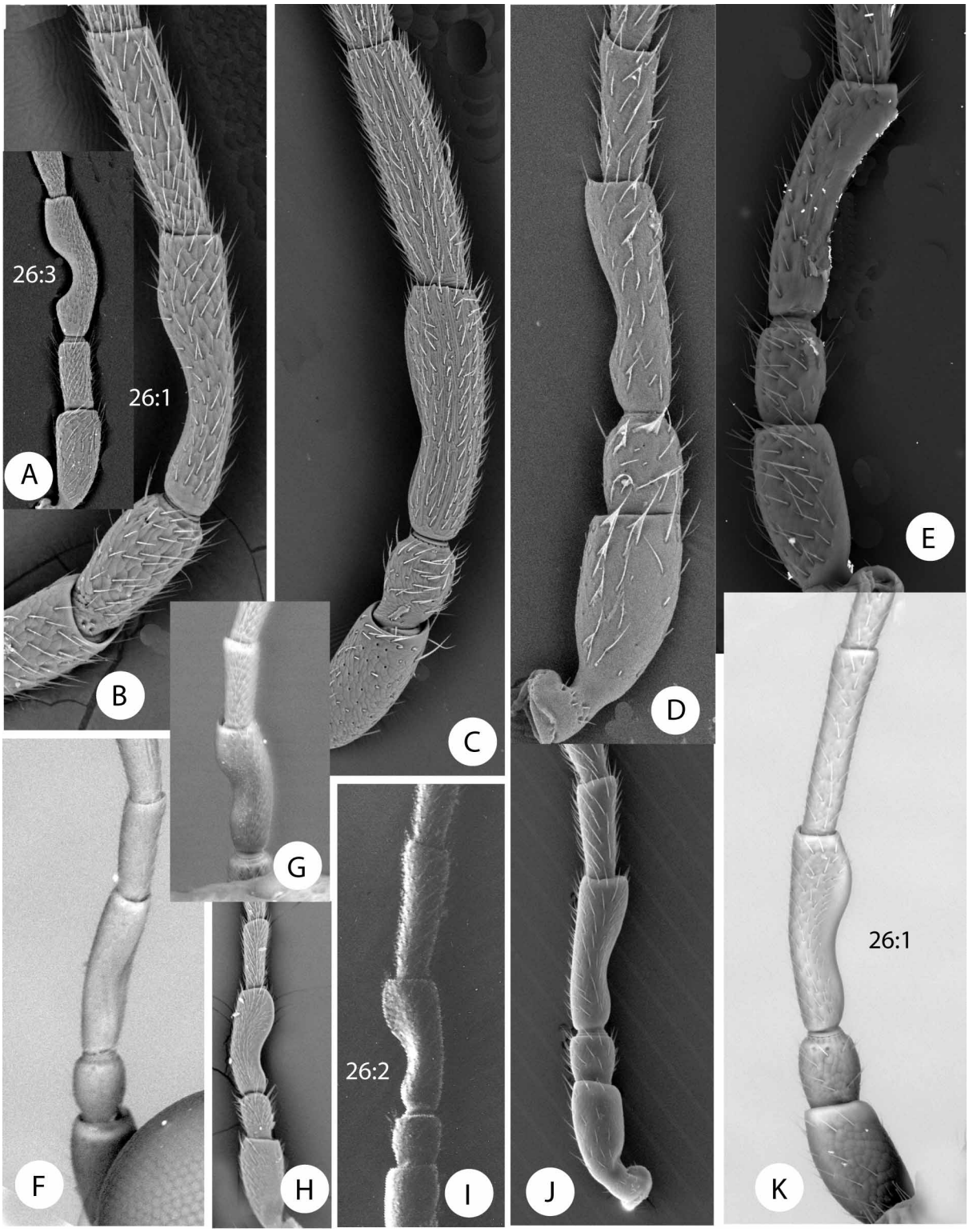

FIGURE 6. Male antennae of inquilines of oak gall wasps: (A) *Agastoroxenia panamensis*. (B) *Synergus elegans*. (C) *Synergus nicaraguensis*. (D) *Synergus chiricanus*. (E) *Synergus luteus*. (F) *Synergus gabrieli*. (G) *Synergus ramoni*. (H) *Synergus mesoamericanus*. (I) *Synergus colombianus*. (J) *Synergus baruensis*. (K) *Synergus rufinotaulis*.

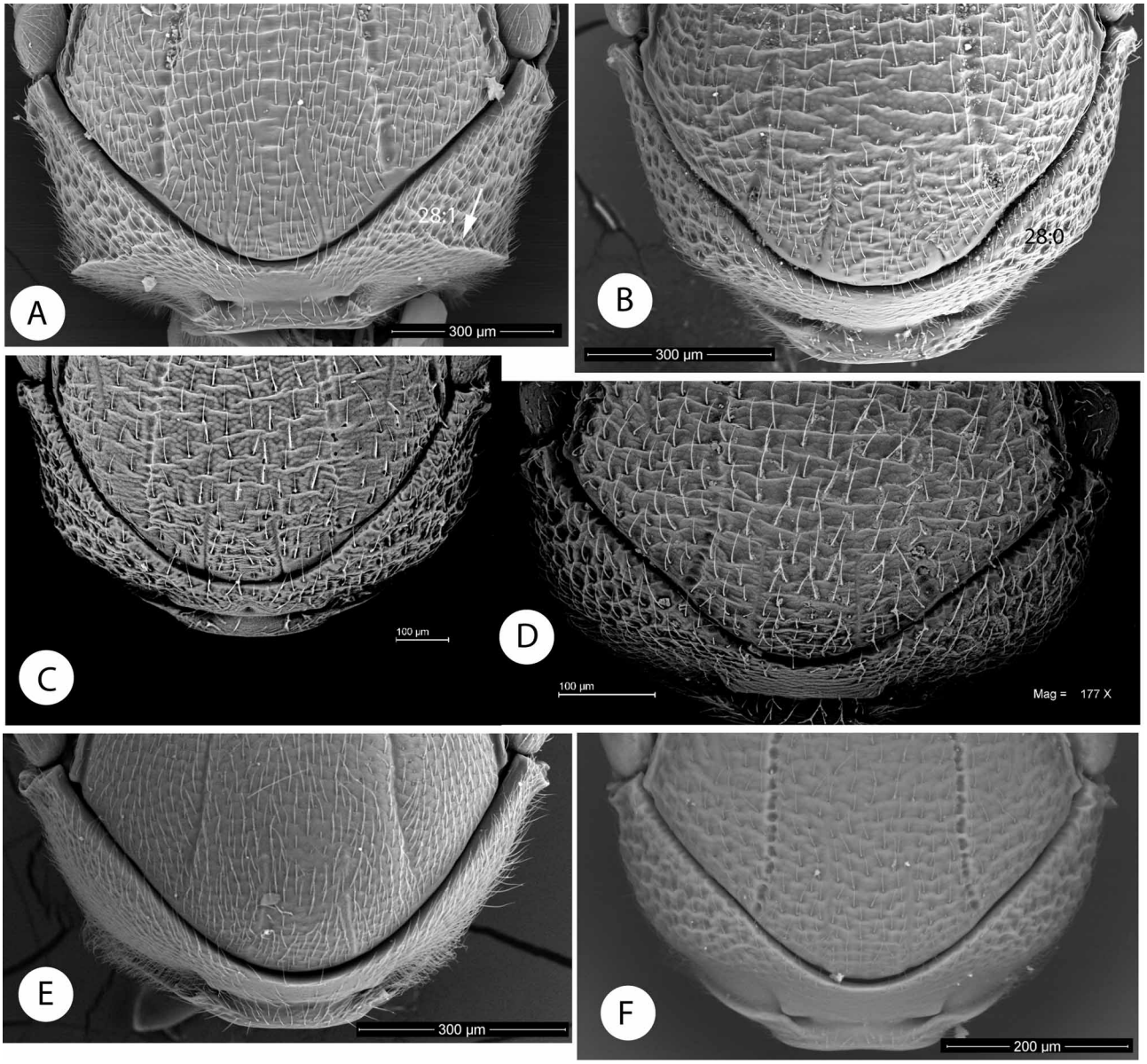

FIGURE 7. Pronotum anterior view of inquilines of oak gall wasps: (A) *Synergus ibericus*. (B) *Synergus ramoni.* (C) *Agastoroxenia panamensis*. (D) *Synergus chiricanus.* (E) *Synergus laticephalus.* (F) *Synergus gabrieli.*

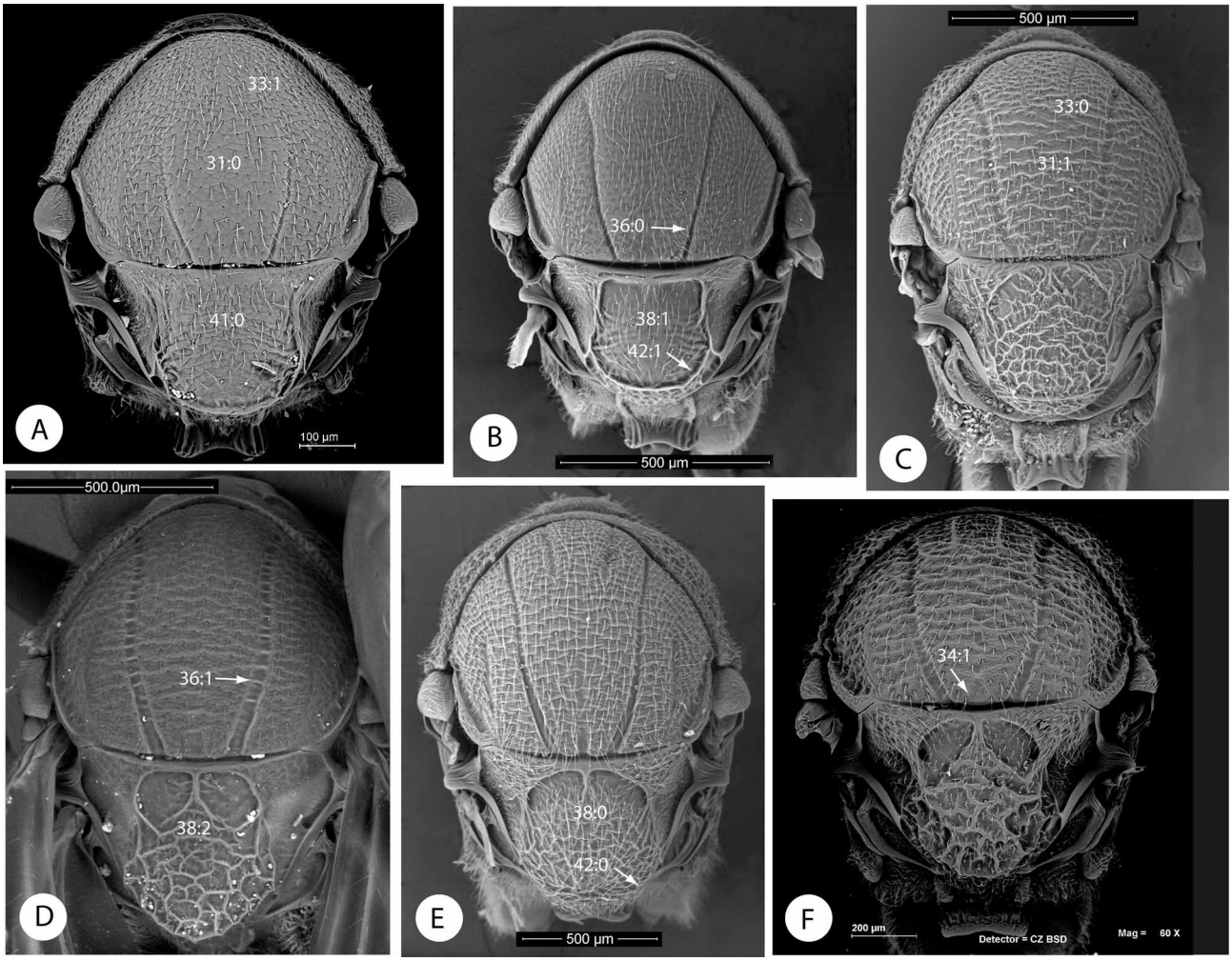

FIGURE 8. Mesosoma dorsal view of *Synergus* species: (A) *Synergus elegans*. (B) *Synergus laticephalus.* (C) *Synergus ramoni.* (D) *Synergus rufinotaulis.* (E) *Synergus mesoamericanus.* (F) *Synergus nicaraguensis.*

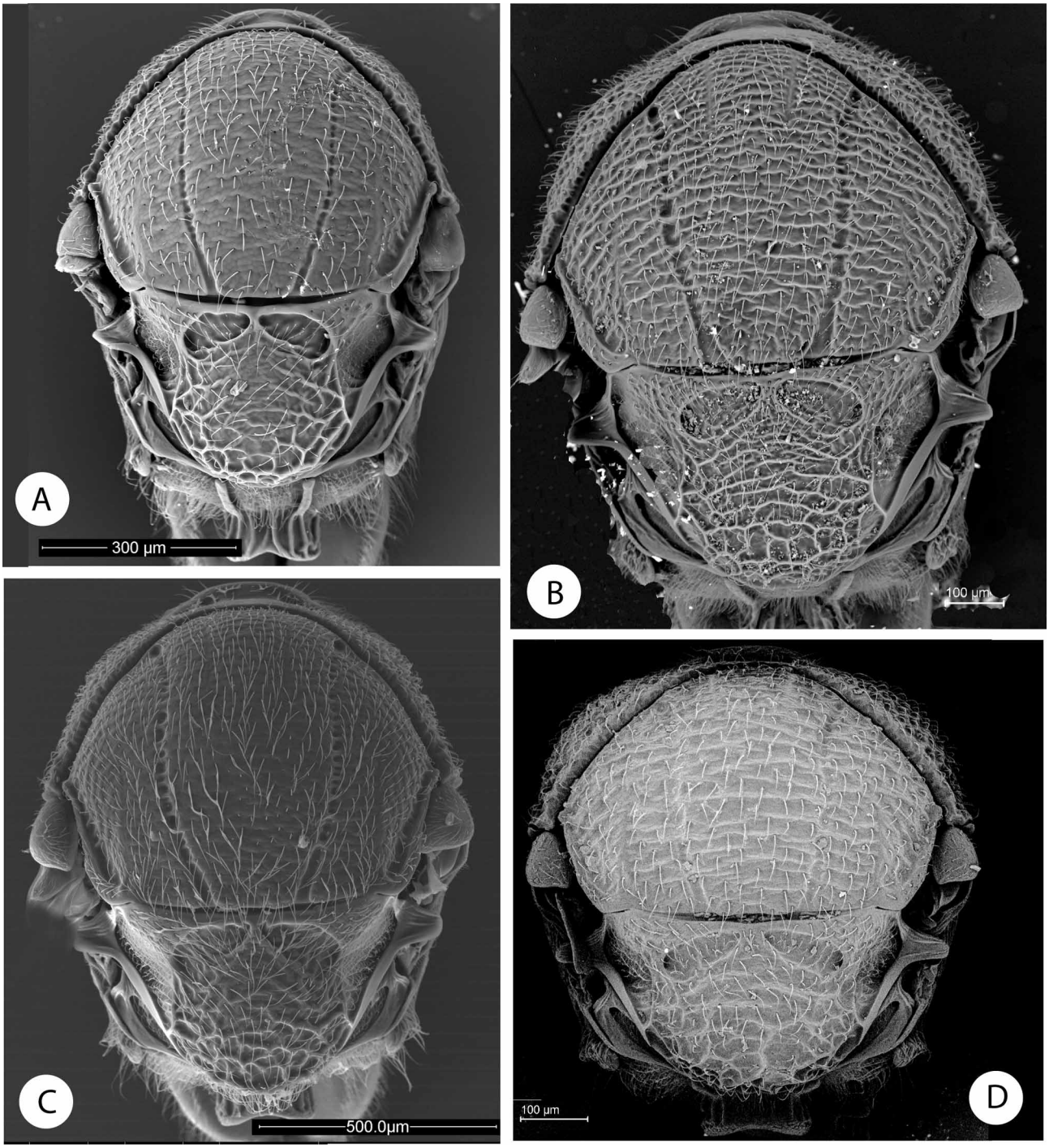

FIGURE 9. Mesosoma dorsal view of *Synergus* species: (A) *Synergus gabrieli*. (B) *Synergus luteus*. (C) *Synergus baruensis*. (D) *Synergus chiricanus*.

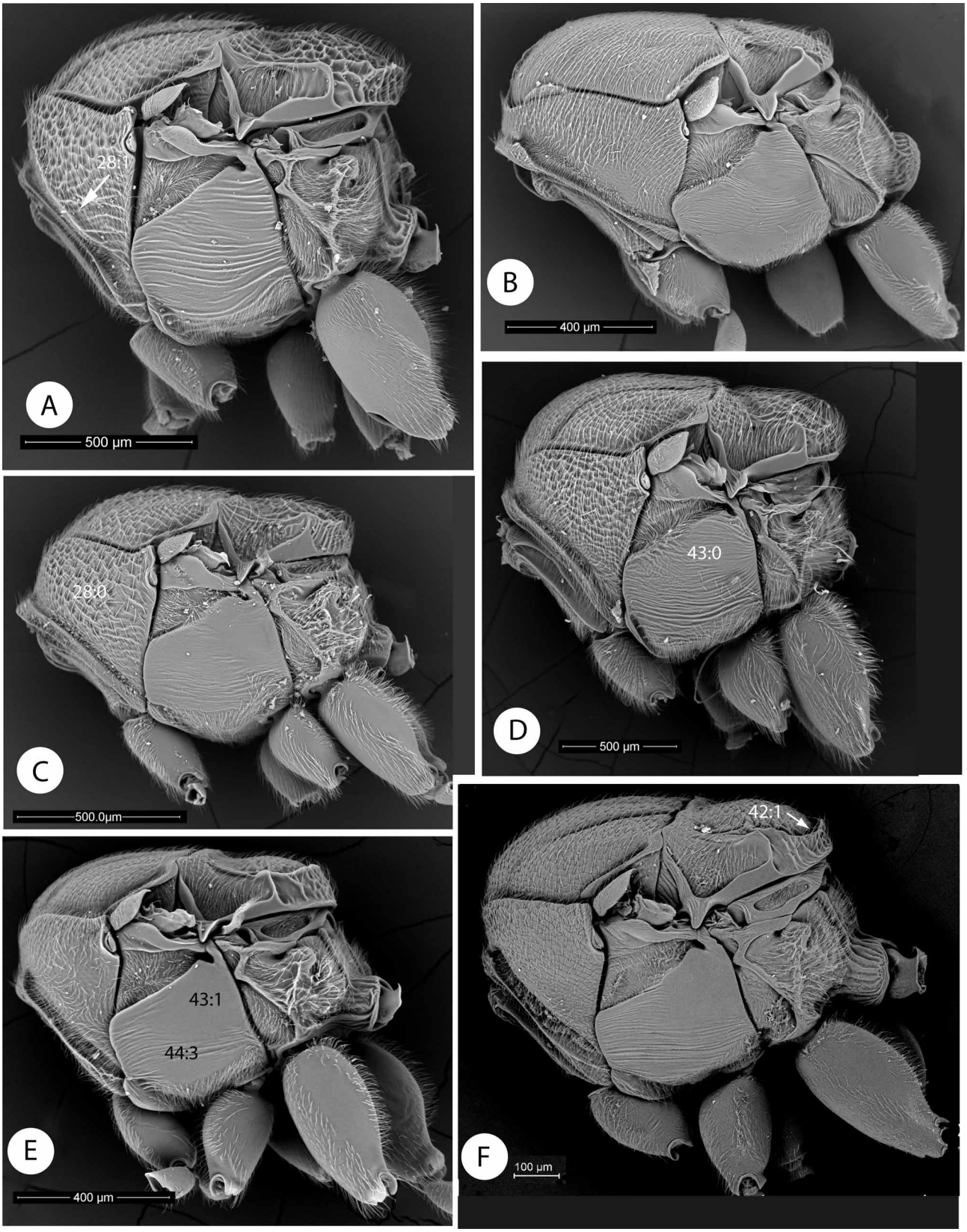

FIGURE 10. Mesosoma lateral view of inquilines of oak gall wasps: (A) *Synergus ibericus*. (B) *Saphonecrus lusitanicus.* (C) *Synergus ramoni.* (D) *Synergus mesoamericanus.* (E) *Synergus laticephalus.* (F) *Synergus elegans.*

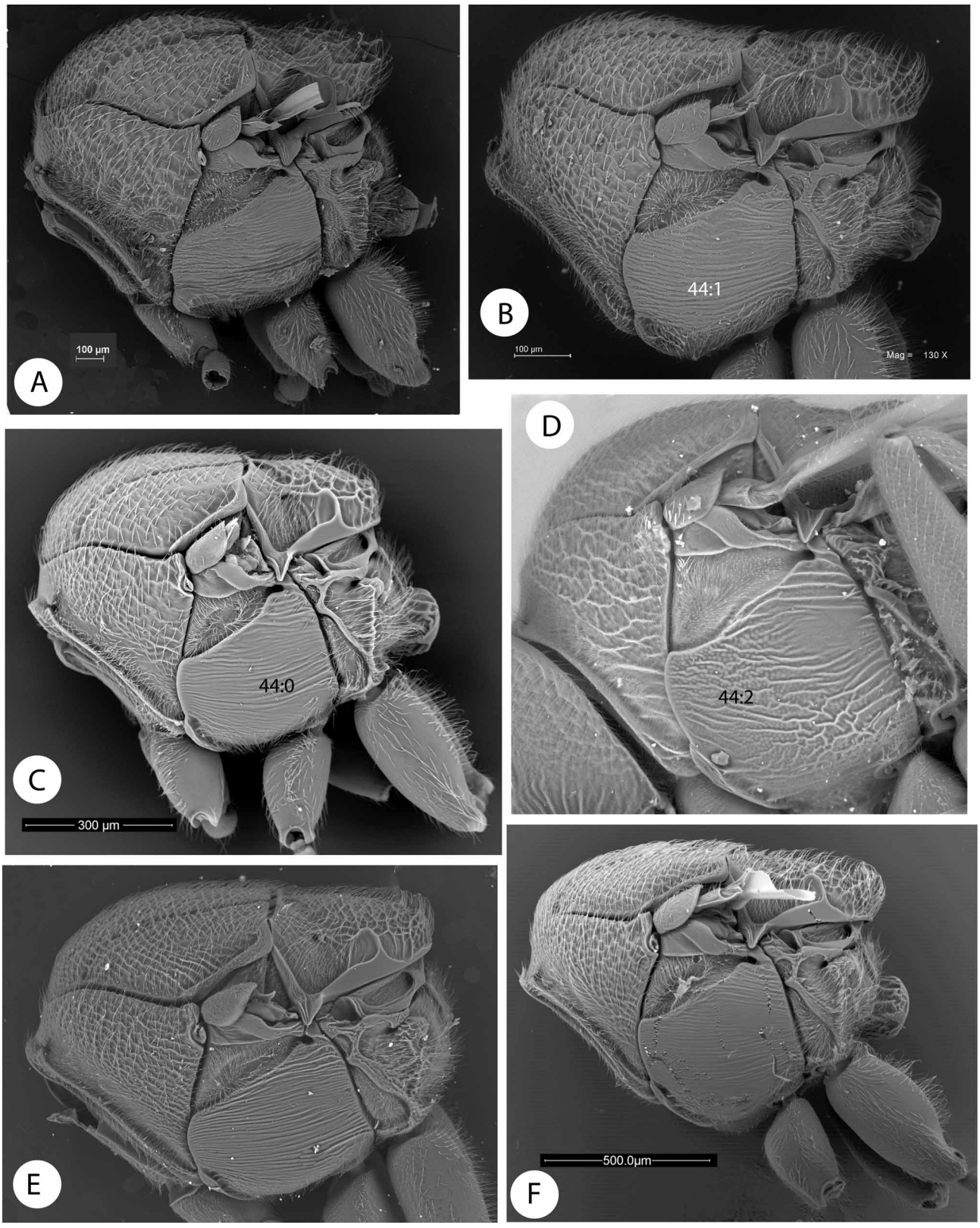

FIGURE 11. Mesosoma lateral view of inquilines of oak gall wasps: (A) *Synergus nicaraguensis*. (B) *Synergus chiricanus.* (C) *Synergus gabrieli.* (D) *Synergus rufinotaulis.* (E) *Synergus luteus.* (F) *Synergus baruensis.*

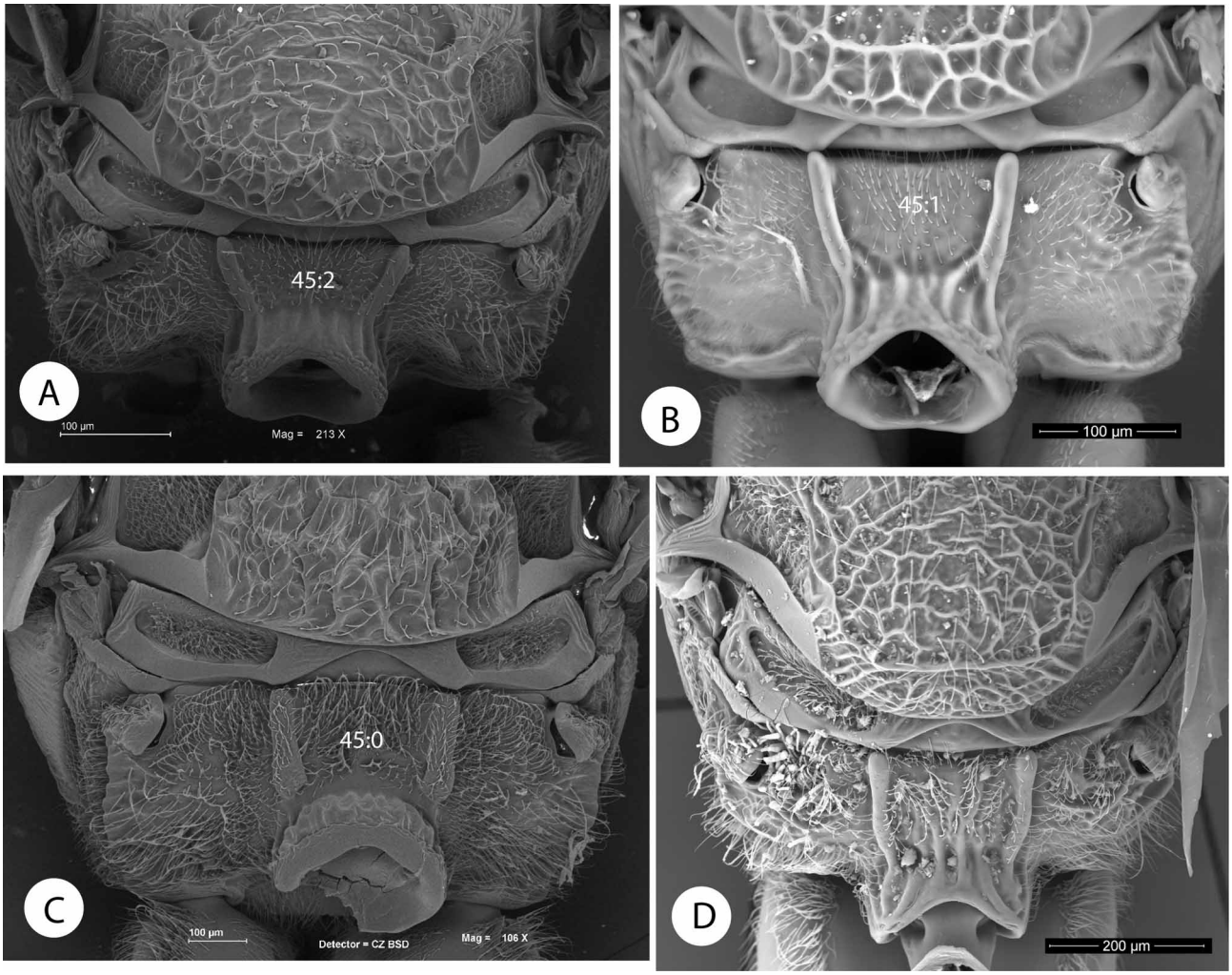

FIGURE 12. Propodeum posterior view of *Synergus* species: (A) *Synergus chiricanus*. (B) *Synergus gabrieli*. (C) *Synergus nicaraguensis*. (D) *Synergus ramoni*.

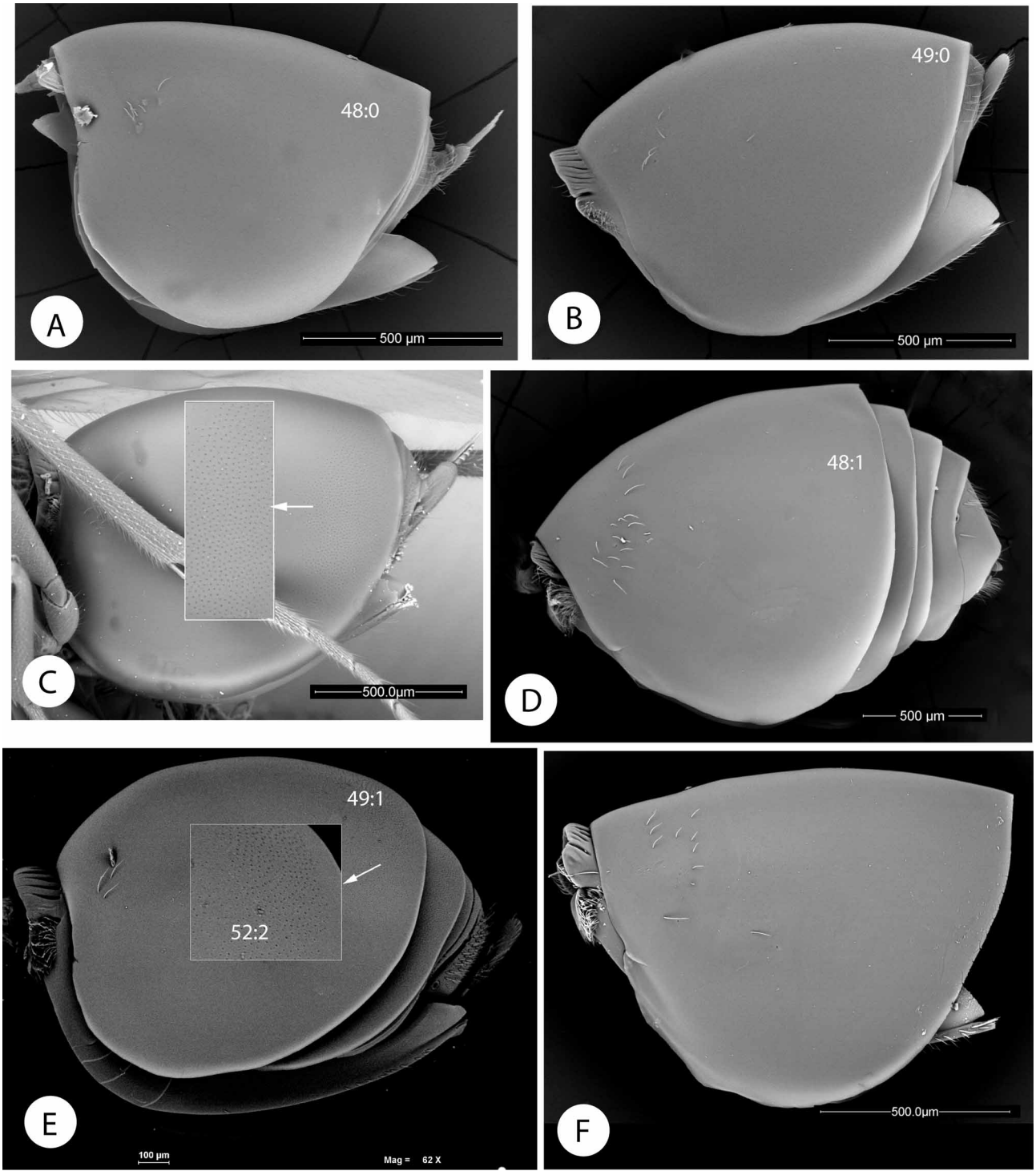

FIGURE 13. Metasoma lateral view of *Synergus* species: (A) *Synergus elegans*. (B) *Synergus laticephalus.* (C) *Synergus rufinotaulis.* (D) *Synergus mesoamericanus.* (E) *Synergus nicaraguensis.* (F) *Synergus ramoni.*

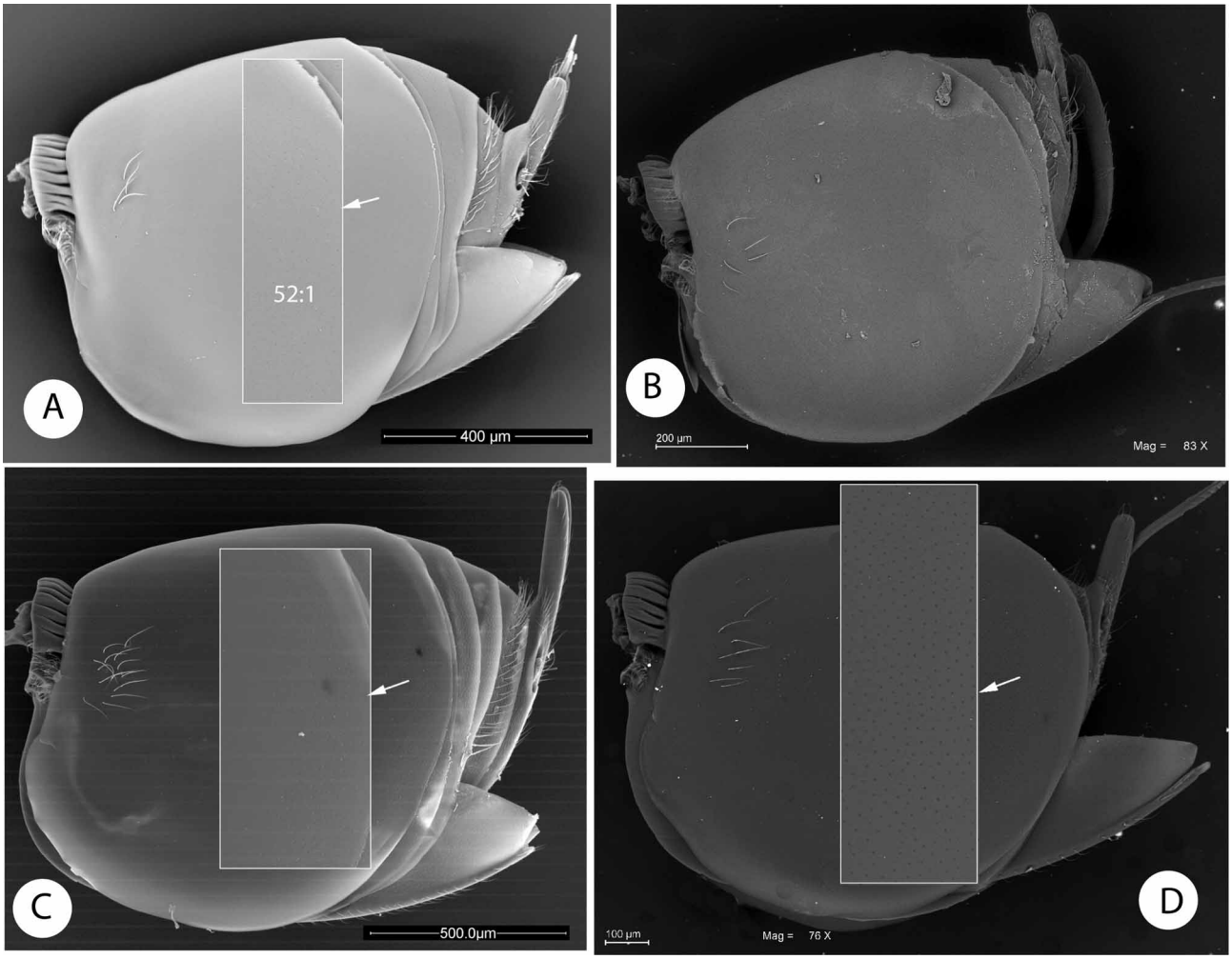

FIGURE 14. Metasoma lateral view of *Synergus* species: (A) *Synergus gabrieli*. (B) *Synergus chiricanus.* (C) *Synergus baruensis.* (D) *Synergus luteus.*

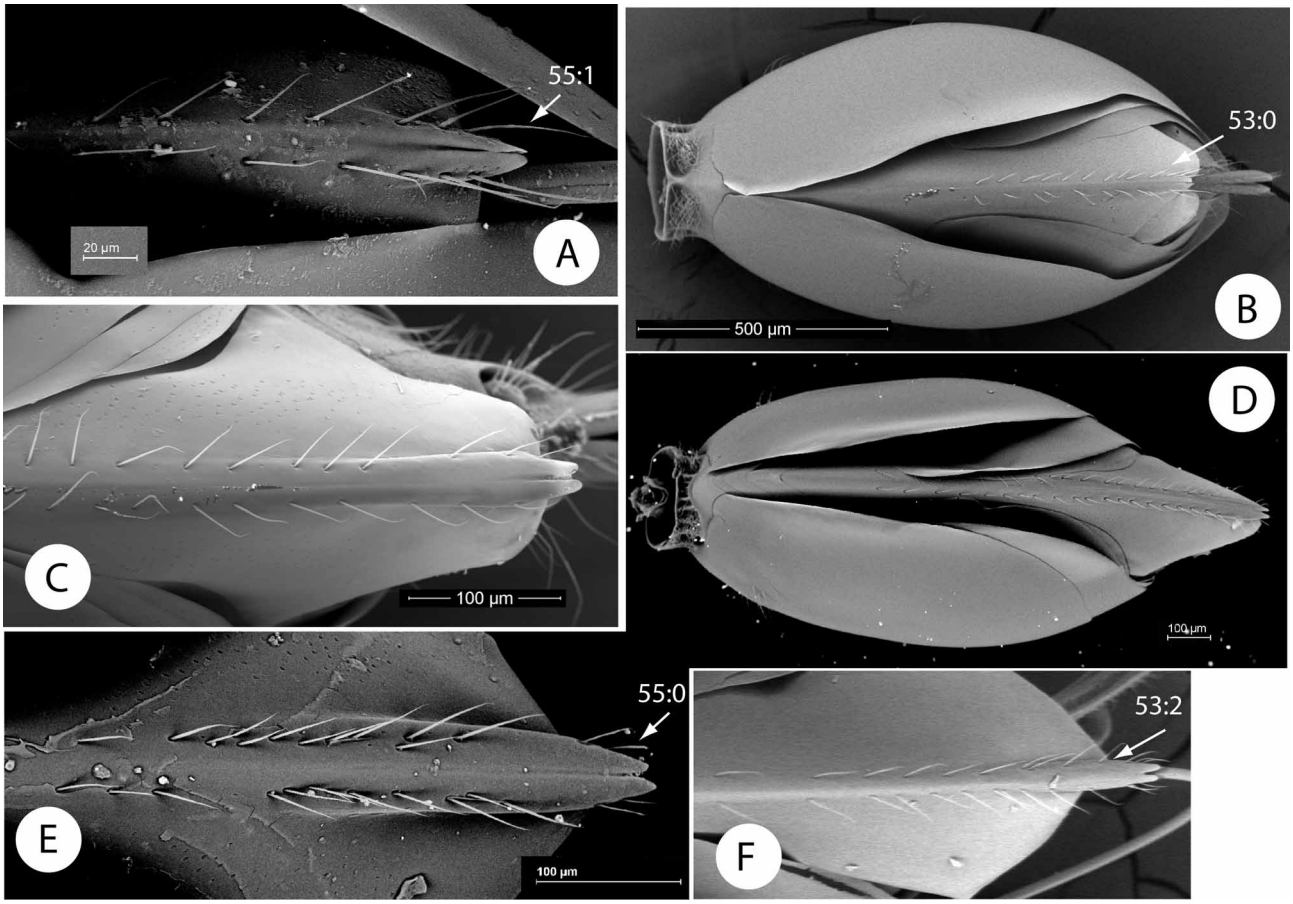

FIGURE 15. Hypopygium ventral view of *Synergus* species: (A) *Synergus elegans*. (B) *Synergus laticephalus*. (C) *Synergus gabrieli*. (D) *Synergus luteus*. (E) *Synergus nicaraguensis*. (F) *Synergus mesoamericanus*.

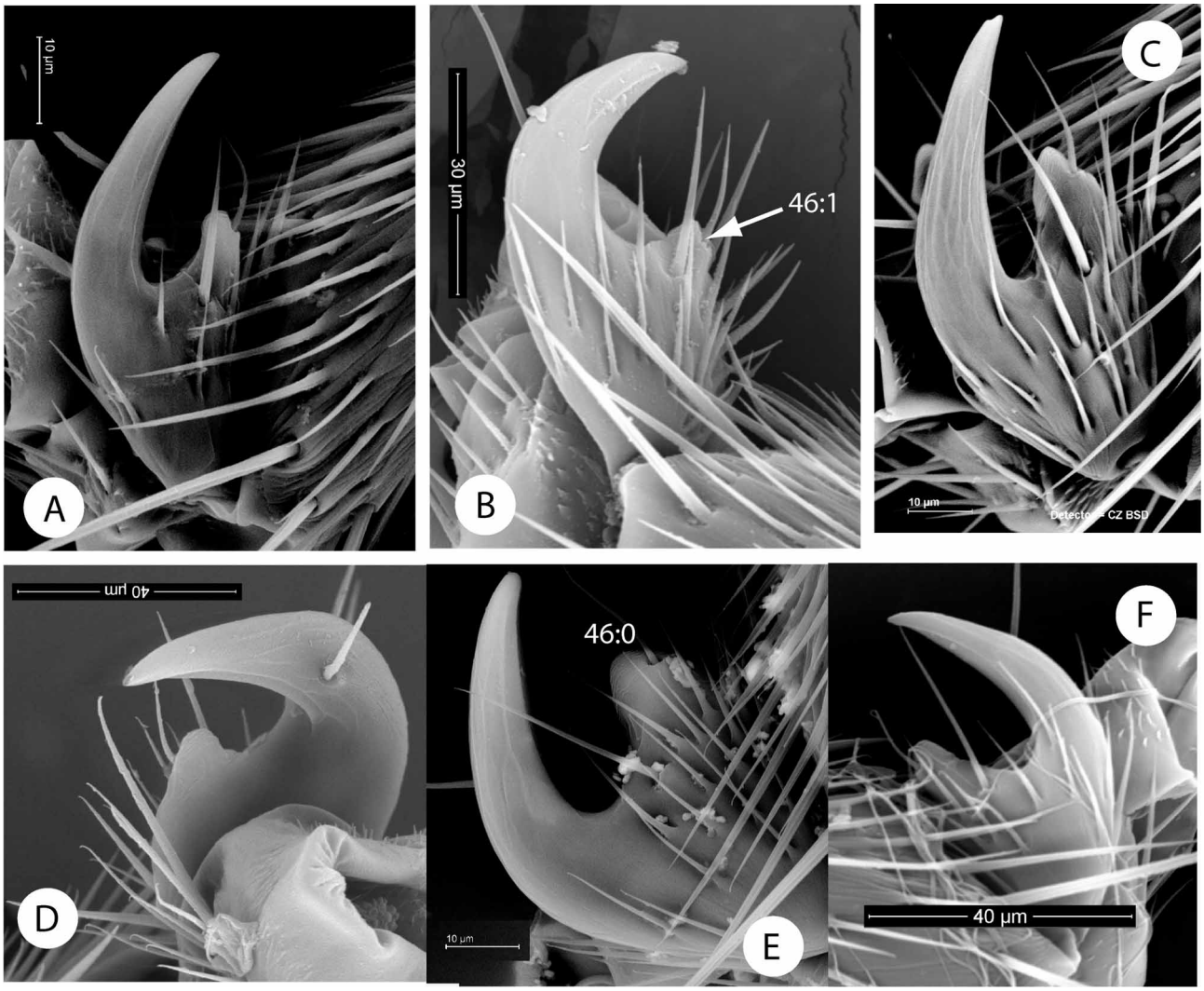

FIGURE 16. Metatarsal claws of *Synergus* species: (A) *Synergus elegans*. (B) *Synergus ramoni.* (C) *Synergus nicaraguensis.* (D) *Synergus mesoamericanus.* (E) *Synergus luteus.* (F) *Synergus gabrieli.*

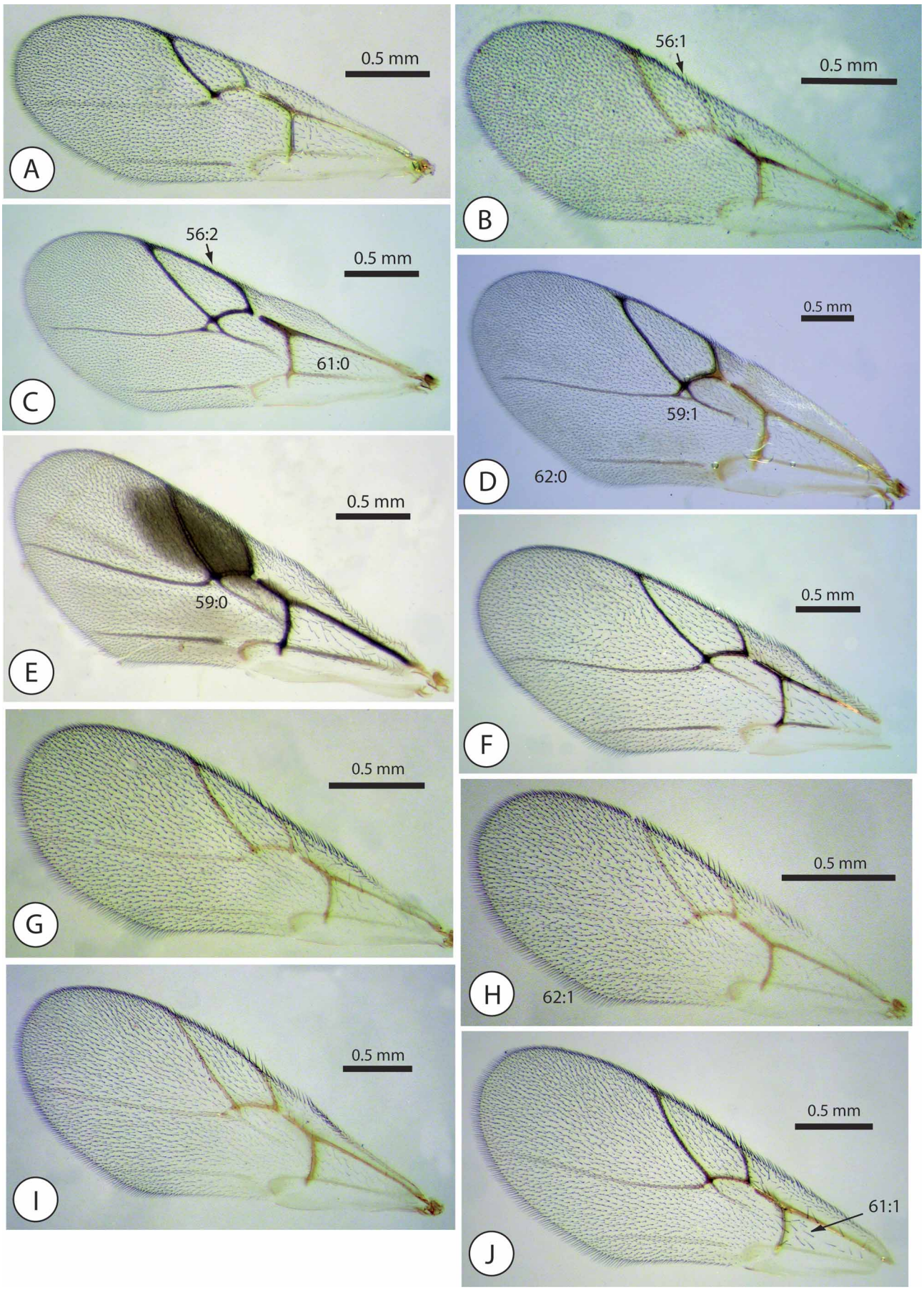

FIGURE 17. Forewing of *Synergus* species: (A) *Synergus laticephalus*. (B) *Synergus elegans*. (C) *Synergus ramoni* (D) *Synergus mesoamericanus*. (E) *Synergus nicaraguensis*. (F) *Synergus rufinotaulis*. (G) *Synergus gabrieli*. (H) *Synergus chiricanus*. (I) *Synergus luteus*. (J) *Synergus baruensis*.

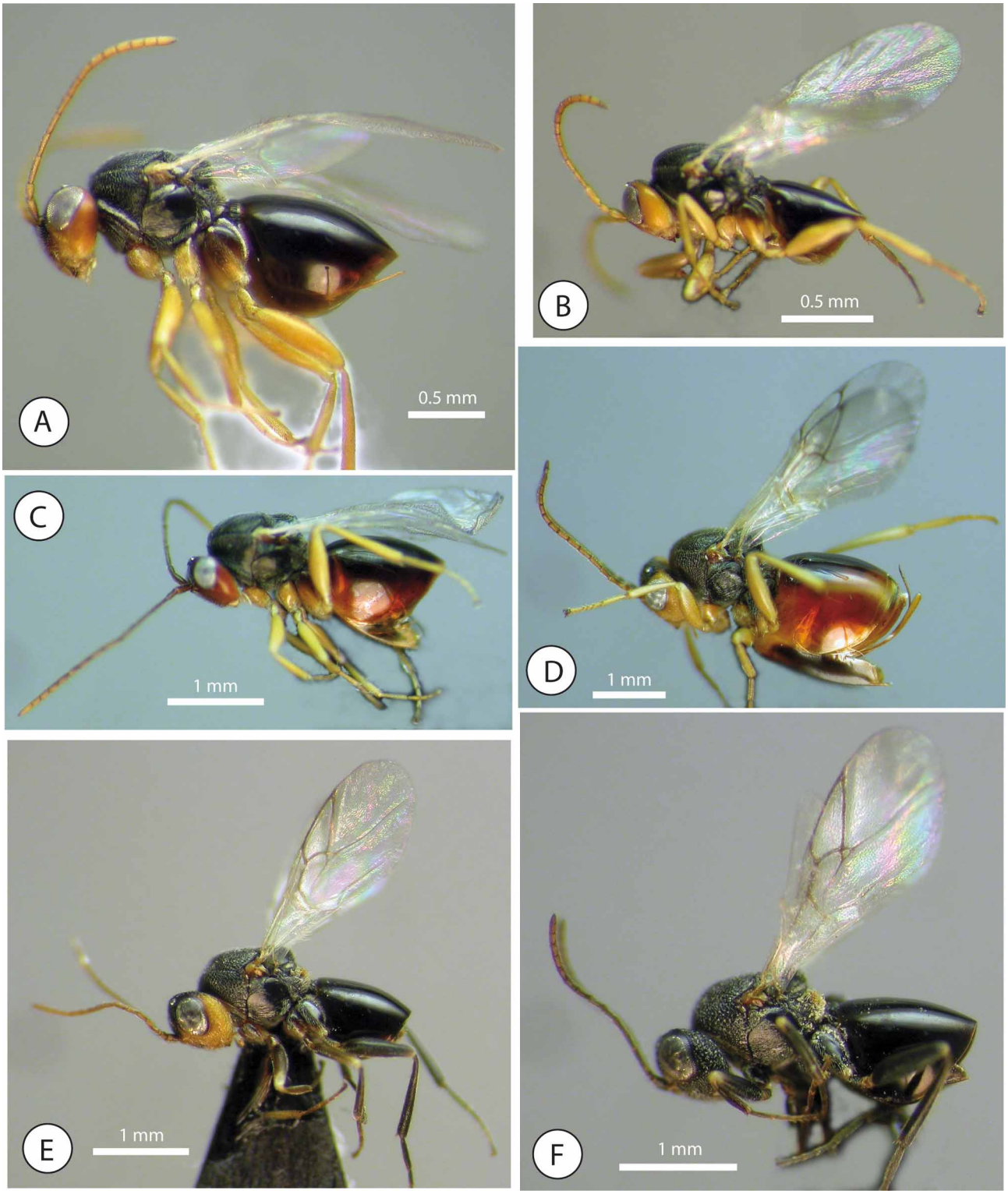

FIGURE 18. Habitus of *Synergus* species: (A) *Synergus elegans*, female. (B) *Synergus elegans*, male. (C) *Synergus laticephalus*, female. (D) *Synergus mesoamericanus*, female (E) *Synergus ramoni*, male. (F) *Synergus ramoni*, female.

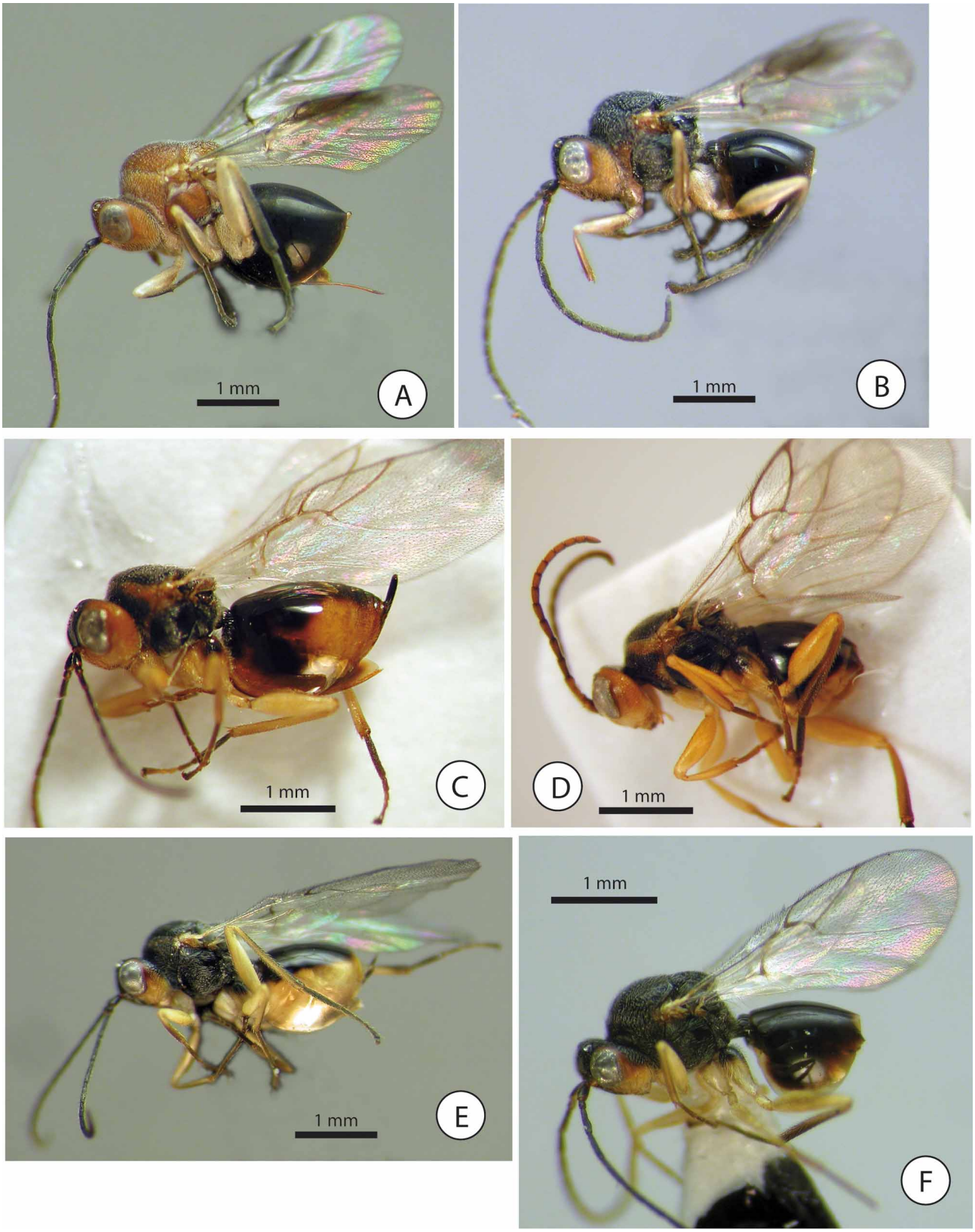

FIGURE 19. Habitus of *Synergus* species: (A) *Synergus nicaraguensis*, female. (B) *Synergus nicaraguensis*, male. (C) *Synergus colombianus*, female. (D) *Synergus colombianus*, male. (E) *Synergus rufinotaulis*, female. (F) *Synergus rufinotaulis*, male.

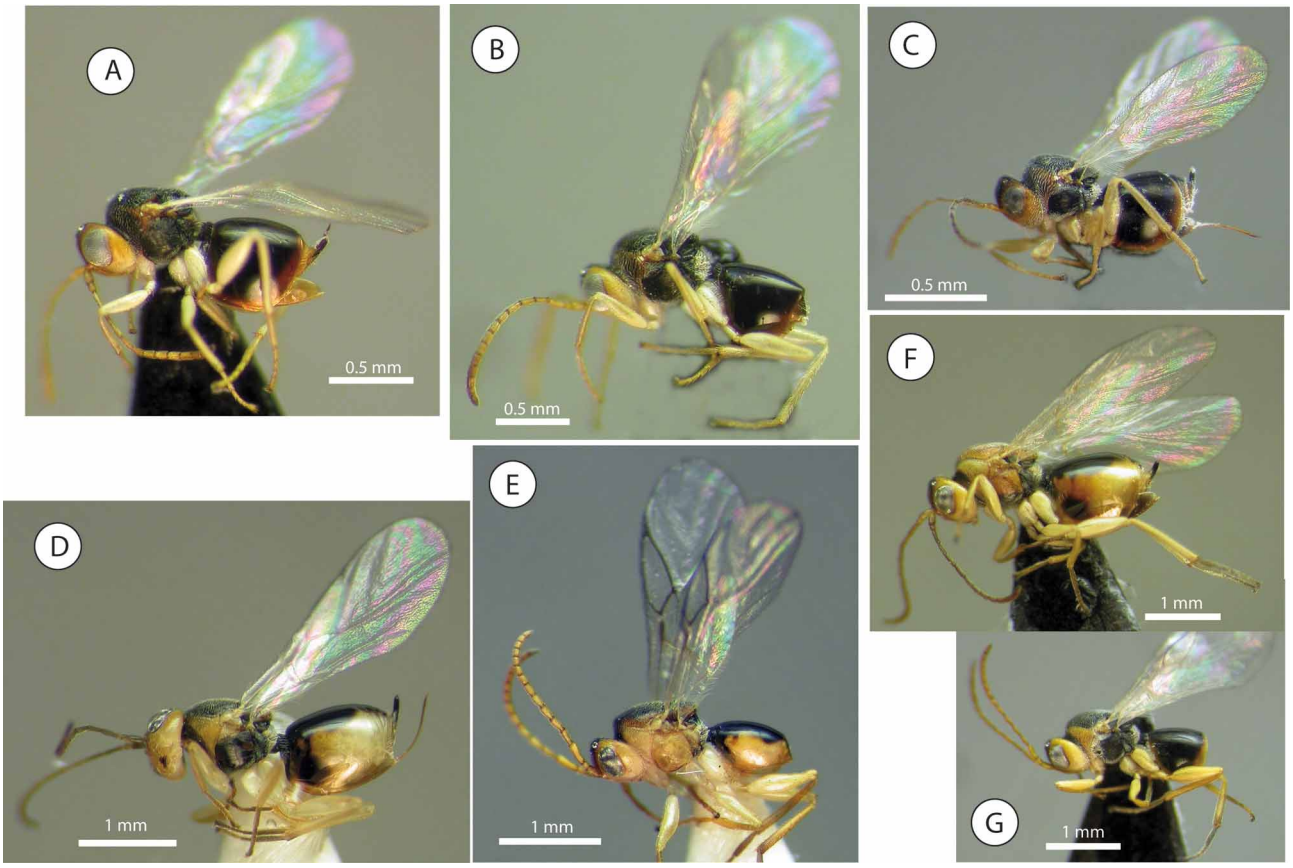

FIGURE 20. Habitus of *Synergus* species: (A) *Synergus gabrieli*, female. (B) *Synergus gabrieli*, male. (C) *Synergus chiricanus*, female. (D) *Synergus baruensis*, female. (E) *Synergus baruensis*, male. (F) *Synergus luteus*, female. (G) *Synergus luteus*, male.

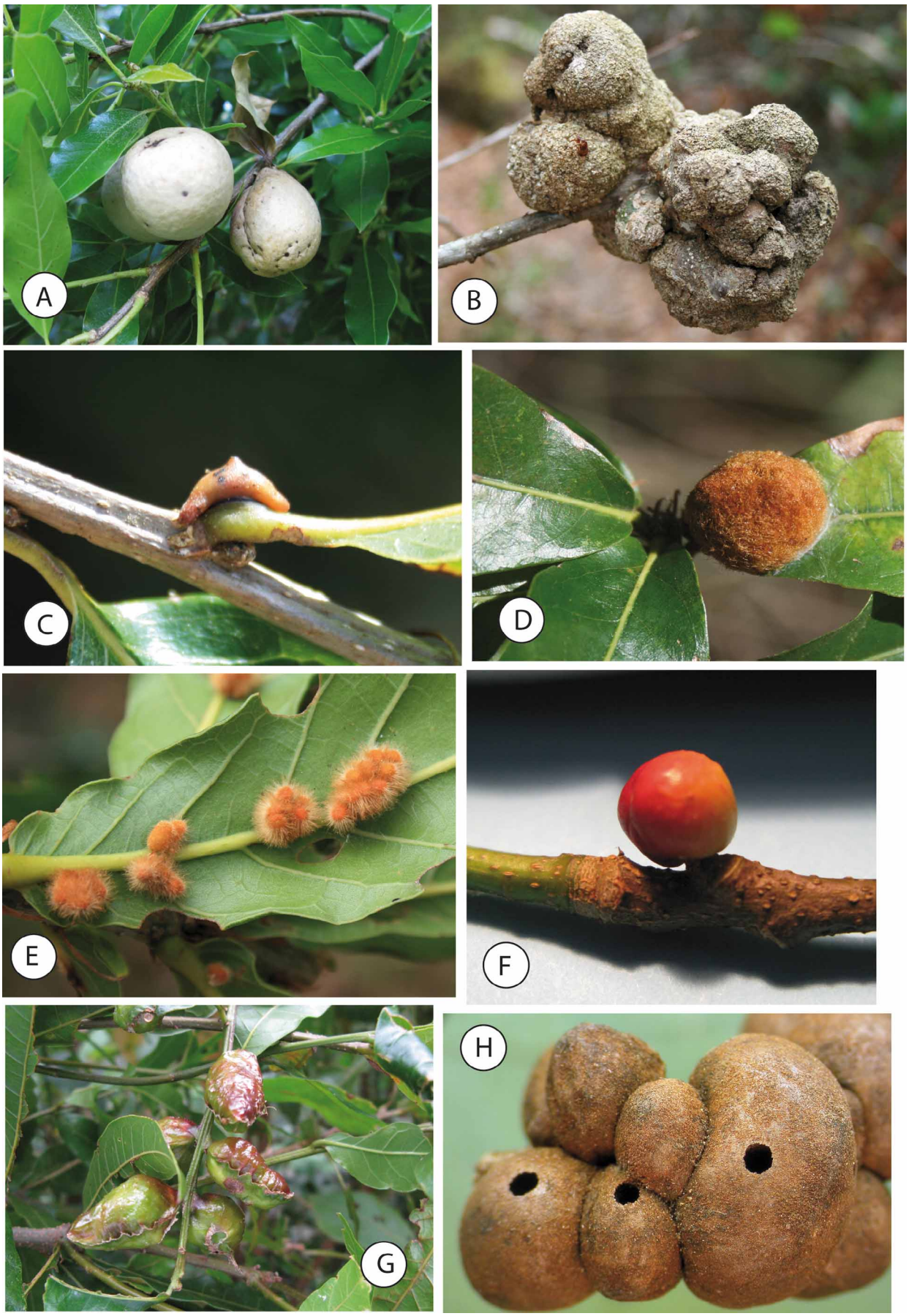

FIGURE 21. Host galls of *Synergus* species from Panama: (A) *Amphibolips castroviejoi*. (B) *Andricus championi*. (C) *Trigonaspis sp. indet.*, female?. (D) *Andricus guatemalensis*. (E) *Neuroterus sp. nov.* (F) *gen. sp. indet.* (G) *Callirhytis sp. nov.* (H) *Disholcaspis sp. nov.*

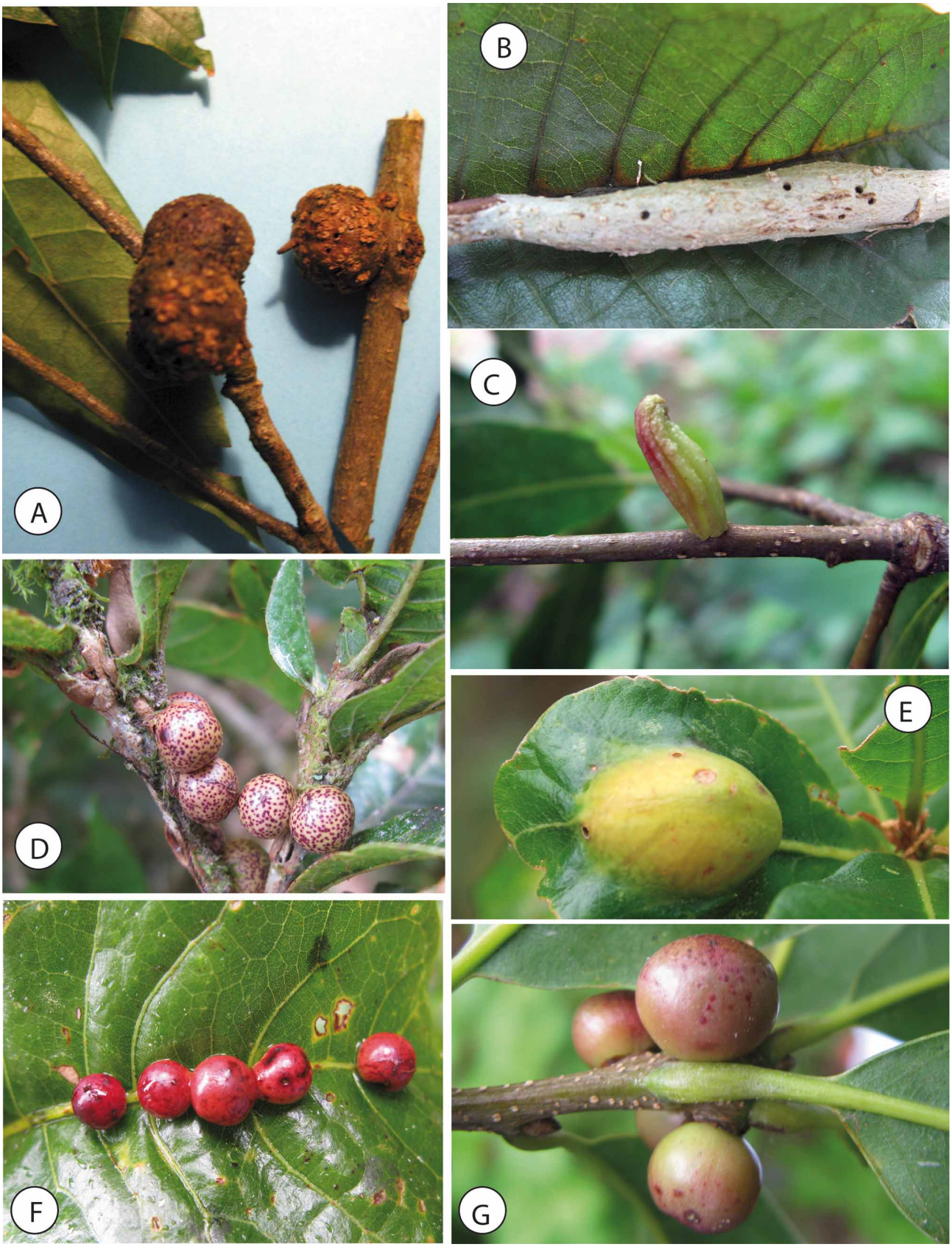

FIGURE 22. Host galls of *Synergus* species from Panama: (A) unidentified cynipid genus on twigs of *Quercus salicifolia*, (B) undescribed species of *Loxaulus* or *Bassettia* genera on *Quercus bumelioides*, (C) gall of an unidentified genus, (D) *Cynips sp. nov.*, (E) *Neuroterus sp. nov.*, (F) *Cynips sp. nov.*, (G) unidentified cynipid genus on *Quercus salicifolia*.

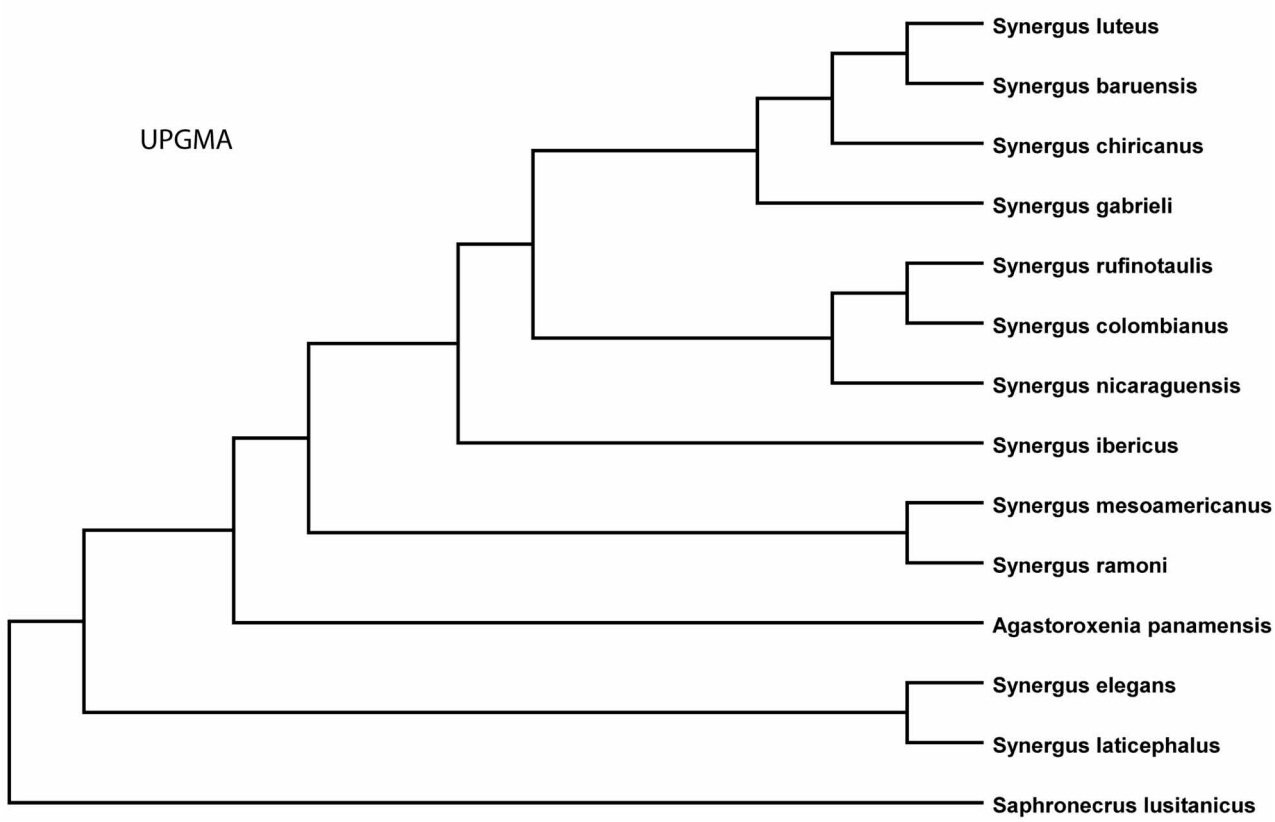

FIGURE 23. Overall similarity phenogram of a UPGMA tree (cluster analysis, unweighted pair group method analysis).

TABLE 1. Data matrix based on the characters listed in Appendix 1. "?" indicates missing data; "-" is used if the character is inapplicable.

	Characters			
Species	1	11	21	31
Synergus elegans	2 0 0 0 0 0 0 - 1 1	1 0 0 0 0 0 1 2 0 0	1 0 0 1 1 1 0 0 0 0	0 - 1 0 - 0 0 1 2 1
Synergus laticephalus	2 0 1 0 0 0 0 - 1 1	1 1 0 0 0 0 1 3 0 0	1 1 1 1 0 ? ? 0 0 0	0 - 0 0 - 0 0 1 2 1
Synergus mesoamericanus	0 0 0 0 1 1 1 0 0 1	2 0 1 1 2 2 0 2 1 1	1 1 0 2 2 2 0 0 1 0	1 0 0 1 0 1 1 0 0 0
Synergus ramoni	0 0 0 0 1 1 1 0 0 1	2 0 0 1 2 2 1 1 1 1	1 1 0 2 2 2 0 0 1 0	1 0 0 0 - 1 1 0 0 0
Synergus nicaraguensis	2 0 0 0 1 0 1 2 0 0	0 0 1 1 2 2 1 1 1 1	1 2 0 3 0 1 0 0 1 0	1 1 0 1 0 1 1 0 0 0
Synergus luteus	1 1 1 0 1 0 1 1 0 0	0 0 1 1 1 1 1 1 1 1	1 1 0 2 1 1 0 0 1 0	1 0 0 0 - 1 1 0 0 0
Synergus baruensis	1 1 0 0 1 0 1 2 0 0	1 0 1 1 1 1 1 1 1 1	1 1 0 3 1 1 0 0 1 0	0 - 0 0 - 1 1 0 1 0
Synergus gabrieli	1 0 1 0 1 0 1 1 0 0	1 0 0 1 1 1 1 1 1 1	1 0 1 2 1 1 0 0 1 0	1 1 0 0 - 1 1 0 1 0
Synergus chiricanus	1 1 0 0 1 0 1 2 0 0	1 0 1 1 1 2 1 1 1 1	1 1 0 1 0 1 0 0 1 0	1 1 0 0 - 1 1 0 0 0
Synergus rufinotaulis	1 0 1 0 1 0 1 1 0 0	0 0 1 1 2 1 1 1 1 1	1 2 0 3 0 1 0 0 1 0	1 1 0 1 0 1 1 2 1 0
Synergus colombianus	1 0 0 0 1 0 1 1 0 0	0 0 1 1 1 1 1 2 1 1	1 1 0 1 0 2 0 0 1 0	1 0 0 1 0 1 1 0 1 0
Synergus ibericus	1 0 0 0 1 0 1 2 0 0	0 0 1 1 2 2 2 0 1 1	1 1 0 3 0 1 0 1 1 0	1 0 0 1 1 1 1 0 2 0
Agastoroxenia panamensis	1 2 1 0 2 1 1 0 0 0	1 0 1 1 2 2 1 1 1 1	0 0 2 0 3 3 2 0 1 0	1 1 1 0 - 1 1 0 0 0
Saphonecrus lusitanicus	1 0 0 1 0 0 0 - 0 0	0 0 0 0 0 1 2 1 0 0	0 0 2 0 1 0 1 0 0 1	0 0 1 0 - 0 0 0 0 1

	Characters		
Species	41	51	61
Synergus elegans	1 1 1 3 0 1 2 0 0 1	0 - 1 1 1 1 0 1 0 0	0 0 2 1 2
Synergus laticephalus	1 1 1 3 0 1 3 0 0 1	0 - 0 1 1 1 0 1 0 0	0 0 1 1 0
Synergus mesoamericanus	0 0 0 1 1 ? 2 1 0 0	0 - 2 1 0 2 0 1 1 2	0 0 0 0 0
Synergus ramoni	0 0 1 2 0 1 2 0 0 1	0 - 1 1 0 2 0 2 1 2	0 0 1 1 0
Synergus nicaraguensis	0 0 0 1 0 0 3 1 1 0	1 2 0 1 0 2 1 0 0 2	1 0 0 1 0
Synergus luteus	0 0 0 0 1 0 1 0 1 0	1 2 0 1 0 1 0 2 0 1	1 1 0 0 1
Synergus baruensis	0 0 0 0 1 0 1 1 1 0	1 1 0 1 0 2 0 2 0 1	1 1 1 0 0
Synergus gabrieli	0 0 0 0 1 1 3 1 1 0	1 0 1 1 0 1 0 2 0 0	1 1 0 1 1
Synergus chiricanus	0 0 0 1 2 0 3 1 1 0	1 1 0 1 0 1 0 1 0 0	1 1 0 0 0
Synergus rufinotaulis	0 0 0 1 1 0 1 0 1 0	1 2 1 1 0 2 0 2 0 1	1 1 0 1 1
Synergus colombianus	0 0 0 0 1 0 1 1 1 0	1 2 1 1 0 2 0 1 0 1	1 0 1 1 0
Synergus ibericus	0 0 0 0 0 0 0 0 0 1	1 2 0 1 0 2 0 1 0 1	0 0 0 1 0
Agastoroxenia panamensis	0 0 0 1 0 1 4 0 0 0	0 - 1 0 0 0 0 1 0 1	1 0 0 0 0
Saphonecrus lusitanicus	1 0 0 0 0 ? 1 0 0 0	1 0 2 0 1 0 0 1 0 0	0 0 3 0 2