Zootaxa 5081 (2): 203–222
https://www.mapress.com/j/zt/
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Article

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

https://doi.org/10.11646/zootaxa.5081.2.2
http://zoobank.org/urn:lsid:zoobank.org:pub:CF7094EB-5966-422E-AECF-FE0E4371974D

A new genus of Neotropical oak gall wasp, *Prokius* Nieves-Aldrey, Medianero & Nicholls, gen. nov. (Hymenoptera: Cynipidae: Cynipini), with description of two new species from Panama

ENRIQUE MEDIANERO[1,5], JAMES A. NICHOLLS[2,6], GRAHAM N. STONE[3,7]
& JOSÉ LUIS NIEVES-ALDREY[4,8*]
[1]*Universidad de Panamá, Departamento de Ciencias Ambientales, Facultad de Ciencias Naturales, Exactas y Tecnología & Programa Centroamericano de Maestría en Entomología, Vicerrectoría de Investigación y Postgrado. C. P. 0824. enrique.medianero@up.ac.pa*
[2]*CSIRO, Australian National Insect Collection, Clunies Ross Street, Acton, ACT 2601, Australia. Email: james.nicholls@csiro.au*
[3]*Institute of Evolutionary Biology, University of Edinburgh, King's Buildings, Charlotte Auerbach Road, Edinburgh EH9 3JT, Scotland, U.K.*
[4]*Museo Nacional de Ciencias Naturales (CSIC), Departamento de Biodiversidad y Biología Evolutiva, C/ José Gutiérrez Abascal 2, ES-28006 Madrid, Spain.*
[5] *enrique.medianero@up.ac.pa; https://orcid.org/0000-0002-8430-9034*
[6] *james.nicholls@csiro.au; https://orcid.org/0000-0002-9325-563X*
[7] *graham.stone@ed.ac.uk; https://orcid.org/0000-0002-2737-696X*
[8] *aldrey@mncn.csic.es; https://orcid.org/0000-0002-4711-7455*
**Corresponding author*

ABSTRACT

A new genus, *Prokius* Nieves Aldrey, Medianero & Nicholls, gen. nov., and two new species of oak gall wasps (Hymenoptera: Cynipidae: Cynipini), *Prokius cambrai* Medianero & Nieves-Aldrey sp. nov. and *Prokius lisethiae* Medianero & Nieves-Aldrey sp. nov., are described from adults reared from galls on *Quercus bumelioides* Liebm (Fagaceae, sect. Quercus, white oaks) collected in Panama. The new genus is phylogenetically and morphologically close to *Dros* Kinsey and forms part of a large clade that includes species from several other genera that appear to require revision, including *Andricus* Hartig and *Phylloteras* Ashmead. Molecular and morphological data, diagnostic characters, gall descriptions, distribution and biological data of the new genus and the new species are given. This new genus represents the fourth recently described genus of Cynipidae endemic to the Neotropical region.

KEYWORDS: Cynipidae, oak gall wasps, phylogeny, *Quercus*, Chiriquí, Panama, white oaks

INTRODUCTION

Species in the family Cynipidae, one of the two largest families included in the Cynipoidea (Insecta: Hymenoptera), are biologically peculiar because all their representatives are associated with plant galls. They either induce the galls themselves or live inside galls caused by other insects, most frequently other cynipids but also chalcidoids and Lepidoptera (Nieves-Aldrey 2001; van Noort *et al.* 2007; Nieves-Aldrey & San Blas 2015; Ronquist *et al.* 2015, Blaimer *et al.* 2020). The most recent classification divides the family Cynipidae into 12 tribes: Aylacini, Aulacideini, Ceroptresini, Cynipini, Diastrophini, Diplolepidini, Eschatocerini, Paraulacini, Pediaspidini, Phanacidini, Qwaqwaiini and Synergini (Ronquist *et al.* 2015). Oak gall wasps (Cynipini) are by far the most species-rich group of gall wasps, with more than 1,000 known species in 50 genera worldwide (Csóka *et al.* 2005, Ronquist *et al.* 2015, Nicholls et al 2018a, Cuesta-Porta *et al.* 2020, Buffington *et al.* 2020, Fang et al 2020, Nieves-Aldrey *et al.* 2021, Melika *et al.* 2021, Melika & Nicholls 2021). Between 90 and 95% of described Cynipini species induce galls on the genus Quercus L. (Fagaceae; Csóka *et al.* 2005), while the remainder induce galls on other genera in the family Fagaceae (*Castanea, Castanopsis, Chrysolepis, Lithocarpus* and *Notholithocarpus*) (Nieves-Aldrey *et al.* 2009, Tang *et al.* 2016, Nicholls *et al.* 2018b). The species richness of oak gall wasps is highest in the

Accepted by S. Van Noort: 23 Nov. 2021; published: 10 Dec. 2021

relatively well-studied faunas of the Western Palaearctic and Nearctic regions (about 900 spp. in total), with only ca. 100 valid species currently known from the Eastern Palaearctic and Oriental Regions (Burks 1979, Pénzes *et al.* 2018, Fang *et al.* 2020).

In the last decade, the known global species richness of the family Cynipidae has increased significantly due to many studies carried out in the Oriental and Neotropical regions that have historically been poorly sampled for their cynipid faunas (see Medianero and Nieves-Aldrey 2011, Fang *et al.* 2020 for a synthesis). Despite being home to a high diversity of potential oak host species, the known Neotropical cynipid fauna is relatively poor. In their review, Medianero & Nieves-Aldrey (2011) listed eight genera of native Cynipini from this region: *Acraspis* Mayr, 1881, *Amphibolips* Reinhard, 1865, *Andricus* Hartig, 1840, *Atrusca* Kinsey, 1930, *Bassettia* Ashmead, 1887, *Disholcaspis* Dalla Torre & Kieffer, 1910, *Loxaulus* Mayr, 1881 and *Odontocynips* Kieffer, 1910. Since then, species from seven more genera have been recorded: *Coffeikokkos* Pujade-Villar & Melika, 2012 (Pujade-Villar *et al.* 2012b, Medianero & Nieves-Aldrey 2013), *Barucynips* Medianero & Nieves-Aldrey, 2013 (Medianero & Nieves-Aldrey 2013), *Striatoandricus* Pujade-Villar, 2020 (Medianero & Nieves-Aldrey 2019, Cuesta-Porta *et al.* 2020), *Melikaiella* Pujade-Villar, 2014 (Medianero & Nieves-Aldrey 2014), *Neuroterus* Hartig,1840 (Medianero & Nieves-Aldrey 2017), *Zapatella* Pujade-Villar & Melika, 2012 (Pujade-Villar *et al.* 2012a) and *Kokkocynips* Pujade-Villar & Melika, 2013 (Nieves-Aldrey *et al.* 2021); this brings the total number of genera of oak gall wasps currently known from the Neotropical region to 15. However, our sampling has revealed further taxa from this region that are morphologically and genetically distinct from known Cynipini genera and hence require formal description.

Here we use a combination of molecular and morphological data to support the description of a new genus of Cynipini, *Prokius* Nieves-Aldrey, Medianero & Nicholls **gen. nov.**. This new genus contains two new species, also described herein, that induce galls on *Quercus bumelioides* Liebm (Fagaceae, sect. Quercus, white oaks). Phylogenetic analysis shows that this new genus is a member of a clade that includes other Nearctic species classified in several genera and which are all associated with white oaks.

MATERIAL AND METHODS

Gall sampling

The adults studied were reared from galls collected on *Quercus bumelioides* Liebm (Fagaceae, sect. *Quercus*, white oaks). Galls were sampled between December 2007 to August 2010 and November 2016 to January 2019 at Volcán Barú, Chiriquí Province, Panama. The adult insects subsequently emerged in the laboratory from rearing cages. The identification of the host *Quercus* species was based on several key references (Breedlove 2001; Burger 1977) as well as on comparisons with herbarium material from the collections of the University of Panama and the Smithsonian Tropical Research Institute. Although some authors consider the name *Q. bumelioides* to be a synonym of *Q. sapotifolia* (a species in section *Lobatae*, the red oaks) we, along with many central American floras, consider that this name refers to a species in section *Quercus* (and note it is sometimes considered synonymous with *Q. copeyensis*). Vouchered adult specimens and their galls were deposited in the entomological collections of the Museo Nacional de Ciencias Naturales, Madrid (Spain) and Maestría en Entomología, Universidad de Panamá (MEUP).

Specimen preparation

For observation under a scanning electron microscope (SEM), adult cynipids were dissected in 96% ethanol, air dried, mounted on a stub and coated with gold. Micrographs of several standardized views were taken using an FEI Quanta 200 microscope (high vacuum technique). The forewings were mounted on slides in Euparal and were later examined under a Wild MZ8 stereomicroscope. Images of the adult habitus and gall dissections were taken with a Nikon Coolpix 4500 digital camera attached to a Wild MZ8 stereomicroscope. Measurements were performed with a calibrated micrometer scale attached to an oculus of this light microscope.

For morphological comparison with the new described genus, we examined SEM photos of *Dros perlentum* Kinsey and *Biorhiza pallida* Olivier deposited in Morphbank repository (http://www.morphbank.net).

Morphological descriptions

The terminology of morphological structures and abbreviations follows Ronquist and Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001) and Liljeblad *et al.* (2008). For the cuticular sculpture, we follow Harris (1979). Measurements and abbreviations used here include: F1–F12, 1st and subsequent flagellomeres; post-ocellar line (POL) is the distance between the inner margins of the lateral ocelli; ocellar-ocular line (OOL) is the distance from the outer edge of a lateral ocellus to the inner margin of the compound eye; and LOL is the distance between the lateral and frontal ocelli. The width of the forewing radial cell is measured from the margin of the wing to the Rs vein.

Molecular phylogenetics

DNA sequence data were used to delimit the genus *Prokius* **gen. nov.** and place it into a broader phylogeny of the Cynipini. One individual of each *Prokius* **gen. nov.** species described herein was sequenced for fragments of three genes (cytochrome *b* [cytb], long-wavelength opsin [opsin] and the D2 loop of the 28S ribosomal RNA gene [D2]) using the protocols and primers presented in Stone *et al.* (2009). Phylogenetic context for these data was provided by combining them with a reduced version of the three gene dataset presented in Nieves-Aldrey *et al.* (2021), supplemented with additional taxa allied to or morphologically similar to the new genus. The final dataset consisted of 44 Cynipini species, rooted using a Synergini inquiline species (details in Supplementary Table 1).

Alignments for each gene were constructed using MAFFT version 7.471 (Katoh 2013). An ambiguously aligned region within the opsin intron plus insertions present only in single taxa were removed, after which the three alignments were concatenated into a single dataset as the phylogenetic histories of these genes show no evidence of significant topological incongruence (Stone *et al.* 2009). The software PartitionFinder v2.1.1 (Lanfear *et al.* 2016) was used to determine both the optimal partitioning scheme and the best type of substitution model applicable to each data partition. The starting partitioning scheme was by gene and within gene by codon position or intron, with linked branch lengths, the BIC for model selection, and a greedy search scheme. This resulted in six partitions: cytb 3rd codon positions with a GTR+G model, cytb 1st codon positions with a GTR+I+G model, cytb 2nd codon positions with a HKY+I+G model, a partition combining all D2 data with opsin 1st codon positions using a GTR+I+G model, opsin 2nd codon positions with a F81 model, and a sixth partition containing the opsin intron and opsin 3rd codon positions with a GTR+G model. Phylogenetic relationships were then estimated using MrBayes v3.2.7a (Ronquist *et al.* 2012) incorporating this partitioning scheme, substitution models and a strict molecular clock. Two independent runs were performed, each for 8 million generations sampled every 1000 generations; this provided effective samples sizes >150 for all model parameters. A majority-rule consensus tree was calculated using samples taken from the final 5 million generations of both runs.

The degree of genetic variation between the two new species belonging to *Prokius* **gen. nov.**, plus their level of divergence from related species falling into the same major clade (from the genera *Dros* Kinsey, 1937, *Phylloteras* Ashmead, 1897 and some *Andricus* species) was assessed using cytb sequence data. A second individual was sequenced for cytb for five of these species to provide estimates of within-species variation (see Supplementary Table 1). Pairwise genetic distances using HKY corrections were calculated between all individuals using the software PAUP* (Swofford 1998), then average distances for within-species, among-congeneric and among-genus comparisons were determined.

Depositories

MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain (Curator Mercedes Paris)
MEUP: Maestría en Entomología, Universidad de Panamá (Curator Enrique Medianero)

RESULTS

Molecular phylogenetics

The total length of alignment used for the phylogenetic analysis was 1496 base pairs (bp), comprising 433bp from cytb (with 58, 22 and 130 variable sites for 1st, 2nd and 3rd codon positions respectively), 574bp from the D2 region (100 variable sites) and 489bp from opsin (24, 8, 99 and 78 variable sites for 1st, 2nd and 3rd codon positions and the intron respectively). All new sequences used in analyses described herein are deposited in GenBank, accession numbers MZ969834–MZ969842, OK001431–OK001445, OK041496–OK041501 and OK042913 (see also Supplementary Table 1).

The multi-gene analysis corroborates the morphological observations that the genus *Prokius* **gen. nov.** forms a distinct lineage, hence supporting the establishment of this taxon as a genus. It falls within a well-supported (100% posterior probability) clade containing other species galling white oaks currently classified in the genera *Phylloteras, Dros* and *Andricus* (Fig. 9). Within this larger clade, the three groups corresponding to *Prokius* **gen. nov.**, *Dros* and the group of *Andricus* species each form strongly-supported monophyletic lineages, while *Phylloteras* appears to be paraphyletic. However, the broader relationships of this larger clade to many other Cynipini genera are unresolved.

The cytb distance data also indicate *Prokius* **gen. nov.** is clearly distinct from allied genera, with this genus being on average 12.2% divergent from *Phylloteras* species, 13.6% divergent from *Dros* species and 11.9% divergent from the lineage of *Andricus* species; these values are comparable with or greater than among-genera distances reported for other Cynipini (e.g. Cerasa *et al.* 2018, Melika & Nicholls 2021). The two new species within *Prokius* **gen. nov.** were 5.90% divergent, comparable to average distances observed among congeneric species in *Dros* (5.44%), *Phylloteras* (8.37%) and the lineage of *Andricus* species (6.27%). In comparison, average within-species divergence for the five species in the broader clade where two individuals were sequenced was 0.19% (range 0 – 0.94%).

Prokius **Nieves Aldrey, Medianero & Nicholls gen. nov.**

Figs 1-8

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Type species: *Prokius cambrai* Nieves-Aldrey & Medianero **sp. nov.**, designated herein.

Etymology. The new genus is named in honor of Alfred Kinsey, eminent cynipidologist and one of the first who studied gall wasps in Central America. The name is derived from Prok, the nickname used for Professor Kinsey by his students.

Gender. Masculine

Diagnosis. The new genus differs from all other known Cynipini genera by the following combination of morphological characters. Head smooth to weakly alutaceous, mesoscutum and mesopleuron smooth. Malar (subocular) sulcus absent, or if present indistinct, sometimes marked by a group of incomplete striae or in the form of a shallow impressed area (Figs 1A, 3A). Facial striae radiating from clypeus inconspicuous to virtually absent. Transscutal articulation present. Antenna with 14–15 antennomeres in the sexual female, 15 antennomeres in male. Lateral propodeal carinae distinct, narrow, subparallel to strongly divergent on the mid-upper part of propodeum, strongly curved and converging below the mid height (Figs 2B, 4A). Median propodeal area smooth, without sculpture. Projecting part of hypopygial spine short, shorter than basal height of spine. In ventral view, hypopygial spine has the same width along entire length and with a blunt cleft apex; the hypopygial spine bears long and thick setae, arranged in pairs perpendicular to spine margins and only just extending beyond apex of spine (Figs 2F, 4D). Notauli complete, smooth, broad, deep and convergent posteriorly. Scutellar foveae distinct, deep, internally the foveae not separated by a septum, with distinct lateral margins but posterior margins indistinct. Mesoscutellum with distinct margins laterally and posteriorly. Metatarsal claws simple, without a basal lobe (Figs 2C, 4B). Associated with white oaks.

In the recently published key to the genera of Nearctic Cynipini that have a transscutal articulation and toothed tarsal claws (Melika *et al.* 2021), the new genus *Prokius* runs close to *Dros*. Both genera share many morphological characters, such as an almost smooth and shiny head, mesoscutum and mesopleuron, a smooth face without striae and without malar sulcus, and the shape and sculpture of the propodeum (Figs 7A, 7B, 7C, 7D). However, the tarsal claws in the two species of the new genus are simple and not toothed as in *Dros* (Fig. 7F), and the hypopygial spine is quite distinct from the known species of *Dros*, which have a long hypopygial spine with an acute apex (Kinsey 1937; Pujade-Villar *et al.* 2017; Fig. 7E).

The new genus is also morphologically similar to species of *Dryocosmus* Giraud, 1859 and *Biorhiza* Westwood, 1840; both genera have a smooth and shiny mesoscutum and mesopleuron and also have simple metatarsal claws. The new genus can be easily distinguished from *Biorhiza* by the absence of a malar (subocular) sulcus (distinctive in *Biorhiza*; Fig. 8C) and by the ventral spine of the hypopygium, which in *Biorhiza* is broad, short, pointed apically and has an apical tuft of setae (Fig. 8D). The new genus differs from *Dryocosmus* (a polyphyletic genus that needs revision; Nieves-Aldrey *et al.* 2021) by the shape and setation of the hypopygial spine, which in *Dryocosmus* has subapical setae extending beyond the apex of the spine (Fig. 8B). In addition, *Dryocosmus* species have radiating striae on the face (Fig. 8A) and a propodeum that is usually sculptured with a median propodeal carina.

Description. Description of this genus is based in the sexual generation of the two known species. The eventual discovery of asexual generations will require revision of the generic definition.

Sexual female slightly pubescent. Head in anterior view generally oval (Fig. 1A, 3A), 1.2-1.3x wider than high, smooth to slightly alutaceous on front and vertex, with gena not expanded behind eyes. Facial striae radiating from clypeus very short, barely discernible (Fig. 1A). Anterior tentorial pits visible; epistomal sulcus apparent, clypeo-pleurostomal lines visible. Clypeus with ventral margin sinuate, moderately projecting over mandibles, slightly pubescent. Malar (subocular) sulcus absent, or if present indistinct, sometimes marked by a group of incomplete striae or in the form of a shallow impressed area (Fig. 1A). Head from posterior view (Fig. 1B) without occipital carina. Gula short, distance between occipital and oral foramina as high as occipital foramen (Fig. 1B). Hypostomal sulci well separated from oral fossa.

Antenna (Fig. 1C, 3E) with 14–15 antennomeres in sexual female, 15 antennomeres in male; flagellum not broadening towards apex.

Mesosoma: Pronotum short medially, slightly pubescent, lateral surface of pronotum smooth; pronotal plate indistinct dorsally (Fig. 2A). Mesoscutum smooth, strongly convex dorsally, sparsely pubescent with scattered setae anteriorly. Notauli percurrent, smooth, well impressed along entire length, reaching pronotum, convergent posteriorly, median mesoscutal impression present. Transscutal fissure present. Mesoscutellum rectangular to slightly trapezoidal, marginated, surrounded by distinct carina. Scutellar foveae distinct, deep, internally the foveae not separated by a septum, with distinct lateral margins but posterior margins indistinct. Mesopleuron smooth, speculum glabrous; mesopleural triangle moderately pubescent (Fig. 1F). Lateral propodeal carinae distinct, narrow, subparallel to strongly divergent in mid to upper part of propodeum, strongly bent and convergent inwards below the mid height. Medial propodeal area smooth, glabrous, lateral propodeal area smooth, with dense white setae (Fig. 2B). Nucha rugose.

Metatarsal claws simple, without an acute basal lobe (Fig. 2C).

Forewing (Figs. 5E, 5F) hyaline, without fuscate spots or stripes, radial cell open along anterior margin; areolet triangular, closed and distinct. Apical margin of wing with short hair fringe.

Metasoma with second metasomal tergum covering about two thirds of metasoma. Projecting part of hypopygial spine short, shorter than basal height of spine. In ventral view, hypopygial spine has the same width along its entire length with a blunt cleft apex; the hypopygial spine bearing long and thick setae, arranged in pairs perpendicular to spine margins and only just extending beyond apex of spine (Figs. 2E, 2F, 4D).

Distribution. Based on our data, the new genus is found only from 1,440m to 3,000m a.s.l. at Volcán Barú, Chiriqui, Panama.

Key to adults of species of *Prokius*

1. Antennae with 14 segments in female, 15 in the male (Figs 1C, 1D). Median mesoscutal impression visible only in posterior one eighth of the mesoscutum (Fig. 1E). Antero-lateral part of second metasomal tergum with a dense patch of setae (Fig. 2D). R1 vein always strongly pigmented and visible, reaching wing margin (Fig. 5F). Body coloration dark brown (Fig. 5C, 5D). . . . . ***P. cambrai* n. sp.**

• Antennae with 15 segments in both sexes (Figs 3E, 3F). Median mesoscutal impression almost complete but shallow, visible in posterior three quarts of the mesoscutum (Fig. 3D). Antero-lateral part of second metasomal tergum with only a few setae (Fig. 4C). R1 vein sometimes depigmented and not reaching wing margin (Fig. 5E). Body coloration amber to light brown in both sexes, lighter in males (Fig. 5A, 5B). . . . . ***P. lisethiae* n. sp.**

Prokius cambrai Nieves-Aldrey & Medianero n. sp.

(Figs. 1-2, 5C-D, 5F, 6A-C)

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Type material. Holotype female Fig.5D; in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted). PANAMA, Chiriquí, Volcán Barú 8°47´50.8” N, 82°29´35.9” W, 1,800 – 2,070 m ; ex gall on leaf of *Quercus bumelioides* Liebm. (Fagaceae), 26.iii.2009, E. Medianero leg.. Paratypes: 2 males and 2 females in MNCN: 1 male, 1 female same data as holotype, collected 15.vi.2008; 1 male and 1 female collected 15.vi.2008, Boquete, Volcancito, 1440 m.; 5 paratypes in Maestría en Entomología, Universidad de Panamá (MEUP): 2 males, 1 female in ethanol, Volcán Baru, 1800 m. 15/vi/2008, E. Medianero leg.

Additionally, 1 male and 1 female from the type series were dissected for SEM observation (in MNCN) and are preserved mounted on the stub.

Additional material (excluded from type material, in ethanol), 5 males, 3 females, Volcan Barú (1800-2070 m), *Q. bumelioides*, 25/x/2008. E. Medianero leg (note: these specimens are darker, predominantly blackish)

Etymology. Named after our colleague and friend Roberto Cambra Torok for his contribution to the development of entomology in Panama.

Diagnosis. Aside from the diagnostic characters of the genus described previously, *P. cambrai* presents the following diagnostic characters that allow differentiation from the other new species described herein: Frons smooth, without visible sculpture. Antennae with 14 segments in female, 15 in the male. Median mesoscutal impression visible only in posterior one eighth of the mesoscutum. R1 vein strongly pigmented and visible, reaching wing margin. Antero-lateral part of second metasomal tergum with a dense patch of setae. Body coloration dark brown. Galls irregular sub-conical to sub-cylindrical.

Description. Body length 2.3 mm (range 2.1 – 2.5 mm; N = 3) for females; 2 mm (range 1.9- 2.1 mm; N = 3) for males. Body uniformly shiny reddish brown to almost black in some specimens; mouth parts yellow, antennal scape, pedicel and basal flagellomeres yellowish, distal flagellomeres darker. Legs yellowish; tibia and tarsomeres darker. Forewing hyaline with some very light infumation; veins dark brown to black.

Sexual female. Head slightly alutaceous to smooth, with sparse white setae, denser on face and malar space, in dorsal view about 2.5× wider than long. POL 1.5× as long as OOL, posterior ocellus separated from inner orbit of eye by about 2× its greatest diameter. Head in anterior view (Fig. 1A) 1.2× wider than high, gena not expanded behind eyes. Vertex, frons and gena slightly alutaceous. Clypeus more or less trapezoidal, 1.4× wider than high, mostly smooth and slightly pubescent; ventral margin sinuate, slightly projecting over mandibles. Anterior tentorial pits visible; epistomal sulcus apparent, clypeo-pleurostomal lines visible. Malar space 0.2× height of compound eye. Malar (subocular) sulcus weak but present, reaching the base of the mandible. Facial striae radiating from clypeus very short, barely discernible. Toruli situated above mid-height of compound eye; distance between antennal rim and compound eye 0.8× width of antennal socket including rim. Ocellar plate raised. Head in posterior view (Fig. 1B) without occipital carina. Gula short; distance between occipital and oral foramina as high as the occipital foramen. Hypostomal sulci well separated from oral fossa.

Mouthparts (Figs. 1B): mandibles exposed, with setae at base, right mandible with three teeth, left with two teeth. Cardo of maxilla visible, maxillary stipes about 2.0× longer than wide. Maxillary palp five-segmented. Labial palp three-segmented.

Antenna (Fig. 1C) of moderate length, as long as 1/2 body length, with 12 flagellomeres; flagellum not broadening towards apex; with relatively long, erect setae, and elongate placodeal sensilla visible only on flagellar segments 3–12. Relative lengths of antennal segments: 17:13:34:24:21:18:15:15:15:13:13:13:12:22. Pedicel subglobose, 0.7× as long as scape; F1–F11, gradually decreasing in length. F1 1.4× as long as F2. F12 2.0× longer than wide, 1.7× as long as F11.

Mesosoma. Smooth, moderately pubescent, in lateral view 1.1× as long as high, strongly convex dorsally. Pronotum smooth, moderately pubescent, with long setae (Fig. 1F). Pronotum short medially, ratio of length of pronotum medially/laterally = 0.2. Pronotal plate indistinct dorsally (Fig. 2A).

Mesonotum (Fig. 1E). Mesoscutum smooth, barely pubescent with scattered setae anteriorly and laterally, with setae scattered along the notauli. Notauli complete, smooth, broad, deep and convergent posteriorly, median mesoscutal impression present but very short, without anteroadmedian signa and parapsidal signa. Transscutal fissure clearly visible, deeply impressed and nearly straight. Scutellar foveae well differentiated, deep, internally the foveae not separated by a septum, their posterior margins indistinct. Mesoscutellum (Fig. 1E), rectangular to slightly trapezoidal, marginated, surrounded by distinct carina, about 0.7× length of mesoscutum, 0.8× as long as wide, smooth and moderately pubescent; in lateral view extended posteriorly over dorsellum. Axillula moderately pubescent, their anterior margins marked and posterior margins indistinct. Mesopleuron smooth, speculum glabrous; mesopleural triangle moderately pubescent (Fig. 1F).

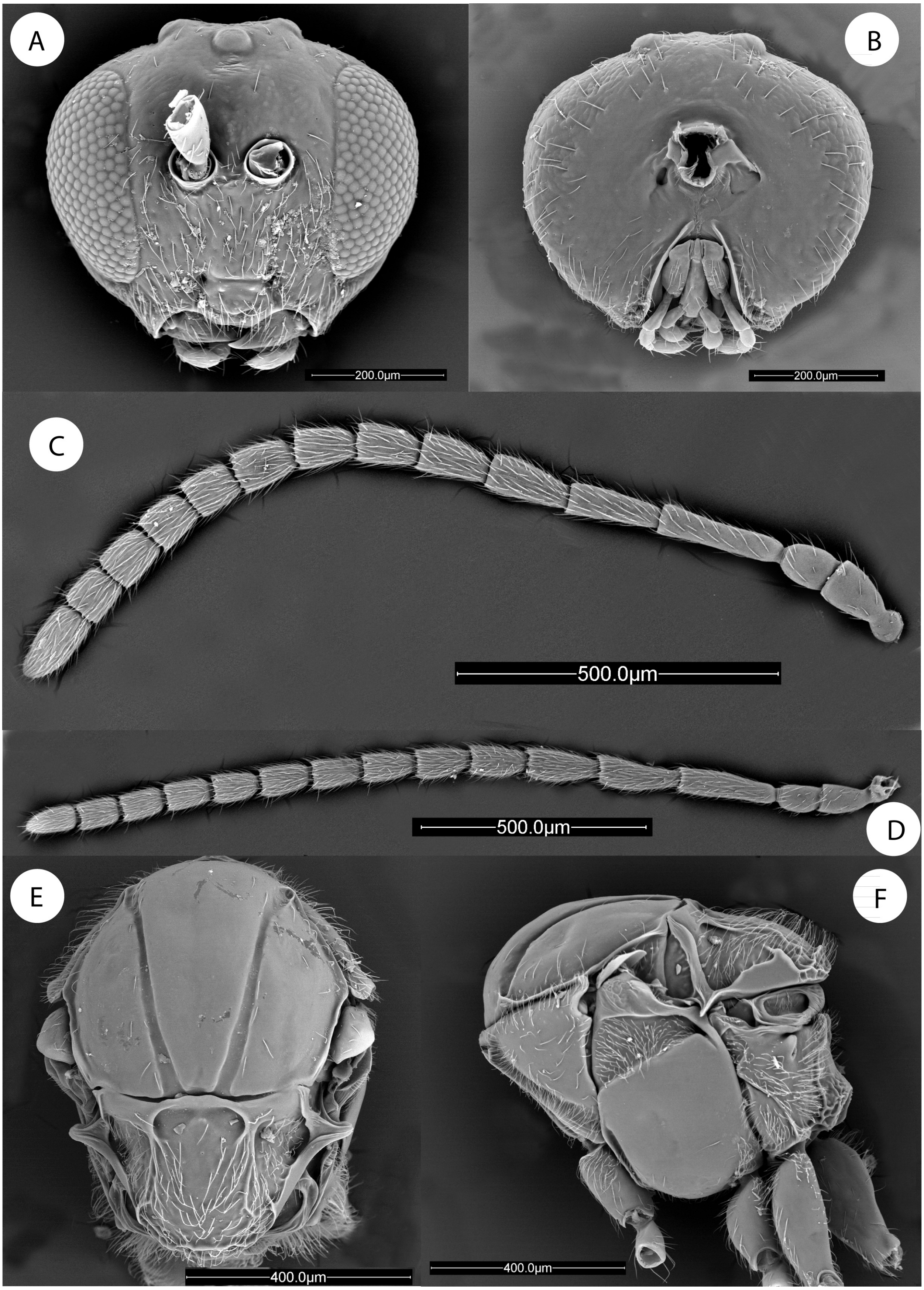

FIGURE 1. *Prokius cambrai*, **sp. nov.**, SEM photos of paratype, sexual female. (A) Head, anterior view. (B) Head, posterior view. (C) Female antenna. (D) Male antenna. (E) Mesosoma, dorsal view. (F) Mesosoma, lateral view.

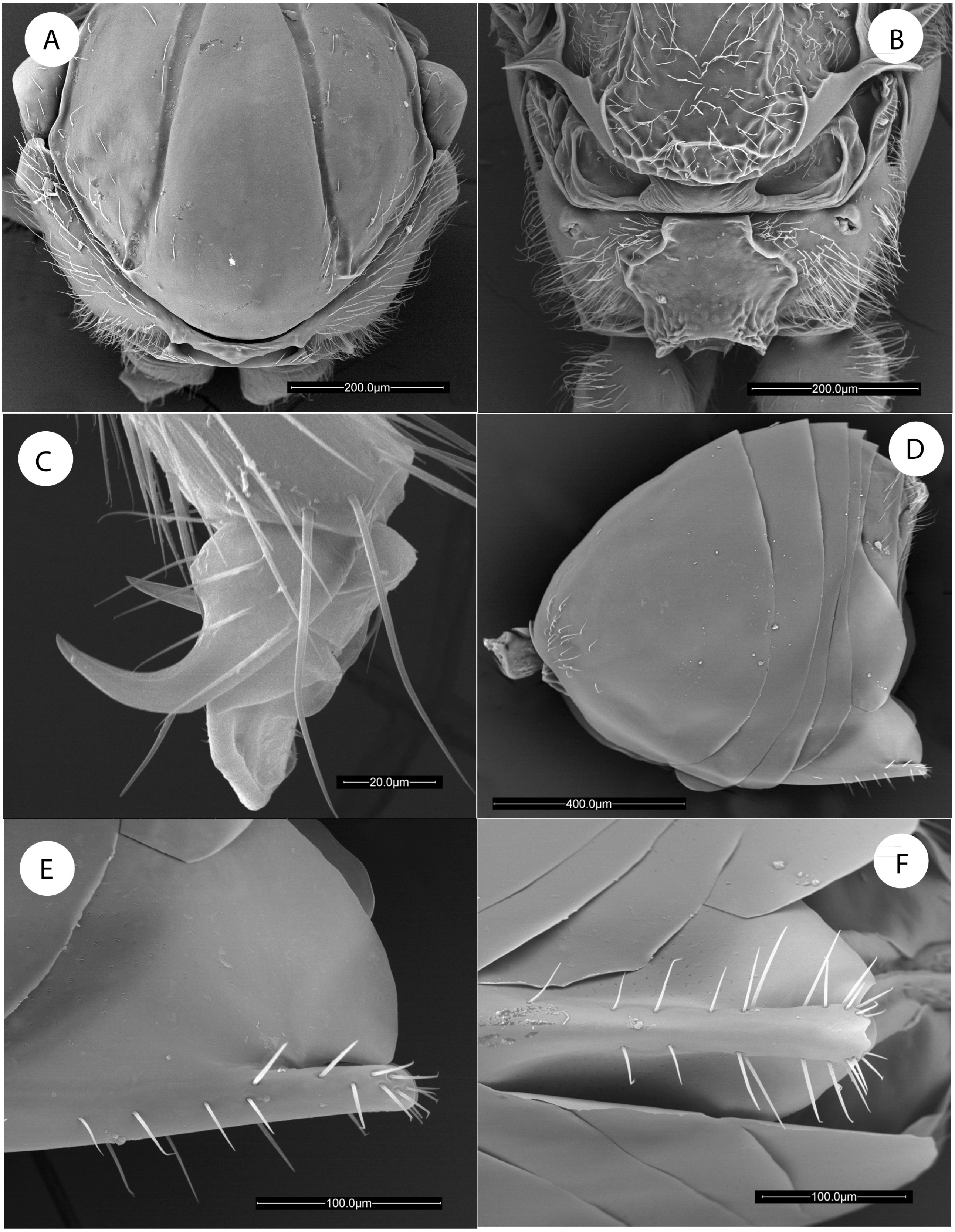

FIGURE 2. *Prokius cambrai*, **sp. nov.**, SEM photos, sexual female. (A) Pronotum, antero-dorsal view. (B) Propodeum. (C) Metatarsal claw. (D) Metasoma, lateral view. (E) Detail of the ventral spine of the hypopygium, lateral view. (F) Detail of the ventral spine of the hypopygium, ventral view.

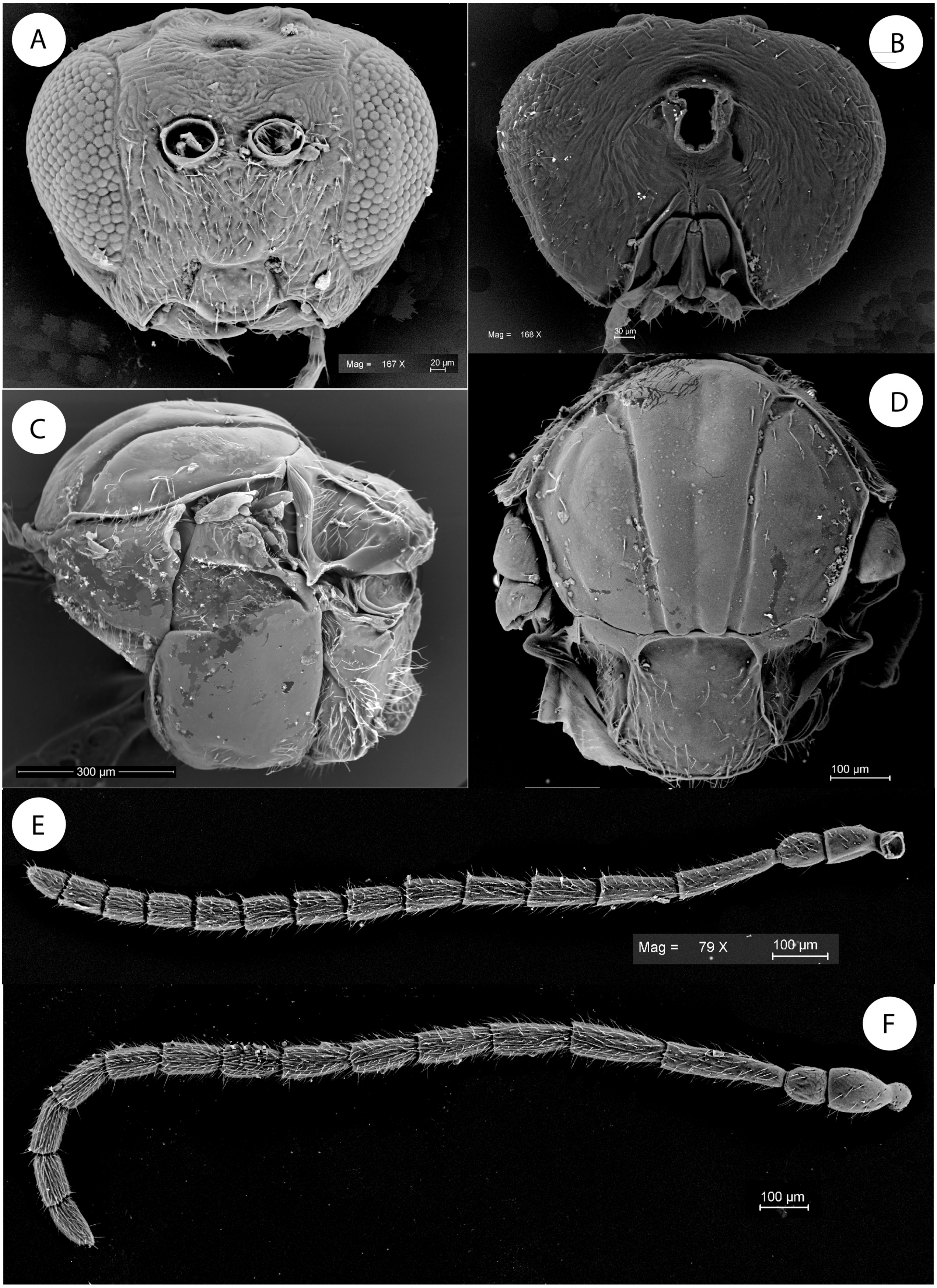

FIGURE 3. *Prokius lisethiae*, **sp. nov.**, SEM photos of paratype, sexual female. (A) Head, anterior view. (B) Head, posterior view. (C) Mesosoma, lateral view. (D) Mesosoma dorsal view. (E) Female antenna. (F) Male antenna.

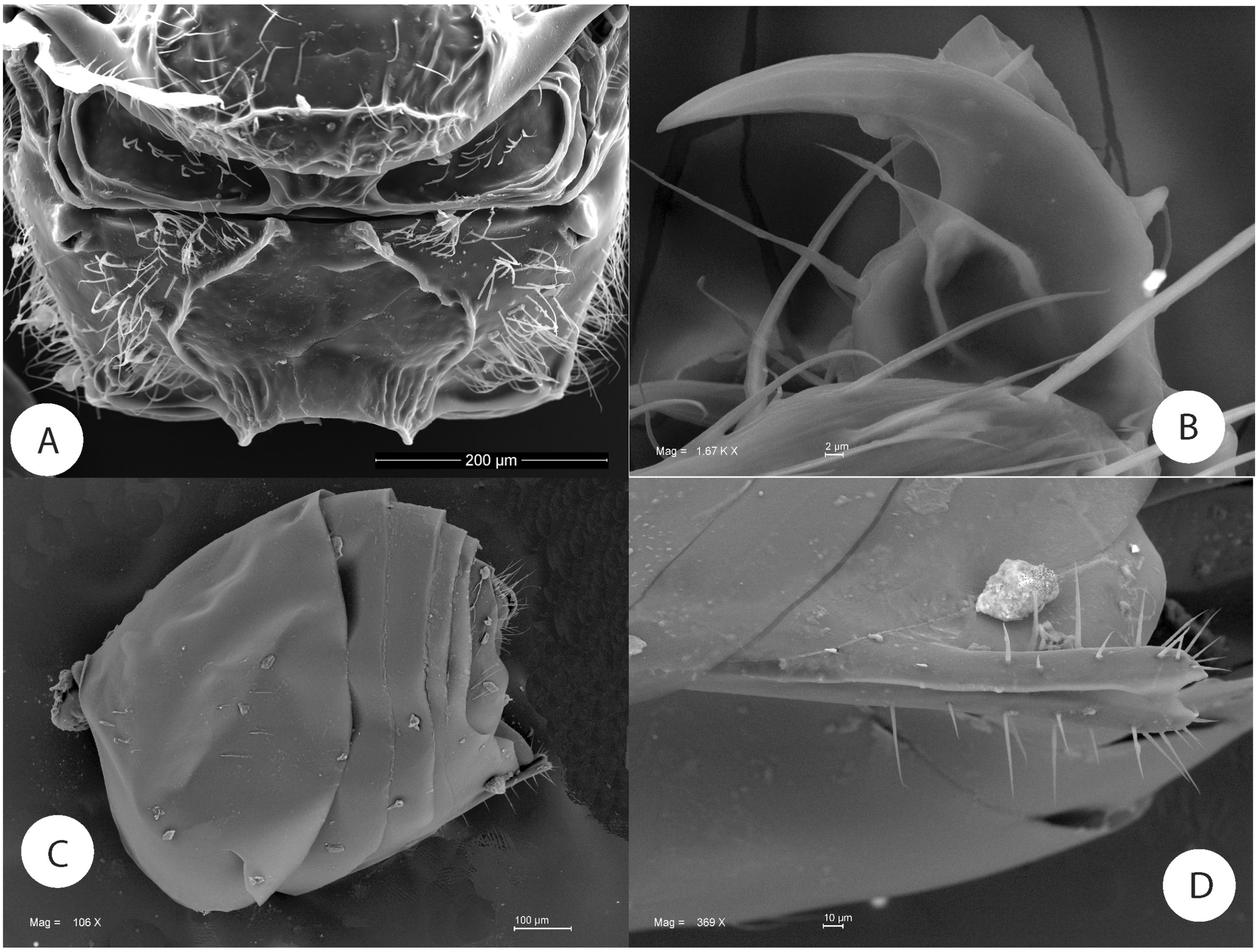

FIGURE 4. *Prokius lisethiae*, **sp. nov.**. SEM photos, sexual female (A) Propodeum. (B) Metatarsal claw. (C) Metasoma, lateral view. (D) Detail of the ventral spine of the hypopygium, ventral view.

Metanotum (Fig. 1F, 2B). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal complex (Fig. 1F). Lateral propodeal carinae distinct, bent outwards distinctly at mid height, central propodeal area smooth, glabrous, lateral propodeal area smooth, with dense white setae (Fig. 2B). Nucha rugose.

Legs. Moderately pubescent; metatarsal claws without a basal lobe (Fig. 2C).

Forewing (Fig. 5F) slightly longer than body; basal cell with some rows of setae; radial cell 4.0× longer than wide; open along anterior margin; areolet triangular, closed and distinct. R1 and Rs nearly straight, reaching wing margin. Rs+M reaching basalis at its mid-height. 2r well pigmented, angulate and projecting slightly medially. Apical margin of wing with a fringe of short hairs.

Metasoma (Fig. 2D) large, as long as head and mesosoma combined, in lateral view as wide as high. Second metasomal tergum covering about 2/3 of metasoma, with a patch of dense setae on its anterior end. Projecting part of hypopygial spine short (Fig. 2E), shorter than basal height of spine; in ventral view, of the same width along its entire length with a blunt cleft apex (Fig. 2F); the hypopygial spine bearing long and thick setae, arranged in pairs perpendicular to spine margins and only just extending beyond apex of spine.

Male (Fig. 5C). Similar to female except as follows: Head almost black; antennal scape and pedicel yellow, flagellum entirely dark yellowish, metatibia distally brown. Antenna with 13 flagellomeres (Fig. 1D); F2 slightly curved at base. Placodeal sensilla present on flagellomeres 1–13. Relative length of antennomeres: 13:13:27:23:20: 15:15:14:14:13:13:12:12:11:14. Metasoma smaller than in female; second tergum 0.7× total metasoma length.

Host plant. *Quercus bumelioides* Liebm. (Fagaceae, Quercus sect. Quercus).

Gall (Figs. 6A-C). Galls are irregularly cylindrical with a smooth surface, measuring 5 × 2 mm, with a single internal larval chamber. Galls develop singly or more frequently in close clusters of 2–5 galls, on the upper side of the leaf blade; the presence of a gall is indicated on the lower side of the leaf by a circular impression (Fig. 6C). The galls are green to red when fresh (Fig. 6A) and black when mature. Galls are relatively abundant on the host plant at Volcán Barú in Panama.

Distribution. *Prokius cambrai* sp. nov. was found between 1,440 – 2,070 m a.s.l. at Volcán Barú, Chiriqui, Panama.

Biology. Only the sexual generation is known, inducing galls on *Quercus bumelioides*. Freshly growing galls are present on new leaves in November during the rainy season. Adult insects emerge in May.

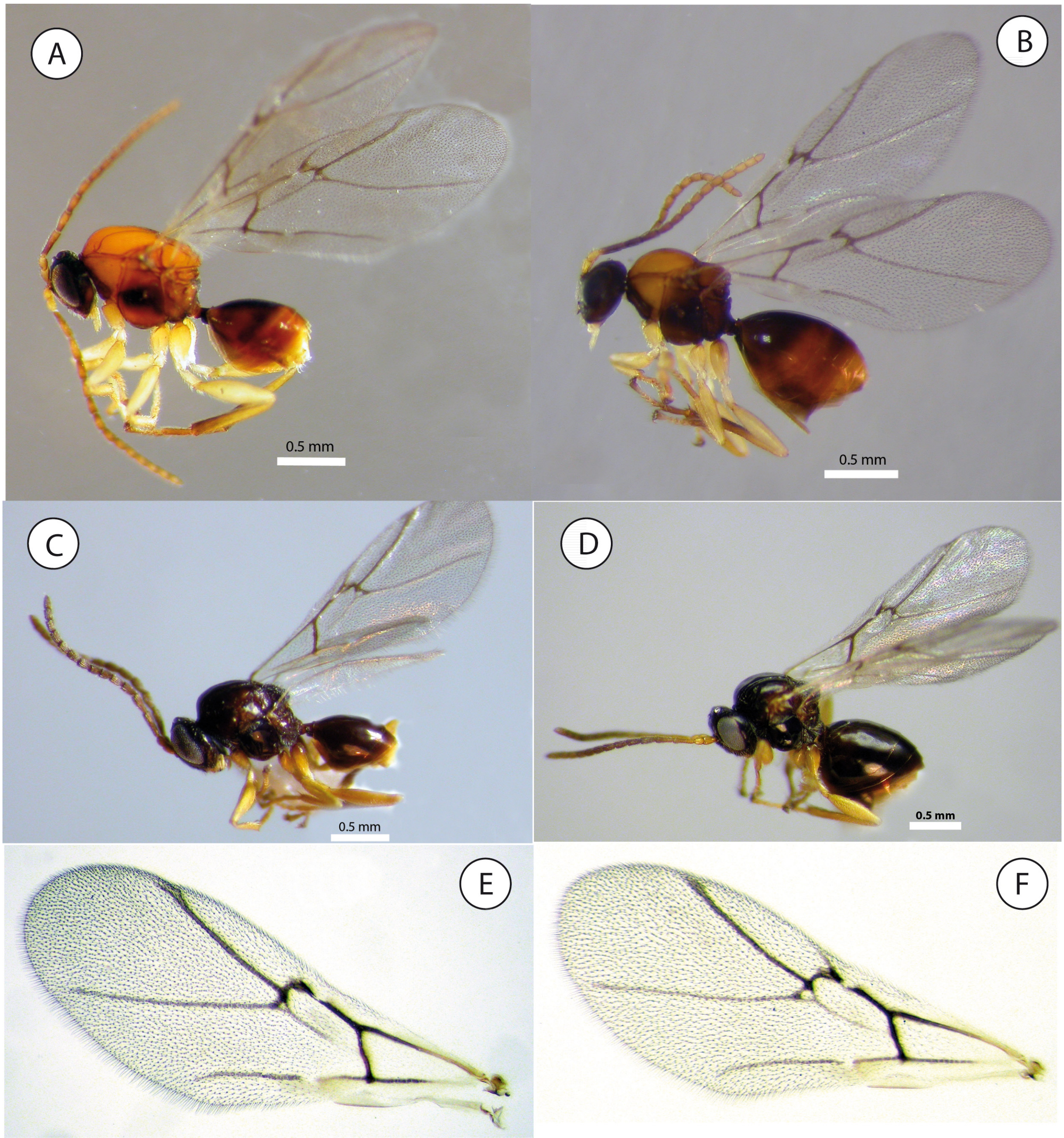

FIGURE 5. *Prokius lisethiae*, **sp. nov.**. Light microscopy photos. (A) Habitus male paratype. (B) Habitus female holotype. (E) Forewing; *Prokius cambrai*, **sp. nov.** (C) Habitus male paratype. (D) Habitus female holotype. (F) Forewing.

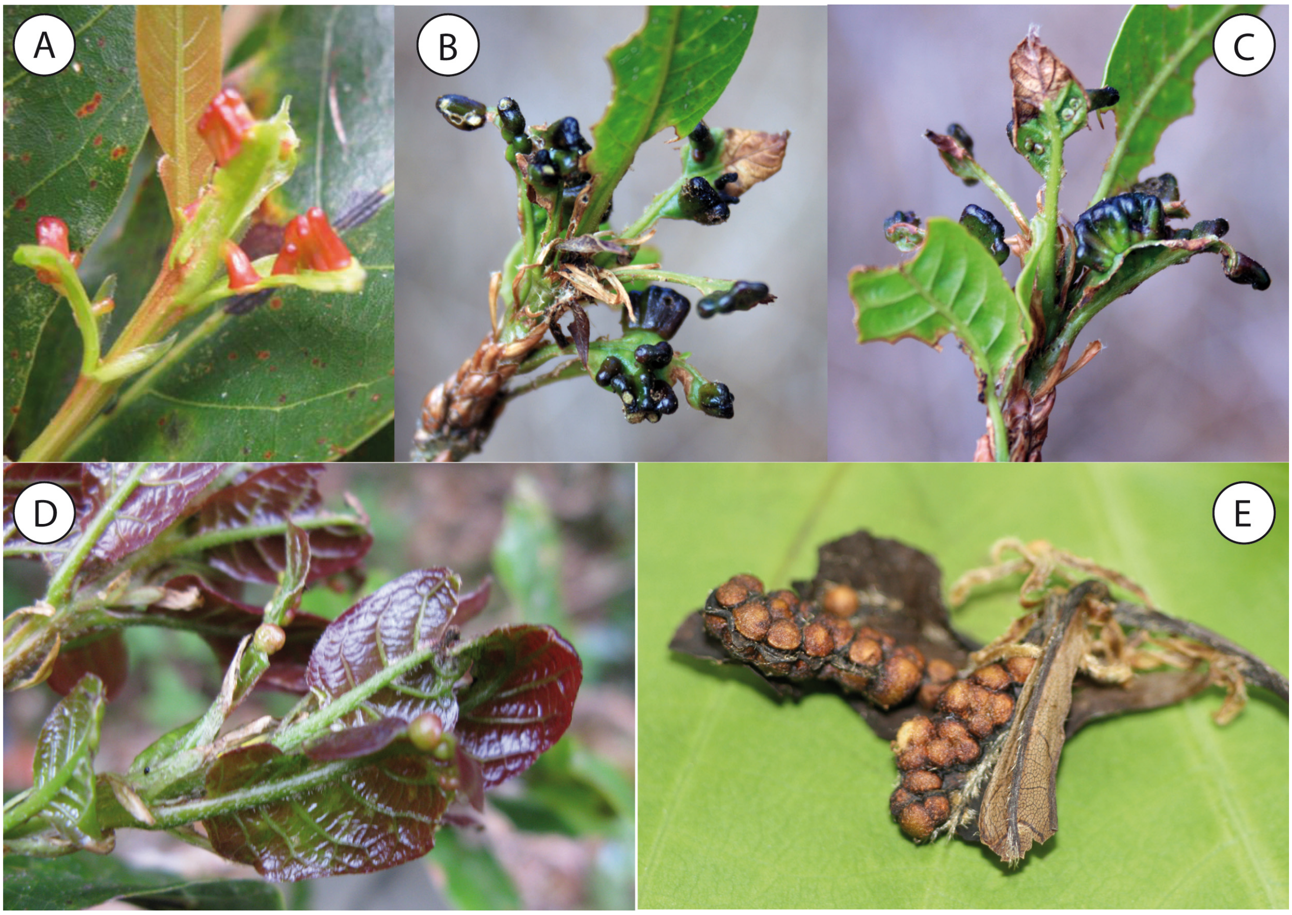

FIGURE 6. *Prokius cambrai*, **sp. nov.**. (A–C) Fresh galls on leaves of *Quercus bumelioides*. *Prokius lisethiae*, **sp. nov.** (D) Fresh galls and (E) Old dried galls on leaves of *Quercus bumelioides*.

Prokius lisethiae Medianero & Nieves-Aldrey n. sp.

(Figs. 3-4, 5A-B, 5E, 6D-E)

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Type material. Holotype female (Fig.5B; in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted). PANAMA, Chiriquí, Volcán Barú 8°46´36.8” N, 82°31´39.9” W, 3000 m; ex gall on leaf of *Quercus bumelioides* Liebm. (Fagaceae), gall collected 12.i.2019, insect emerged i.2019, E. Medianero leg. Paratypes: 4 males and 13 females; 7 females with same data as holotype; 3 males and 4 females, Volcan Barú, 2681-2780 m, galls collected 27.i.2009, E. Medianero leg. 1 male and 2 female paratypes in ethanol; 1 female paratype extracted for DNA. 11 paratypes in MNCN, 6 paratypes (in ethanol) in Maestría en Entomología, Universidad de Panamá (MEUP).

Additionally, 1 male and 1 female paratype of the type series were dissected for SEM observation (in MNCN) and are preserved mounted on their stubs.

Etymology. Named after Liseth, daughter of the first author.

Diagnosis and comments. Closely resembles *P. cambrai* in most morphological characteristics. The species differs mainly in the sculpturing of the head, the relative width and height of head in anterior view, number of antennal segments, and lengths of the median mesoscutal impression and R1. The front of the head in *P. lisethiae* is alutaceous whereas in *P. cambrai* it is smooth to slightly alutaceous. In anterior view the head of *P. lisethiae* is 1.3× wider than high whereas in *P. cambrai* it is 1.2× wider than high. *Prokius lisethiae* has antennae containing 15 segments in both sexes whereas *P. cambrai* has antennae with 14 segments in females and 15 in males. The median mesoscutal impression in *P. lisethiae* is complete whereas in *P. cambrai* it is present but very short. In *P. cambrai* R1 is always complete, reaching the wing margin, whereas in *P. lisethiae* the R1 is sometimes faint or absent (Fig. 5A). A minor difference is that *P. cambrai* has a dense patch of setae at the anterior end of the second metasomal tergum whereas in *P. lisethiae* the second metasomal tergum has scattered setae rather than a dense patch. In *P. cambrai* the posterior margins of the axillula are indistinct whereas in *P. lisethiae* they are distinct. Finally, in *P. lisethiae* the apical margin of the wing has a fringe of long hairs, whereas in *P. cambrai* the apical margin of wing has a fringe of short hairs.

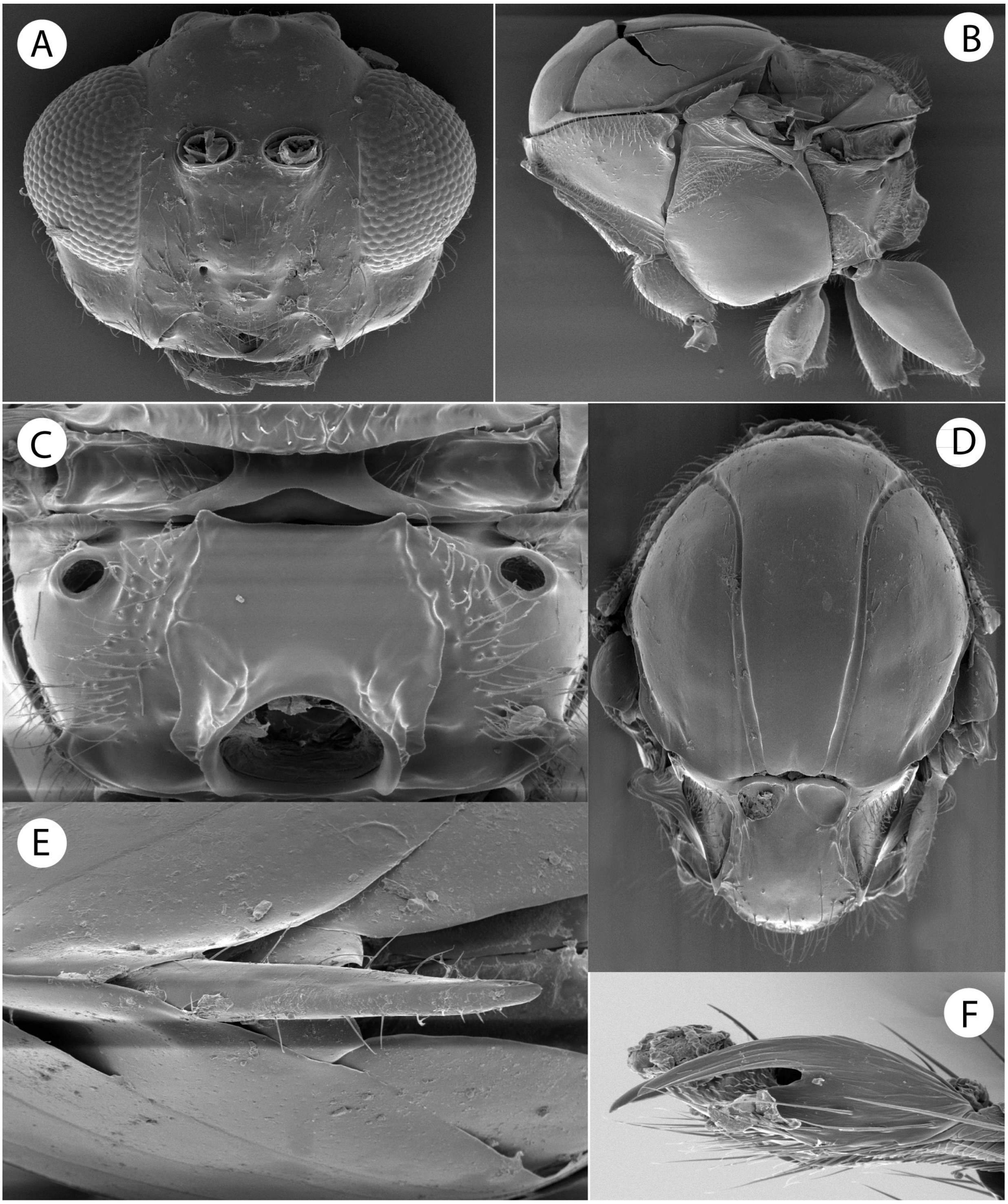

FIGURE 7. *Dros perlentum* Kinsey, 1937. SEM photos of asexual female. (A) Head, anterior view. (B) Mesosoma, lateral view. (C) Propodeum. (D) Mesosoma, dorsal view. (E) Detail of the ventral spine of the hypopygium, ventral view. (F) Metatarsal claw. Reproduced with permission from Johan Liljeblad and Fredrik Ronquist, copyright holders of the images in Morphbank.

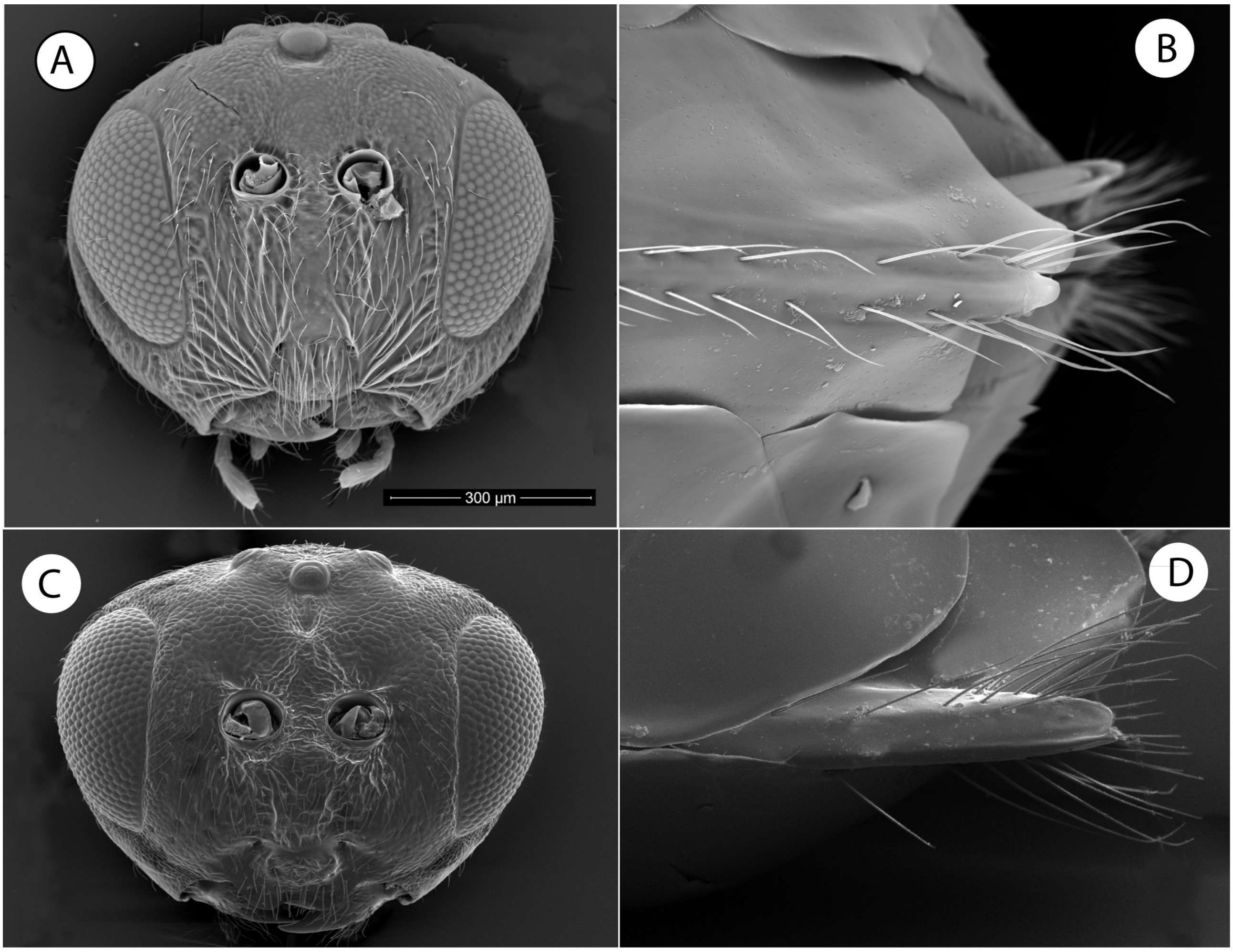

FIGURE 8. Selected SEM photos of Cynipini genera morphologically similar to *Prokius* **gen. nov**. (A–B) *Dryocosmus kuriphilus* Yasumatsu, 1951, asexual female. (A) Head, anterior view. (B) Spine of hypopygium, ventral view. (C–D) *Biorhiza pallida* (Olivier, 1791), sexual female. (C) Head, anterior view. (D) Spine of hypopygium, ventral view (C and D images reproduced with permission from Johan Liljeblad and Fredrik Ronquist, copyright holders of the images in Morphbank.

Description. Body length 2.2 mm (range 1.9 – 2.4; N = 4) for females; 2 mm (range 1.9 – 2.1 mm; N =3) for males. Body predominantly orange to reddish orange; frons and sides of the head orange-brownish; lower head and mouth parts orange; mesosoma orange, parts of mesopleuron, metapleuron and propodeum darker; metasoma orange-reddish; scape and pedicel of antenna yellowish, antennal flagellum darker; legs entirely yellow except for distally darker metatibia. Forewing hyaline with some very light infumation; veins dark brown to black.

Sexual female. Head alutaceous, with sparse white setae, denser on face and malar space; in dorsal view about 2.3× wider than long. POL 2× as long as OOL, posterior ocellus separated from inner orbit of eye by 2× its greatest diameter. Head in anterior view (Fig. 3A) 1.3× times wider than high, gena not expanded behind eyes. Vertex, frons and gena slightly alutaceous. Face smooth and moderately pubescent with piliferous punctures. Clypeus more or less trapezoidal, 1.4× as wide as high, mostly smooth and slightly pubescent; ventral margin straight, slightly projecting over mandibles. Anterior tentorial pits visible; epistomal sulcus apparent, clypeo-pleurostomal lines visible. Malar space 0.26× height of compound eye. Malar (subocular) sulcus absent. Facial striae radiating from clypeus very short, barely distinct. Toruli situated above mid-height of compound eye; distance between antennal rim and compound eye 0.8× width of antennal socket including rim. Ocellar plate not raised. Head from posterior view (Fig. 3B) without occipital carina. Gula short; distance between occipital and oral foramina as high as the occipital foramen (Fig. 3B). Hypostomal sulci clearly separated from oral fossa.

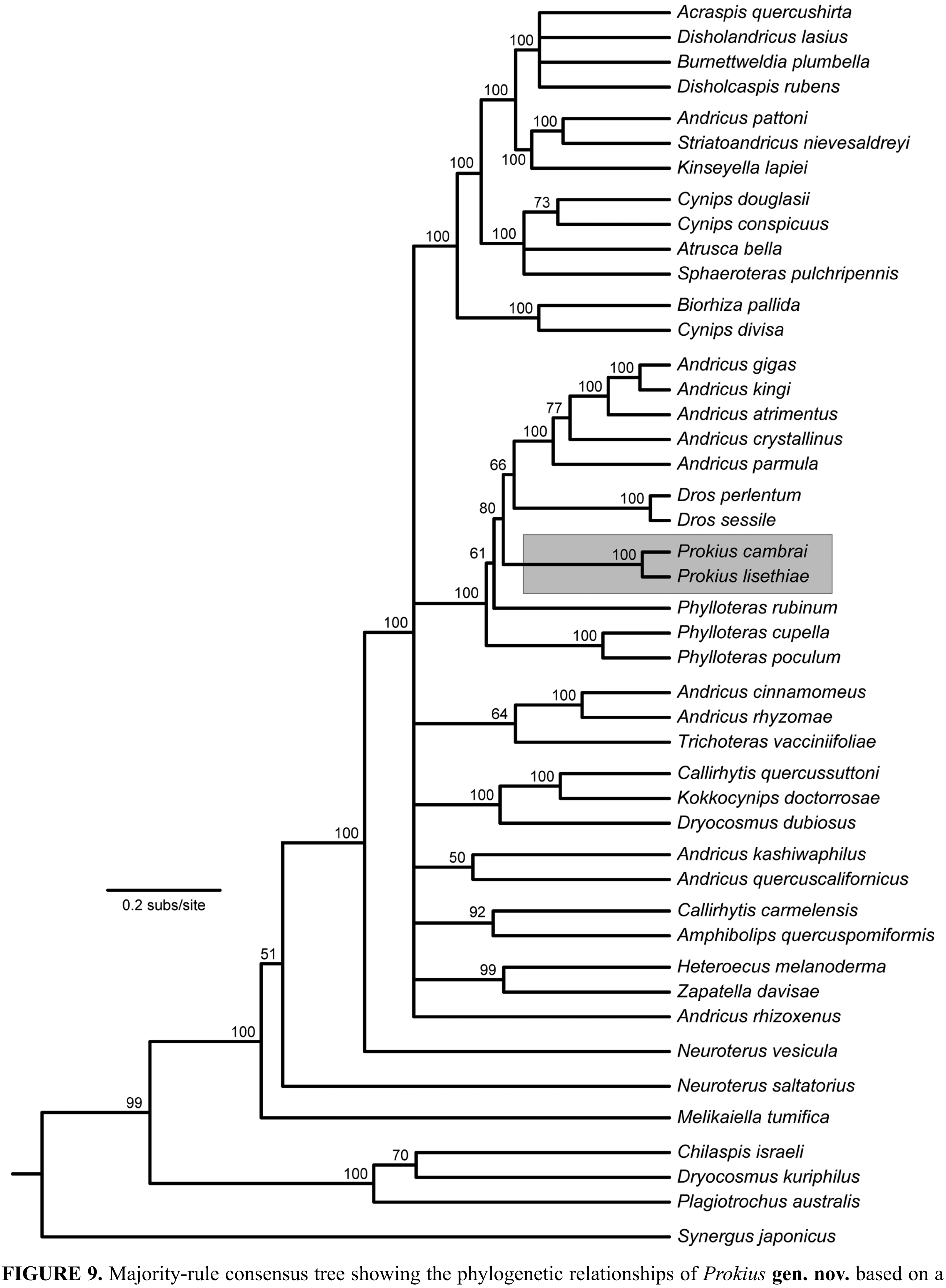

FIGURE 9. Majority-rule consensus tree showing the phylogenetic relationships of *Prokius* **gen. nov.** based on a Bayesian analysis of a concatenation of three loci (cytochrome b, the D2 region of the 28S rRNA gene and long-wavelength opsin). Numbers above nodes indicate posterior probability support; the new genus is highlighted by the grey shaded box.

Mouthparts (Figs 3 A-B): mandibles exposed, with setae at base, right mandible with three teeth, left with two teeth. Cardo of maxilla visible, maxillary stipes about 2.0× longer than wide. Maxillary palp five-segmented. Labial palp three-segmented.

Antenna (Fig. 3E) of moderate length, as long as 1/2 body length, with 13 flagellomeres; flagellum not broadening towards apex; with relatively long, erect setae, and elongate placodeal sensilla visible only on flagellar segments 3–12. Relative lengths of antennal segments: 17:16:32:25:22:21:18:18:17:16:16:15:14:14:13. Pedicel sub-globose, 0.9× as long as scape; F1–F11 gradually decreasing in length. F1 1.3 times as long as F2. F13 1.4× longer than wide, 0.9× as long as F12.

Mesosoma. Smooth, slightly pubescent, in lateral view as high as long, strongly convex dorsally. Pronotum smooth, slightly pubescent; with long setae (Fig. 3C). Pronotum short medially, ratio of length of pronotum medially/ laterally = 0.2. Pronotal plate indistinct dorsally (Fig. 3D).

Mesonotum (Fig. 3C, D). Mesoscutum smooth, sparsely pubescent with scattered setae anteriorly and laterally, with setae scattered along the notauli. Notauli complete, smooth, broad, deep and convergent posteriorly, median mesoscutal impression visible without anteroadmedian signa and parapsidal signa. Transscutal fissure clearly visible, deeply impressed and nearly straight. Scutellar foveae well differentiated, deep, internally the foveae not separated by a septum, their posterior margins indistinct. Mesoscutellum (Fig. 3D), rectangular to slightly trapezoidal, marginated, delimited completely by distinct carina, about 0.5× length of mesoscutum, 0.8× as long as wide, smooth and slightly pubescent; in lateral view extended posteriorly over dorsellum. Axillula moderately pubescent, their anterior and posterior margins marked. Mesopleuron smooth, speculum glabrous; mesopleural triangle slightly pubescent (Fig. 3C).

Metanotum (Fig. 3C, 4A). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about two thirds its height (Fig. 3C). Lateral propodeal carinae distinct, bent strongly outwards at mid height, central propodeal area smooth, glabrous, lateral propodeal area smooth, with dense white setae (Fig. 4A). Nucha rugose.

Legs. Slightly pubescent; metatarsal claws without a basal lobe (Fig. 4B).

Forewing (Fig. 5E) slightly infused and longer than body; basal cell with some rows of setae; radial cell 4.0× longer than wide; open along anterior margin; areolet triangular, closed and distinct. Rs nearly straight, reaching wing margin. R1 absent. Rs+M reaching basalis at its mid-height. 2r well pigmented, angulate and projecting slightly medially. Apical margin of wing with fringe of long hairs.

Metasoma (Fig. 4C) large, as long as head and mesosoma combined, in lateral view as wide as high. Second metasomal tergum covering about 2/3 of metasoma, with scattered setae. Projecting part of hypopygial spine short (Fig. 4D), as long as wide in lateral view; in ventral view the same width along its entire length and with a blunt cleft apex; the hypopygial spine bearing long and thick setae, arranged in pairs perpendicular to spine margins and extending slightly beyond apex of spine (Fig. 4D).

Male (Fig. 5A). Similar to female except as follows: Placodeal sensilla present on flagellomeres 1–13 (Fig. 3F). Relative length of antennomeres: 20:15:42:31:26:25:23:22:20:20:19:19:17:17:17. Metasoma smaller than in female; second tergum 0.6× total metasoma length.

Host plant. *Quercus bumelioides* Liebm (Fagaceae, Quercus section Quercus).

Gall (Figs. 6D-E). Galls have a spherical to lenticular shape with a smooth surface. They grow on the edge of the leaf blade, deforming the new leaf, measuring 5 × 2 mm. Galls typically grow in close clusters of 2–20 galls per leaf. The galls are reddish green when fresh and brown when mature. Galls are relatively abundant around Volcán Barú in Panama.

Distribution. *Prokius lisethiae* was found to 3,000 m a.s.l. at Volcán Barú, Chiriqui, Panama.

Biology. Only the sexual generation is known. Young galls are present in January during the dry season, growing on new leaves. The adult insects emerge from mature galls in late January and February.

DISCUSSION

Prokius **gen. nov.** is the fourth recently described cynipid genus that is endemic to the Central American section of the Neotropical region, after *Barucynips, Coffeikokkos* and the inquiline genus *Agastoroxenia*, (Nieves-Aldrey & Medianero 2010, Pujade-Villar *et al.* 2012, Medianero & Nieves-Aldrey 2013). The gall wasp fauna of this geographical region has traditionally been very poorly studied. However, the present and ongoing studies will serve to expand our knowledge of the unique cynipid fauna of the Neotropical region.

The status of the new genus described here is supported by both molecular and morphological evidence. The combined use of morphological and molecular characters, as well as biological traits (host plant lineage, for example), has allowed recent studies to resolve some of the unstable classification and taxonomic status of the main lineages of Nearctic and Neotropical oak gall wasps (Nicholls *et al.* 2018b, Cuesta-Puerta *et al.* 2020, Nieves-Aldrey *et al.* 2021; Melika *et al.* 2021, Melika & Nicholls 2021). The previous unstable taxonomy of the Cynipini reflects in part historical causes, since much of the current generic level taxonomy still follows Weld (1952) and is based to some extent upon diagnostic characters that are inconsistent within genera (Nicholls *et al.* 2018a). This in turn reflects both the great diversity of this group of cynipids and the apparent high level of homoplasy that exists in many of the taxonomic characters used in this group (Liljeblad *et al.* 2008). However, recent studies based on more solid evidence have helped to re-define the generic limits of previously described and newly discovered taxa from the Nearctic and Neotropical regions.

An example of one such taxon, allied to the new genus described in this study, is the genus *Dros*. This genus was described by Kinsey (1937), synonymized with *Andricus* by Melika and Abrahamson (2002), but recently re-established as a valid genus by Pujade-Villar *et al.* (2017). The phylogenetic results presented here highlight that other genera in the clade containing *Dros* and *Prokius* **gen. nov.** require further revision; for instance, *Phylloteras* appears to be paraphyletic. In addition, previous studies have shown that Nearctic *Andricus* is a polyphyletic complex (e.g. Nicholls *et al.* 2018b, Melika *et al.* 2021, Nieves-Aldrey *et al.* 2021) and the *Andricus* species allied to *Prokius* **gen. nov.** are likely different from typical *Andricus* known from the Western Palaearctic and Asia. Further revisions within this broader group are ongoing tasks and fall outside the scope and objectives of the current work; however, the new genus we describe here serves as another step in clarifying the taxonomy of this broader clade.

Interestingly, known sexual generations of other species in the broader clade containing *Prokius* **gen. nov.** induce fleshy integral leaf galls, often on the edges of the leaf blade (see Doutt 1960, Dailey & Sprenger 1973a, b), which is a gross morphology consistent with the sexual generation galls of the two species described herein. Most of the species allied to *Prokius* **gen. nov.** are known only from their asexual generations, e.g. those in *Dros* and *Phylloteras* (Melika & Abrahamson 2002, Pujade-Villar *et al.* 2017), but we predict that their yet-to-be discovered sexual generations will induce small, somewhat inconspicuous leaf galls. As these sexual generations are found, generic characters will need re-circumscription, further refining our understanding of generic limits in Nearctic and Neotropical Cynipini.

ACKNOWLEDGMENTS

EM was funded by the Sistema Nacional de Investigación of the SENACYT in Panama, the University of Panama and research project SENACYT 52-2016-4-ITE15-05 and No. 266-20218. JLNA was supported by the research project MINECO/FEDER, UE CGL2015-66571-P. We thank Johan Liljeblad and Fredrik Ronquist for granting us permission to reproduce the copyrighted images from Morphbank which are cited within figure captions. We also thank to two anonymous reviewers for their useful comments and corrections and to Miguel Angel Alonso Zarazaga for nomenclatorial advice.

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SUPPLEMENTARY Table 1. Information for specimens sequenced in this study, including collection details, global bioregion and host oak species. GenBank accession numbers (for new data from this study and previously published sequences) are provided for each specimen/gene combination.