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Re-description and systematic re-appraisal of the genus *Kokkocynips* Pujade-Villar & Melika, (Hymenoptera: Cynipidae: Cynipini), including new combinations of Nearctic species and the description of a new species from Panama

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ABSTRACT

The monophyly and taxonomic validity of some currently accepted genera of gall wasps in the Cynipini (Hymenoptera: Cynipidae) are being challenged by recent systematic studies. Here we used morphological and molecular data to re-describe and revise the taxonomic limits of the monotypic genus *Kokkocynips* Pujade-Villar & Melika, previously recorded only from Mexico.

We describe a new species from Panama, *Kokkocynips panamensis* Medianero & Nieves-Aldrey, reared from galls on *Quercus salicifolia* Neé, and add new records from Mexico for the type species of the genus *K. doctorrosae* Pujade-Villar. Six Nearctic species, *Dryocosmus rileyi* (Ashmead, 1896), *D. imbricariae* (Ashmead, 1896), *D. coxii* (Basset, 1881), *D. deciduus* (Beutenmueller, 1913), *Callirhytis difficilis* (Ashmead, 1887) and *C. attractans* (Kinsey, 1922) are transferred to *Kokkocynips*. Species of *Kokkocynips* are associated only with red oaks (*Quercus* section Lobatae (Fagaceae)) and are distributed in the Nearctic and Neotropical regions, from Canada through Mexico and Panama. Taxonomic limits of *Kokkocynips* are discussed in light of the molecular phylogenetic relationships of the studied species. Diagnostic characters, gall description, distribution, and biological data of *Kokkocynips* species are given, including a key for the identification of the asexual generations of seven species.

KEYWORDS: oak gall wasps, key, *Dryocosmus*, *Callirhytis*, Chiriquí, *Quercus,* Lobatae, red oaks

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INTRODUCTION

Gall wasps (Hymenoptera, Cynipidae) are a biologically interesting family within the Cynipoidea; most species are highly specialized phytophages that induce complex galls on plants, although some inhabit galls induced by other cynipids (Nieves-Aldrey 2001, Melika 2006, Liljeblad *et al*. 2008, Blaimer *et al*. 2020) and rarely, also inhabit galls induced by chalcidoids (Nieves-Aldrey *et al*. 2009), gall midges (e.g. Wachi *et al.* 2011) and moths (van Noort *et al.* 2007). The current classification divides the Cynipidae into 12 tribes: Aylacini, Aulacideini, Ceroptresini, Cynipini, Diastrophini, Diplolepidini, Eschatocerini, Paraulacini, Pediaspidini, Phanacidini, Qwaqwaini and Synergini (Ronquist *et al*. 2015, Buffington *et al*. 2020). The Cynipini is the most species-rich gall wasp lineage, comprising the "oak gall wasps", so named because they induce galls on plants in the family Fagaceae, primarily oaks. More than 1,000 species of Cynipini are known in 46 genera worldwide (Melika & Abrahamson 2002; Csóka *et al*. 2005; Ronquist *et al*. 2015; Nicholls *et al*. 2018b; Buffington *et al*. 2020), distributed mainly in the Holarctic region (Weld 1952, Burks 1979, Liljeblad *et al*. 2008; Stone *et al*. 2009; Melika *et al*. 2010). However, in recent years, significant new faunas of oak gall wasps have been discovered in the Neotropical and Oriental regions, leading to the description or re-establishment of 17 genera. Eight of the recently described genera belong to the American fauna; two are endemic to Central America, *Coffeikokkos* Pujade-Villar & Melika (Pujade-Villar *et al*. 2012b) and *Barucynips* Medianero & Nieves-Aldrey (Medianero & Nieves-Aldrey 2013); one, *Protobalandricus* Melika, Nicholls & Stone, is known only from California (Nicholls *et al*. 2018b); and five genera are more widely distributed in North America and Central America: *Kinseyella* Pujade-Villar & Melika (Pujade-Villar *et al*. 2010), *Zapatella* Pujade-Villar & Melika (Pujade-Villar *et al*. 2012a), *Kokkocynips* Pujade-Villar & Melika (Pujade-Villar *et al*. 2013), *Melikaiella* Pujade-Villar (Pujade-Villar *et al*. 2014) and *Striatoandricus* Pujade-Villar (Cuesta-Porta *et al*. 2020).

In the Neotropical Region, recent studies have unveiled a rich diversity of Cynipidae in the high mountains of western Panama, associated with nine oak species in the *Quercus* sections Lobatae (red oaks) and *Quercus sensu stricto* (white oaks) (see Medianero and Nieves-Aldrey 2011 for a synthesis). However, much of this fauna requires more thorough taxonomic study, as some specimens show combinations of morphological characters that make assignment to any known genus problematic.

Among these problematic taxa we found specimens of an undescribed species whose diagnostic morphological characters did not fit any currently described genus of Cynipini, suggesting that it should be placed within a new genus. To test this hypothesis, we sequenced the new species from Panama and included it in ongoing molecular phylogenetic analyses of global Cynipini (Nicholls *et al.* in prep.; Tang *et al.* in prep.). The resulting preliminary trees placed the new species in a large clade associated only with red oaks (*Quercus* section Lobatae) and, more specifically, within a sub-clade that included some Nearctic species currently classified within *Dryocosmus* and *Callirhytis*. Morphological study of these Nearctic species indicated that they shared the main diagnostic characters of the new species from Panama but not the diagnostic characters as originally defined for *Dryocosmus* and *Callirhytis*. Furthermore, specimens of *Kokkocynips doctorrosae* Pujade-Villar & Melika, 2013, the only species within a recently-described genus from Mexico, also nested within this same clade of mis-placed *Dryocosmus*, *Callirhytis* and the new unplaced Panamanian species. These results indicated the need for some generic-level revision. Since the name *Kokkocynips* has nomenclatorial priority it is not necessary to describe a new genus but only to re-circumscribe the generic limits of *Kokkocynips* in the light of these new findings. This includes the re-appraisal of the diagnostic characters of *Kokkocynips*, which in the original description were focused around the reticulate sculpture on the metasomal terga, and logically must reflect characters of all the member species. Here we test this taxonomic hypothesis, with an appropriate sample of species, using both morphological and molecular techniques.

This work aims to contribute to the clarification of the currently uncertain (even chaotic) limits of the genera and species associated with *Quercus* species of the section Lobatae. To this end, we test expansion of the current concept of *Kokkocynips* into a defendable taxonomic unit, incorporating both description of a new species from Panama and re-analysis of other mis-placed species from the genera *Dryocosmus* and *Callirhytis*. Furthermore, this work continues the ongoing description of new species in the rich cynipid fauna of Panama.

MATERIAL AND METHODS

Gall sampling

Adults of the new species were reared from galls collected on *Quercus salicifolia* Neé (Fagaceae, sect. Lobatae). Galls were sampled from December 2007 to August 2010 and from June 2016 to January 2019 at Volcán Barú and El Salto, Boquete, Chiriquí Province, Panama. The adult insects emerged in the laboratory from rearing cages. 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). The identification of the *Quercus* species was based on several key references (Breedlove 2001; Burger 1977) as well as on comparisons with material in the collections of the University of Panama and the Smithsonian Tropical Research Institute.

Specimen Preparation

Specimens of *Kokkocynips panamensis* and *Kokkocynips doctorrosae* were observed in the MNCN 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 standardised views were taken using an FEI Quanta 200 microscope (high vacuum technique). The forewings were mounted on slides in Euparal and 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 eye piece of the light microscope.

One exemplar of each specimen series of *K. imbricariae*, *K. difficilis*, *K. coxii* and *K. rileyi* deposited in USNM were also examined under a SEM. Images were generated using a Hitachi®™ TM3000 desktop scanning electron microscope; specimens were coated in 25–30 nm gold-palladium alloy (Cressington®™ 108 auto sputtercoater), with an 'analysis' voltage and a 'compo' mode. High resolution images in color for *K. coxii*, *K. decidua*, *K. difficilis*, *K. imbricariae* and *K. rileyi* were photographed using a Macroscopic Solutions Macropod Micro Kit (Tolland, CT, USA) and stacked using Zerene Stacker (Richland, WA, USA).

Morphological descriptions

The terminology of morphological structures and abbreviations follows Ronquist and Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001), Melika (2006) and Liljeblad *et al*. (2008). For 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 analysis

DNA sequence data were used to support the delimitation of the genus *Kokkocynips* and place this genus within a broader phylogeny of the Cynipini. One individual of each *Kokkocynips* 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). These data were combined with a slightly reduced version of the three gene dataset presented in Nicholls *et al*. (2017) to provide context for this genus within global Cynipini diversity. Some additional taxa were sequenced to provide increased sampling of cynipid species galling section Lobatae oaks including species from several recently described genera (*Melikaiella*, *Zapatella*). Two *Striatoandricus* species were included to assess the phylogenetic distribution of the distinctive metasomal sculpturing shared by *Kokkocynips* and *Striatoandricus*. Finally, a phylogenetically-closer outgroup taxon, *Synergus japonicus*, was used instead of the outgroups from Nicholls *et al*. (2017). The final dataset consisted of 60 Cynipini species, including eight *Kokkocynips* species (details in Supplementary Table 1).

Alignments for each locus were constructed using MAFFT version 7.471 (Katoh 2013). The cytb alignment was partitioned by codon position, the opsin alignment was divided into three partitions (first and second codon positions in a single data partition as they contained only a small number of variable sites; third codon positions; and the intronic section of this gene fragment), while the D2 fragment was treated as a single partition. Appropriate substitution models were determined for each partition using the software jModeltest v2.1.7 (Darriba *et a*l. 2012), and these models then simplified if not all substitution types specified in the jModeltest output were actually present in the respective partition. Phylogenetic relationships were estimated using MrBayes v3.2.7a (Ronquist *et al*. 2012) using a concatenated matrix of the three genes given that these genes show no evidence of significant topological incongruence (Stone *et al*. 2009). Independent HKY+I+G models were estimated for the cytb 1st position and cytb 2nd position partitions, HKY+G models for the cytb 3rd position and opsin 3rd position partitions, HKY+I models for the opsin 1st+2nd position and opsin intron partitions, and a GTR+I+G model for the D2 partition. A strict molecular clock model was also imposed. Two independent runs were performed, each for 6 million generations and sampled every 1000 generations; this provided effective samples sizes >200 for each model parameter. A majority-rule consensus tree was calculated using samples taken from the final 3 million generations of both runs.

The degree of variation among and within species belonging to the re-defined genus *Kokkocynips* was assessed using cytb sequence data from additional individuals sequenced for this study or from Nicholls *et al*. (2018a), with between two and four individuals per species sampled (see Supplementary Table 1). Pairwise genetic distances using HKY corrections were calculated between all individuals using the software PAUP* (Swofford 1998), then average within- and among-species distances determined.

RESULTS

Molecular phylogenetics

Kokkocynips, as redefined in this study, forms a well-supported monophyletic clade within the broader multi-locus Cynipini phylogeny (Figure 1). It is related to other species from a range of genera galling section Lobatae oaks in the Nearctic (*Zopheroteras*, *Callirhytis*, *Dryocosmus*). The new species, *K. panamensis,* clusters with the Arizonan species *K. coxii*, albeit with only moderate support, but consistent with their shared gall morphology of swellings integral within twigs. The type species *K. doctorrosae* is placed with strong support in a clade containing two eastern Nearctic species inducing similar round detachable stem galls (*K. imbricariae*, *K. difficilis*) and the leaf-galling species *K. decidua*. As highlighted in preliminary analyses, most of these species were formerly placed within *Callirhytis* and *Dryocosmus* and hence are transferred here to *Kokkocynips*.

Genetic distances for the mitochondrial cytb gene among species within *Kokkocynips* (Table 1) ranged from 5.1% (*K. imbricariae* vs. *K. difficilis*) to 12.8% (*K. coxii* vs. both *K. decidua* and K. *doctorrosae*). These genetic distances are consistent with those found among congeners in other cynipid genera (5.1% in *Cyclocynips*, Melika *et al*. 2013; 4.1% to 16.7% in *Dryocosmus* and 10.8% in *Chilaspis*, Cerasa *et al*. 2018; 2.4% to 5.3% in *Callirhytis*, Nicholls & Pujade-Villar 2020; 8% to 27% in *Cycloneuroterus*, Tang *et al*. 2020). All new sequences are deposited in GenBank, accessions MW326677-MW326729.

Morphology-based taxonomy of *Kokkocynips*

Kokkocynips Pujade-Villar & Melika, 2013

Type species: *Kokkocynips doctorrosae* Pujade-Villar, 2013.

Diagnosis. Kokkocynips differs from all other known Cynipini genera by the following combination of characters: Malar (subocular) sulcus absent or sometimes visible in the form of a short and shallow impressed area marked by some irregular striae; rarely complete, but weakly impressed. Facial striae radiating from clypeus indistinct or very short to absent. Anterior and posterior tentorial pits large and very deeply impressed and distinctive. Epistomal line strongly curved. Gular sulci widely separated at hypostomata. Female antennae 14-segmented, F1 1.4 to 2x as long as F2. Notauli percurrent, well-marked. Median mesoscutal impression either absent or if present only short and weakly impressed. Scutellar foveae rounded or ovate, usually indistinctly margined posteriorly; widely separated in *K. panamensis* n. sp. but narrowly in other species. Mesoscutum with delicate and shiny coriaceous sculpture, almost smooth in some species. Mesopleuron medially with a longitudinal band of coriaceous sculpture, sometimes also with some longitudinal rugae or carina; upper and lower parts of mesopleuron reticulate in the type species *K. doctorrosae*, but more usually without visible sculpture. Lateral propodeal carinae distinct, more often subparallel but slightly divergent dorsally and curved ventrally in *K. panamensis* n. sp.; central and lateral propodeal areas dull rugose. Forewings with open radial cell; distal margin of forewing with fringe of short setae. Metatarsal claws simple, without acute basal lobe or tooth. Metasoma with a group of sparse setae latero-basally. Terga entirely and regularly reticulate in the type species; with conspicuous micropunctures to almost smooth in other species. Projecting part of hypopygial spine long, 4.5x to 6x as long as wide in ventral view, laterally with some setae, basal setae longer while the apical ones are short and not reaching apex of the spine.

One of the diagnostic morphological characters mentioned in the original description in support of a monotypic *Kokkocynips* was the presence of a striking feature, namely the reticulate sculpture on the metasomal terga (Pujade-Villar *et al*. 2013). A similar morphological feature is present in a group of *Andricus* species (*A. georgei* Pujade-Villar, 2011 and *A. nievesaldreyi* Pujade-Villar, 2011), leading to comparison of *Kokkocynips* with this group. However, as mentioned in Pujade-Villar et al. (2013), these species have toothed claws, are associated with white oaks and have recently been moved into their own new genus *Striatoandricus* (Cuesta-Porta *et al*. 2020). In fact, *Kokkocynips* is placed in a very different part of the phylogeny to *Striatoandricus* (see Fig. 1), implying that the distinct sculpturing on the metasomal tergites shared by these genera has been independently derived. Hence it can be concluded that within the Cynipini this character of reticulate sculpturing of the metasoma is not reliable for assessing relationships among genera but only for determining relatedness within genera.

In the original description of *Kokkocynips* the new genus and species was not compared with some Nearctic species that were originally classified within *Dryocosmus* and *Callirhytis*, which we show here share other important diagnostic characters such as the simple tarsal claw, similar antennae, particular sculpturing of the mesoscutum and mesopleuron, their gall morphology and an association with red oaks. Hence, we provide the following more detailed diagnoses.

TABLE 1. Percentage pairwise genetic distances among the eight species of *Kokkocynips*, based upon 433 base pairs of the cytochrome *b* gene using a HKY correction. The number of individuals sequenced per species is indicated next to the species name. Values on the diagonal (in bold) indicate variation within a species; off-diagonal values indicate between-species distances.

	K. attractans	*K. coxii*	*K. decidua*	*K. difficilis*	*K. doctorrosae*	*K. imbricariae*	*K. panamensis*	*K. rileyi*
K. attractans (n=2)	**0.5**							
K. coxii (n=4)	11.5	**1.4**						
K. decidua (n=2)	9.9	12.8	**0.2**					
K. difficilis (n=2)	7.6	10.0	6.0	**0.5**				
K. doctorrosae (n=2)	9.8	12.8	8.2	5.4	**0.0**			
K. imbricariae (n=4)	9.6	12.6	9.6	5.1	5.5	**1.3**		
K. panamensis (n=2)	10.3	12.2	11.1	8.7	10.4	10.7	**0.0**	
K. rileyi (n=2)	9.9	12.2	9.9	6.2	7.9	9.3	11.3	**0.5**

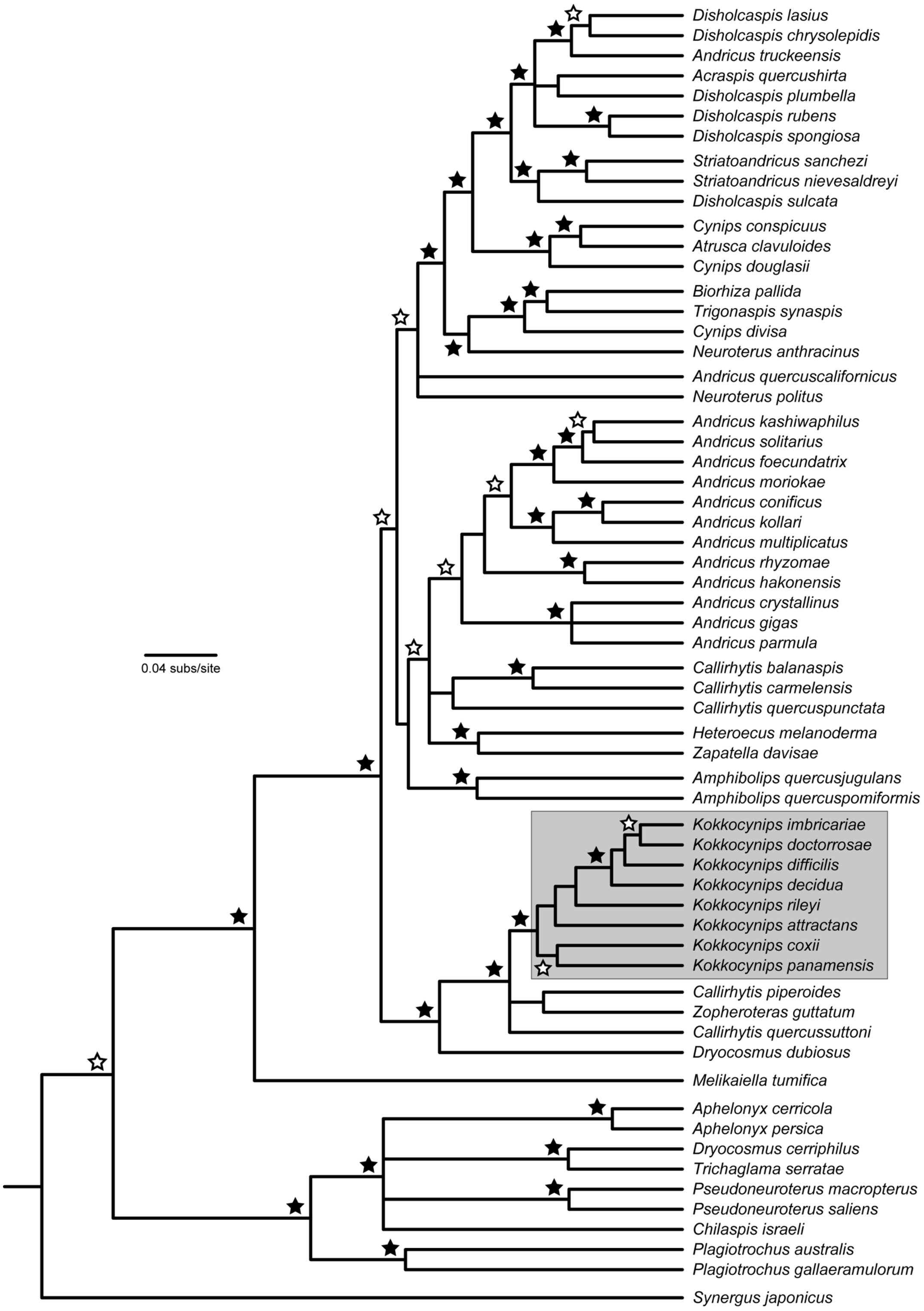

FIG. 1. Majority-rule consensus tree of species sampled from across the Cynipini, based on a Bayesian analysis of a concatenation of three loci (cytochrome *b*, long-wavelength opsin, and the D2 region of the 28S rRNA gene). Black stars at nodes indicate ≥95% posterior probability support; white stars indicate 70%-94% posterior probability support. The revised limits of the genus *Kokkocynips* are indicated by the grey shaded box.

Within the group of the Cynipini genera with a transscutal fissure and fully winged asexual females, *Kokkocynips* is most similar to *Dryocosmus*, *Callirhytis*, *Loxaulus* and *Plagiotrochus*. *Kokkocynips* differs from *Dryocosmus* (sensu Giraud 1859, not Weld 1926b), in the long spine of the hypopygium without long subapical setae, absence of radiating facial striae, presence of a band of sculpture on the mesopleuron, and the absence of a median carina in the propodeal sculpture. It differs from *Plagiotrochus* in lacking radiating facial striae from the clypeus, the relatively longer hypopygial spine and difference in sculpture of the mesoscutum. The indistinct malar sulcus, distal forewing margin with setae, the sculpture of propodeum, and the structure of the hypopygial spine, readily differentiate *Kokkocynips* from *Callirhytis* and the allied genera *Melikaiella* and *Zapatella*. *Kokkocynips* differs from *Andricus* by having simple metatarsal claws, not having a whitish band of dense setae on metasomal terga, nor radiating striae from the clypeus reaching or almost reaching the ventral margin of the eye, and having a weak but still discernible malar sulcus (if the metasoma is not reticulated). It differs from *Belonocnema* by the apex of the fore tibia, which in *Belonocnema* extends far behind the base of fore tarsomere I, and the 2nd abscissa of Rs is strongly curved. *Loxaulus* differs from *Kokkocynips* by the finely transversely coriaceous sculpture of the mesoscutum, the presence of the median propodeal carina and the short prominent part of the ventral spine of the hypopygium, which is always less than 3.5 times as long as broad while in *Kokkocynips* it is always longer. Finally, *Erythres* differs from *Kokkocynips* by the sculpture of the head, mesosoma and dorsal surface of legs, which are uniformly and finely punctate-rugose; the notauli are also incomplete in *Erythres*.

Re-description

Asexual female largely glabrous, hardly pubescent. Head in anterior view wider than high, genae slightly expanded behind eyes. Facial striae radiating from clypeus very short, barely distinctive. Anterior and posterior tentorial pits large and very deeply impressed and distinctive. Epistomal line strongly curved. Clypeus trapezoidal with ventral margin sinuate, moderately projecting over mandibles. Malar sulcus absent or only present in the form of a shallow impressed area; rarely complete but weak impressed. Head, in posterior view, without occipital carina. Gular sulci widely separated at hypostomata. Antenna 14-segmented, F1 1.4 to 2x as long as F2. Pronotum short medially, pronotal plate indistinct dorsally. Mesoscutum reticulate or delicately coriaceous to almost smooth and shiny in the middle lobe, overall weakly pubescent. Notauli percurrent, deeply impressed. Median mesoscutal impression present, usually short and weakly impressed. Transscutal fissure present. Scutellar foveae rounded or oval, more or less widely separated medially and usually with indistinct posterior margins. Mesopleuron medially with a longitudinal band of fine coriaceous sculpture variably extended, some weak longitudinal rugae also present in some species; the upper and lower parts of the mesopleuron smooth except in *K. doctorrosae*. Lateral propodeal carinae distinct, slightly divergent dorsally and curved ventrally. Metatarsal claws simple, without acute basal lobe or tooth. Forewing with open radial cell along anterior margin; areolet triangular; apical margin of wing with short hair fringe.

Metasoma with a group of sparse setae latero-basally. Projecting part of hypopygial spine long, about 4.5 to 6 times as long as wide in ventral view, laterally with some setae, basal setae longer, the apical ones short and not reaching apex of the spine (Figs. 3E-G).

Gall structures: the galls induced by asexual forms of *Kokkocynips* species range from multilocular (many-chambered) stem swellings to unilocular (single-chambered) solitary or aggregated galls on stems or leaves (Figs. 4D-F and 11).

Host plant association: *Kokkocynips* species are associated only with red oaks, in *Quercus* section Lobatae.

Biology: all but one *Kokkocynips* species are known only from their asexual generations. However, *Callirhytis attractans* (Kinsey, 1922) (= *Callirhytis uvellae* Weld, 1944), that our phylogenetic analysis shows is included in the genus *Kokkocynips*, is known only from its sexual generation.

Distribution: Nearctic and Neotropical. Currently known from Panama, Mexico, the United States and Canada.

Key to asexual females of *Kokkocynips*

1. Scutellar foveae with inner margins widely separated by a broad septum; with distinct posterior margins (Fig. 3B). Lateral carinae of propodeum narrow and clearly divergent in anterior 2/3 of propodeum (Fig. 2D). Head and body contrasting in colour with antennae and metatibia (Fig. 4B) . . . . **_K. panamensis_ n. sp.**

• Scutellar foveae with inner margins in contact anteriorly or narrowly separated by a carina or narrow septum; posterior margins usually indistinct (Figs. 5B, 6C, 7C, 8C). Lateral carinae of propodeum usually broader, subparallel or only slightly divergent (Figs. 7E, 8E, 9E). Head and body usually not contrasting in colour with legs and antennae (Figs. 10A, 10C, 10D, 10E, 10F) **2**

2. Metasomal terga with regular coriaceous-reticulate sculpture (Figs. 5F-G). Sculpture of mesopleuron extended beyond the medial area towards upper and lower areas of mesopleuron (Fig. 5C). Scutellar foveae with rugose sculpture (Fig. 5B) . . . . ***K. doctorrosae*** **Pujade-Villar**

- Metasomal terga punctate to almost smooth (Figs. 6E, 7F, 8F, 9F). Sculpture of mesopleuron usually present only in the medial area; upper and lower areas of mesopleuron smooth (Fig. 6D, 7D, 8D, 9D). Scutellar foveae smooth or only with some longitudinal rugae (Figs. 6C, 7C, 8C, 9C) 3

3. Head, mesosoma and metasoma dark brown to black (Fig. 10A). Notauli subparallel or only slightly converging towards the transscutal fissure; mid lobe of mesoscutum almost smooth (Fig. 10B) . . . . ***K. decidua*** **(Beutenmueller)**

- Head, mesosoma and metasoma amber to reddish (Figs. 10C, 10D, 10E, 10F). Notauli more converging towards transscutal fissure (Figs. 6C, 7C, 9C); mid lobe of mesoscutum with fine coriaceous sculpture (Figs. 7C, 8C, 9C) **4**

4. Malar sulcus well defined but weakly impressed (Fig. 7B). Projection of ventral spine of hypopygium relatively short, less than 4x as long as broad in lateral view (Fig. 7H). Scutellum not marginated and coriaceus at its centre (Fig. 7E); scutellar foveae smooth, not margined posteriorly. Metasomal punctures absent (Fig. 7F). Mesosoma, metasoma and coxae darker than rest of body in lateral view (Fig. 10C). . . . . ***K. coxii*** **(Basset)**

- Malar sulcus usually shallowly impressed, sometimes indistinct (Figs. 6A, 8B, 9B). Projection of ventral spine of hypopygium longer, more than 4 times as long as broad in lateral view (Figs. 6E, 8H, 9H). Scutellum marginated and surface rugose (Figs. 6C-D, 8C-D, 9C-D); scutellar foveae smooth or with some longitudinal rugae, margined posteriorly in *K. difficilis* (Figs. 9C, 9E). Metasomal punctures sometimes weak but present (Figs. 6E, 8F, 9F). Mesosoma, metasoma and coxae concolorous with the rest of body in lateral view (Figs. 10D, 10E, 10F) **5**

5. Notauli strongly converging posteriorly, only slightly separated at the junction with the transscutal fissure (Fig. 6C); scutellar foveae with indistinct posterior margins, separated medially by a longitudinal carina (Fig 6C). . . . ***K. imbricariae*** **(Ashmead)**

- Notauli only weakly converging posteriorly, more widely separated at the junction with the transscutal fissure (Figs. 8C, 9C); scutellar foveae posteriorly margined or not, separated medially by an anterior contact point or by a carina (Figs. 8C, 9C) . . **6**

6. Projection of ventral spine of hypopygium relatively short, 4.5x as long as wide in lateral view (Fig. 7H). Scutellar foveae with some rugae; not margined posteriorly. (Fig. 7C). . . . . ***K. rileyi*** **(Ashmead)**

- Projection of ventral spine of hypopygium long, 6x as long as wide in lateral view (Fig. 8H). Scutellar foveae smooth; with distinct margins (Fig. 8C).. . . . . ***K. difficilis*** **(Ashmead)**

Kokkocynips panamensis **Medianero & Nieves-Aldrey n. sp. (Figs. 2–4)**

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Type material. Holotype ♀ (Fig. 4B) (in MNCN, Madrid, Spain), card-mounted. PANAMA, Chiriquí, Boquete, El Salto, 8º 47’ 32.08” N, 82º 27’ 37.09” W, 1,431 m; ex gall of twigs of *Quercus salicifolia* Née (Fagaceae) (Fig. 4E); gall collected 21.x.2008; insect emerged xi.2008, E. Medianero leg. Paratypes: 1♀, same data as holotype. 2♀, same data as holotype but collected 25-x-2008; insect emerged xi-2008. 7♀ PANAMA, Chiriquí, Volcán Barú, 8°47´50.8” N, 82°29´35.9” W, 1,800 m; ex gall of twigs of *Quercus salicifolia* Née (Fagaceae); gall collected 5-xi-2018; insect emerged xi-2018, E. Medianero leg. 3♀, paratypes in Maestría en Entomología, Universidad de Panamá (MEUP).

Etymology. The species name refers to Panama, the country of origin of the new species.

Diagnosis

The new species differs from the type species of the genus, *K. doctorrosae,* by the absence of reticulate sculpture on the metasomal terga. It is easily distinguished from the other species transferred here to *Kokkocynips* by having mesoscutellar foveae with distinct posterior margins and inner margins that are widely separated by a broad septum (Fig. 3B). The gall morphology of the new species is similar to *K. coxii*, and this similarity is reflected in the phylogenetic analysis, with both species falling into the same clade that is sister to the remaining *Kokkocynips* species (Fig. 1).

General Description

Body length, 3.5 mm (range 3.23-3.70 mm; *N* = 6) for females.

Head, mesosoma and metasoma predominantly reddish-amber; frons above clypeus, parapsidal furrows and anterior parallel lines, transscutal fissure, scutellar foveae, sides of mesoscutellum and postero-lateral parts of mesopleuron brown to black. Antennae brown; legs the same colour as body, except for brown metatibia and metatarsi. Forewing very slightly infuscate.

Asexual Female

Head, with frons, face and genae coriaceous. Face with radiating striae from clypeus very short, barely distinctive, that do not reach across half the malar space. Face slightly carinate below torulus. Face and occiput moderately pubescent. Head in dorsal view 2.5x as wide as long (Fig. 2C). POL 1.5x longer than OOL; posterior ocellus separated from inner orbit of eye by 2.0x its longest diameter (Fig. 2C). Head in anterior view generally oval (Fig. 2A), 1.3x as wide as high. Genae slightly expanded behind eyes. Clypeus trapezoidal, 2.4x as wide as high, coriaceous, moderately pubescent, ventral margin moderately sinuate and clearly projected over mandibles. Anterior and posterior tentorial pits large and very deeply impressed and distinctive; epistomal line strongly curved, clypeo-pleurostomal lines distinct. Malar space 0.3x height of compound eye, malar (subocular) sulcus weak but present in the form of a shallow impressed area from compound eye almost reaching to the base of the mandible. Distance between antennal rim and compound eye 1.0x width of antennal socket including rim. Ocellar plate raised. Head, posterior view (Fig. 2B) with coriaceous sculpture and with moderately long setae at the sides. Gular sulci widely separated at hypostomata; distance between occipital and oral foramina as long as the occipital foramen. Without an occipital carina.

Mouthparts (Fig. 2A). Mandibles strong and exposed, moderately pubescent; right mandible with three teeth, left with two teeth. Cardo of maxilla visible, maxillary stipes approximately 2.0x as long as wide. Maxillary palp five-segmented. Labial palp three-segmented (Fig. 2B).

Antennae (Fig. 2E) as long as 1/2 body length, with 14 segments; flagellum not broadening toward apex, with short, erect setae and elongate placodeal sensilla visible only on flagellar segments 2–12. Relative lengths of antennal segments 20:15:50:35:26:26:22:22:18:17:17:16:15:29. Pedicel globose, small, 0.7 times as long as scape; F1 1.4x as long as F2 (Fig. 2E); F12 2.6x longer than wide and 1.9x as long as F11 (Fig. 2F).

Mesosoma (Figs. 3A-C). Mesonotum as long as high in lateral view, strongly convex dorsally (Fig. 3C). Pronotum, moderately pubescent; with long and dense white setae, lateral surface of pronotum with longitudinal wrinkles (Fig. 3C). Pronotum short medially, ratio of length of pronotum medially/laterally = 0.2. Anterior part of pronotal plate with a posterolateral tooth-like section present; dorsal part of pronotal plate distinctly offset, with anterolateral corners, ventral and lateral margins marked (Fig. 3A).

Mesoscutum finely coriaceous; only slightly pubescent with scattered setae anterior and laterally, with a row of setae along the notauli. Notauli percurrent, deep, smooth, well impressed along entire length, reaching pronotum, convergent posteriorly. Median mesoscutal impression present but very short. Anteroadmedian signa clearly visible. Parapsidal signa broad, smooth. Transscutal fissure narrow; distance between the fissure and the anterior margin of scutellar foveae wide (Fig. 3B). Scutellum (Fig. 3B), rounded, approximately 0.4x as long as mesoscutum, coriaceous with some lateral carinae, posterior margin not emarginate, scutellar foveae well differentiated, deep, smooth and quite widely separated, the space between them being almost as wide as a fovea. Scutellum overlapping the dorsellum posteriorly in lateral view. Axillula barely pubescent, their anterior margins and posterior marked. Mesopleuron medially with a longitudinal band of coriaceous sculpture and with some shallow longitudinal rugae; the upper and low parts of the mesopleuron without sculpture; the mesopleural triangle, moderately pubescent (Fig. 3C).

Metanotum (Figs. 2D and 3C). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at mid-height of metapectal-propodeal complex (Fig. 3C). Lateral propodeal carinae distinct, slightly divergent dorsally and curved ventrally. Median propodeal area wide and bare, with only some weak rugae. Lateral propodeal area moderately pubescent. Nucha rugose.

Legs (Fig. 3D). Moderately pubescent, Metatarsal claws simple, without acute basal lobes or teeth (Fig. 3F).

Forewing (Fig. 4A). As long as body; veins strongly pigmented. Radial cell 3.4x as long as wide, open along anterior margin, areolet large, triangular, closed. Rs nearly straight, reaching wing margin. R1 slightly bowed not reaching wing margin. M nearly straight, not reaching wing margin. Rs+M reaching basalis at mid-height. First abscissa of radius (2r) slightly angled. Basal cell pubescent. Apical margin of wing with moderately long hair fringe.

Metasoma rounded (Fig. 3E). Large, as long as head and mesosoma combined, 1.1x as long as high in lateral view. Second metasomal tergite about 0.5x length of metasoma, with a group of sparse setae latero-basally, following tergites finely but densely micropunctate (Fig. 3E). Projecting part of hypopygial spine long, about 4.5x as long as wide in ventral view, laterally with some setae, basal setae longer, the apical ones short and not reaching apex of the spine (Fig. 3G).

Gall (Figs. 4C–E, 11H)

Kokkocynips panamensis induces an elongated multilocular swelling gall in young stems, oval to spindle-shaped, with the same colour and surface texture as the bark of twigs (Figs. 4D & E). The galls have an average length of 35 mm (range 20 to 60 mm) and diameter 51 mm (range 30 to 85 mm) (n = 12). The internal structure of the gall is highly lignified and is multilocular, containing several larval cells (Figs. 4C, 4D and 11H). The outer layers crack and peel in older galls.

The gall of *Kokkocynips panamensis* resembles those induced by *Kokkocynips coxii* (Bassett, 1881), *Protobalandricus spectabilis* (Kinsey, 1922) and *Dryocosmus asymmetricus* (Kinsey, 1922) from North America, *Andricus costaricensis* Pujade-Villar & Melika, 2009 from Costa Rica and some galls of *Plagiotrochus* species (e.g., *P. gallaeramulorum* (Boyer de Fonsc., 1832)) and *Pseudoneuroterus macropterus* (Hartig, 1843) from Europe; however, the morphology of the adults is very different as are the *Quercus* hosts.

Host plant: *Quercus salicifolia* Née (Fagaceae, *Quercus* sect. Lobatae).

Distribution: *Kokkocynips panamensis* was found from 1,400–1,800m above sea level at Volcán Barú and El Salto, Chiriquí Province, Panama.

Biology: only the asexual generation of *Kokkocynips panamensis* is known. The galls are found between October and November, during the rainy season. The adult insects emerge from mature galls in November.

Kokkocynips doctorrosae Pujade-Villar, 2013 (Figs. 5, 10B and 11A)

Kokkocynips doctorrosae Pujade-Villar, 2013. *Act. Zool. Mex.,* 29(1): 211.

Material examined: holotype. Female (deposited in the collection J.P-V, UB), labeled as "MEX, Michoacán, Carretera Federal Maravatío-Morelia, 19º54'22.91''N100º34'28.35''W, 2391 m" (white label), "Ex. *Q. acutifolia*, (08.xii.2011), 21.xii.2011" (white label); "Holotype *Kokkocynips doctorrosae* desig. JP-V 2012" (red label).

Other material examined: 2 females, ex gall *Quercus castanea*, MEXICO, Oaxaca, Hunduchii. 2192 m., 08.xi.2008. Y. Maldonado leg.; *Q. castanea*, MEXICO, Oacaxa, Santa Catarina Ixtepeji, 10.vii.2012: 3♀, R. Clark leg. (MEX553, MEX567); *Q. crassipes*, MEXICO, Mexico State, near to Santa Rita Tlahuapan, 18.vii.2012, A. Equihua-Martínez & E. Estrada-Venegas leg. (only galls: S350); *Q. castanea*, MEXICO, Michoacán, Federal highway Maravatío-Morelia, 14.vi.2019, JP-V leg. (only galls: C-C1); *Quercus* sp., MEXICO, Puebla, Tetela de Ocampo, 22.ix.2014, A. Equihua-Martínez & E. Estrada-Venegas leg. (only galls: S435); *Q. crassifolia*, Tetela de Ocampo, 15.vi.2018, JP-V leg. (only galls: S505); *Quercus* sp., MEXICO, Puebla, Chignahuapan, 25.vi.2016 & 27.vi.2016, JP-V leg. (only galls: S475**,** S476 S485).

Gall: the gall (Fig. 11A) is unilocular on twigs, nearly spherical, 8–10 mm in diameter, slightly flattened basally, with a smooth surface, lacking pubescence, yellowish with concentric circular red-brown lines, apically reddish-pink. The gall stays soft when mature, but not fragile. Larval chamber ovate, 1.4 × 1.8 mm, with thin walls (0.16 mm), surrounded by a sponge-like tissue, located in the centre of the gall. Exit hole usually located laterally. There is always a longitudinal crack in the bark where the gall is inserted.

Host plant: Quercus acutifolia, *Q. castanea*, *Q. crassifolia* and *Q. crassipes* (section Lobatae within *Quercus*).

Biology: only known from an asexual generation.

Distribution: currently known only from Mexico. Originally recorded only from the state of Michoacan. New records from Oaxaca, Puebla and Mexico states added here extend the distribution of this species.

Remarks: K. doctorrosae can be easily distinguished from the other known species of *Kokkocynips* by the regular well-marked reticulate sculpture on the metasomal terga. Congruent with the morphological similarity of both adults and galls, this species is sister to the Nearctic species *K. imbricariae* in the multi-locus phylogenetic analysis (Fig. 1), and forms a close cluster with *K. imbricariae* and *K. difficilis* based on cytb distances (all just over 5% divergent; Table 1).

Kokkocynips decidua (Beutenmueller, 1913) n. comb. (Figs. 10A, 11D)

Andricus decidua Beutenmueller, 1913. *Insecut. Inscit. Menst.,* 1: 131-132.
Dryocosmus deciduus (Beutenmueller): Weld, 1926b. *Proc. U.S. Nat. Mus*., 68: 41.

Material examined: holotype. Female. Black Mountains, NC, 1912. Beutenmuller, type, *Andricus decidua* type Beutm., Beut Coll rec'd 1935, USNM Type No. 52978, *Dryocosmus deciduus* (Beut), USNMENT00802028, USNM.

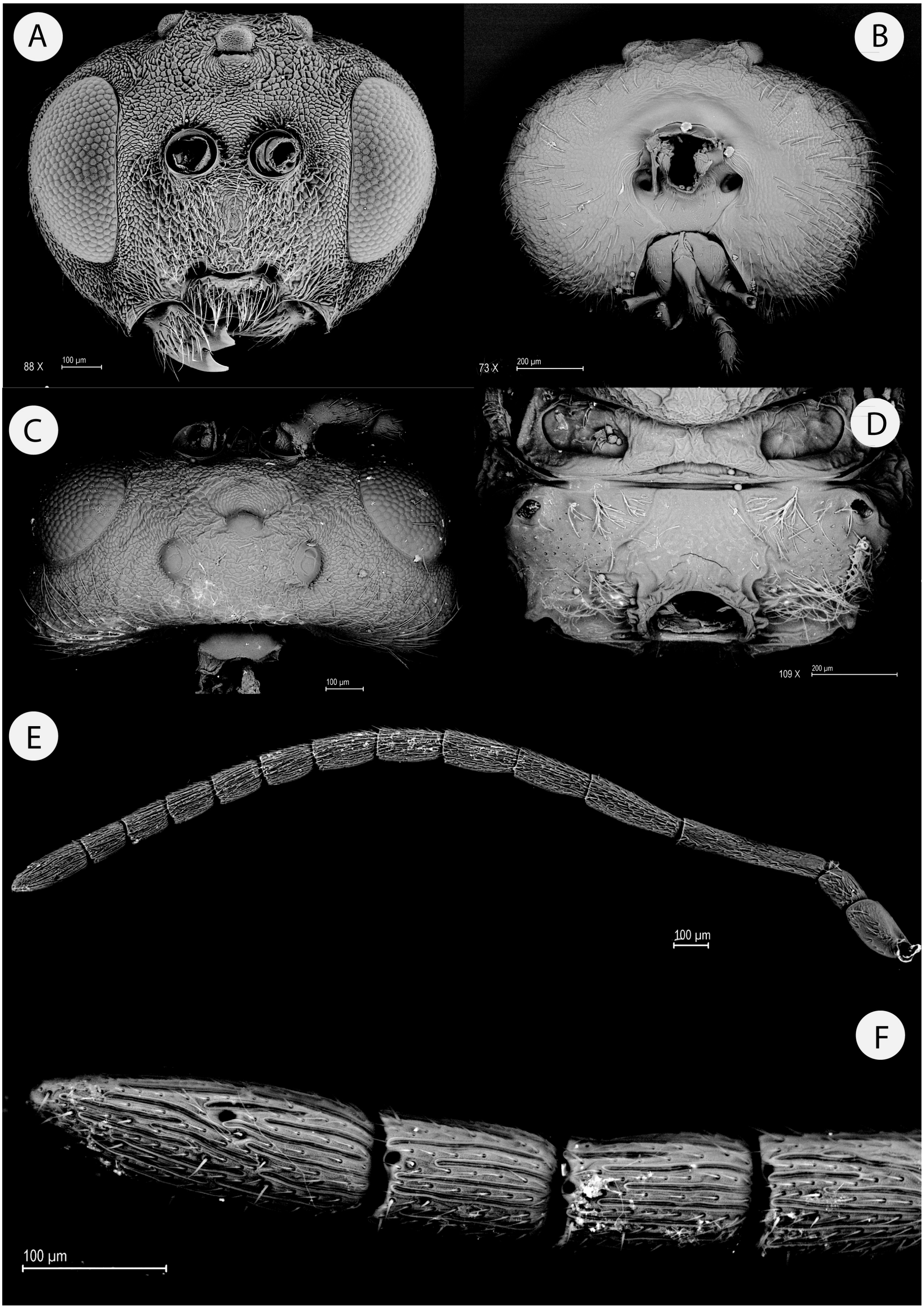

FIG. 2. *Kokkocynips panamensis*, **new species**, asexual female. (A) Head, anterior view. (B) Head, posterior view. (C) Head, dorsal view. (D) Propodeum. (E) Female antenna. (F) Detail of the last flagellomeres.

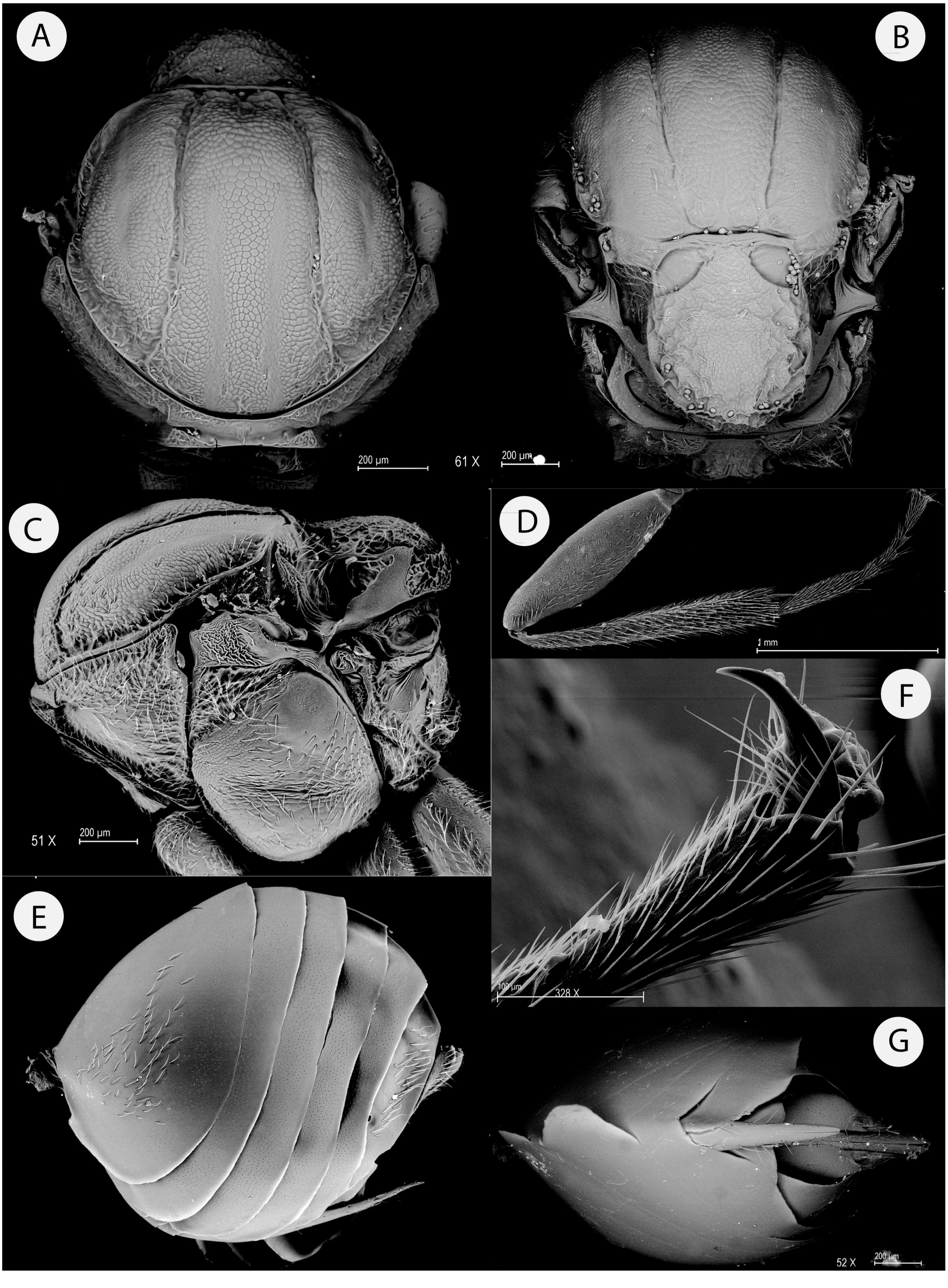

FIG. 3. *Kokkocynips panamensis*, **new species**, asexual female. (A) Pronotum, antero-dorsal view. (B) Mesosoma, dorsal view. (C) Mesosoma, lateral view. (D) Hind leg. (E) Metasoma, lateral view. (F) Metatarsal claw. (G) Detail of the ventral spine of the hypopygium, ventral view.

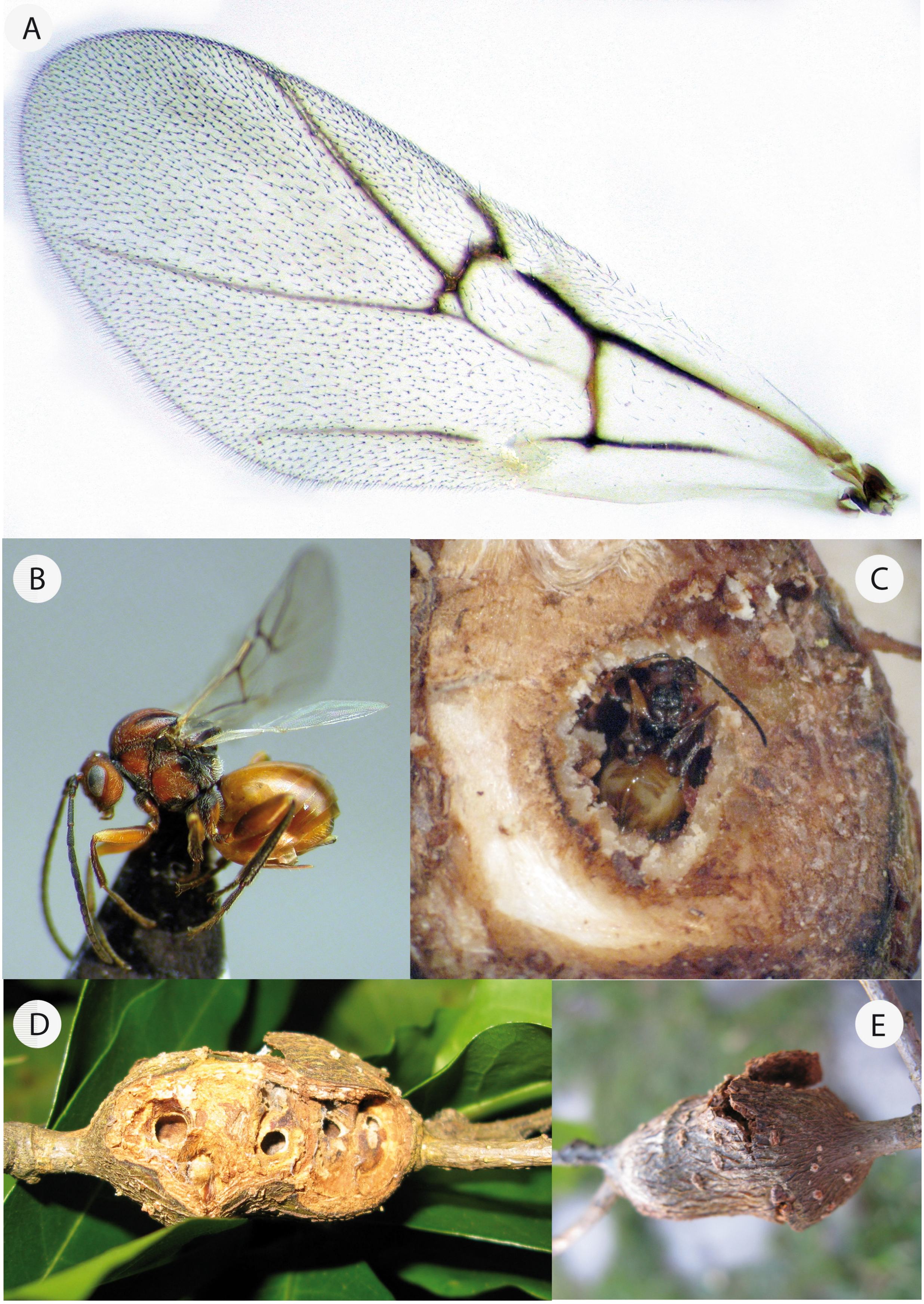

FIG. 4. *Kokkocynips panamensis*, **new species**, asexual female. (A) Forewing. (B) Habitus. (C) Section of gall showing the alive cynipid. (D) Section of a mature galls on *Quercus salicifolia.* (E) External view of a gall.

Other material examined: USA. Maryland. '709Q on *Q. rubra*. 4 females. USNMENT01735091-USNMENT01735094 (USNM). Illinois. Evanston. Cut out Nov 16, 1917. LH Weld Coll., 259. *Andricus decidua* WB Beutt., Beutt coll. Rec'd 1935. 1 female. USNMENT01735090 (USNM). Michigan. Through CV Riley. *D. deciduus*, det. Weld 1943. 1 female. USNMENT01735095 (USNM).

Gall: galls (Fig. 11D) are multilocular clusters of rounded or elongated swellings on the midribs of the leaves that contain from a few to about 40 oblong larval chambers, depending upon the size of the gall (Beutenmueller, 1913).

Host plant: initially described from red oak (*Quercus rubra*) and black oak (*Q. velutina*), but Weld (1959) lists this species from most section Lobatae oaks in eastern North America.

Biology: only known from an asexual generation. The gall is fully-grown by September or October, when it falls to the ground.

Distribution: USA, from New England states southwards at least as far as North Carolina and westwards to the eastern Midwest.

Remarks: this species was transferred to *Dryocosmus* by Weld (1926b) based on the following morphological account: "mesoscutum smooth, parapsidal grooves complete, head sculptured, no malar groove, antennal segment 3 longer than 4 and claws simple". These characters match those for *Kokkocynips*. However, Weld does not mention some other important diagnostic characters that make placement of this species within *Dryocosmus* problematic, such as the long hypopygial spine without long subapical setae and a sculptured mesopleuron, not smooth as in *Dryocosmus* (Fig. 10A). According to these morphological features and molecular evidence, this species should be included in *Kokkocynips* and we herewith formally transfer the species into this genus. The multi-locus phylogeny (Fig. 1) places *K. decidua* as the sister taxon of the *K. imbricariae*, *K. doctorrosae*, *K. difficilis* complex.

Kokkocynips imbricariae **(Ashmead, 1896) n. comb. (Figs. 6, 10F, 11B)**

Andricus imbrecariae Ashmead, 1896. *Proc. U.S. Nat. Mus*., vol. 19, p.122.
Holcaspis fasciata Bassett, 1900. *Trans. Amer. Ent. Soc*., vol, 26, p.328. [Syn. by Weld, 1926b: 43].
Dryocosmus fasciatus (Bassett): Weld, 1922a. *Proc. U.S. Nat. Mus*., vol. 61, art. 18, p.7.
*Dryocosmus imbricariae** (Ashmead): Weld, 1926b. *Proc. U.S. Nat. Mus*., 68, 43.

* The original spelling 'imbrecariae' is a typographical error and Ashmead had corrected it in his own copy of the paper to align it with the name of the host oak (Weld, 1926b).

Material examined: *syntypes. Andricus imbrecariae.* Through CV Riley, No. 714 P on *Q. imbricariae*, St. L. Mo., Oct 12. 81, Type number 3072, USNM, *Andricus imbrecariae*, USNMENT00802135 (USNM).

Missouri. No. 714 P on *Q. imbracariae*, St. Louis, MO. 12 Oct 1881, CV Riley, USNM type #3072. Two females. USNMENT01735157 and USNMENT01735158 (USNM).

Cotypes. *Disholcaspis fasciata*. Connecticut. Waterbury, HF Bassett, cotype, USNM type # 27177, *Holcaspis fasciata* WB Bassett. 17 females. USNMENT01735140-USNMENT01735156 (USNM).

Other material examined: USA. Alabama and Florida. Hopkins 15632a. Troy and Dothan, AL; Cottondate, FL. *Quercus marilandica* and *Quercus falcata*, October 1919., LH Weld. 10 females. USNMENT01735100-USNMENT01735109 (USNM). Missouri. Hopkins 10776a. Iorton, *Quercus rubra*. 12 Oct. 1918. Galls collected on ground, some from twigs; wasps emerged Oct. 1919. 5 females, USNMENT10735116-USNMENT01735120 (USNM). Poplar Bluff, IX.20.1918, LH Weld, ex *Q. digitata*, Beutt coll. record 1935, 1 female, USNMENT01735159 (USNM). St. Louis, MO., No. 136 on *Q. imbracariae*, CV Riley, 2 females, USNMENT01735171 and USNMENT01735172 (USNM). Texas. Hunter 2701, Victoria, ex black jack spkld., X.29.1910; emerged II.1.1912. 11 females. USNMENT01735123, USNMENT01735125-USNMENT01735134 (USNM). Hunter 1369, Victoria, bd stem gall oak, X,17.1905, JD Mitchell, coll. 7 females. USNMENT01735122, USNMENT01735124, USNMENT01735135-USNMENT01735139 (USNM). Victoria Co., Colleto Creek. 29 Oct. 1905, JD Mitchell, Coll. Issued 20 Nov 1906. 10 females, USNMENT01735160-USNMENT01735169 (USNM). Virginia. Hopkins 10773q. East Falls Church. 3 Oct 1018. Galls collected by Penelope Brown just before falling. Cynipini emerged/mounted Oct. 1919. 5 females. USNMENT01735110-USNMENT01735114 (USNM). Unknown locality. '714P' Sept. 10, 1909, 2 females, USNMENT01735173 and USNMENT01735174 (USNM).

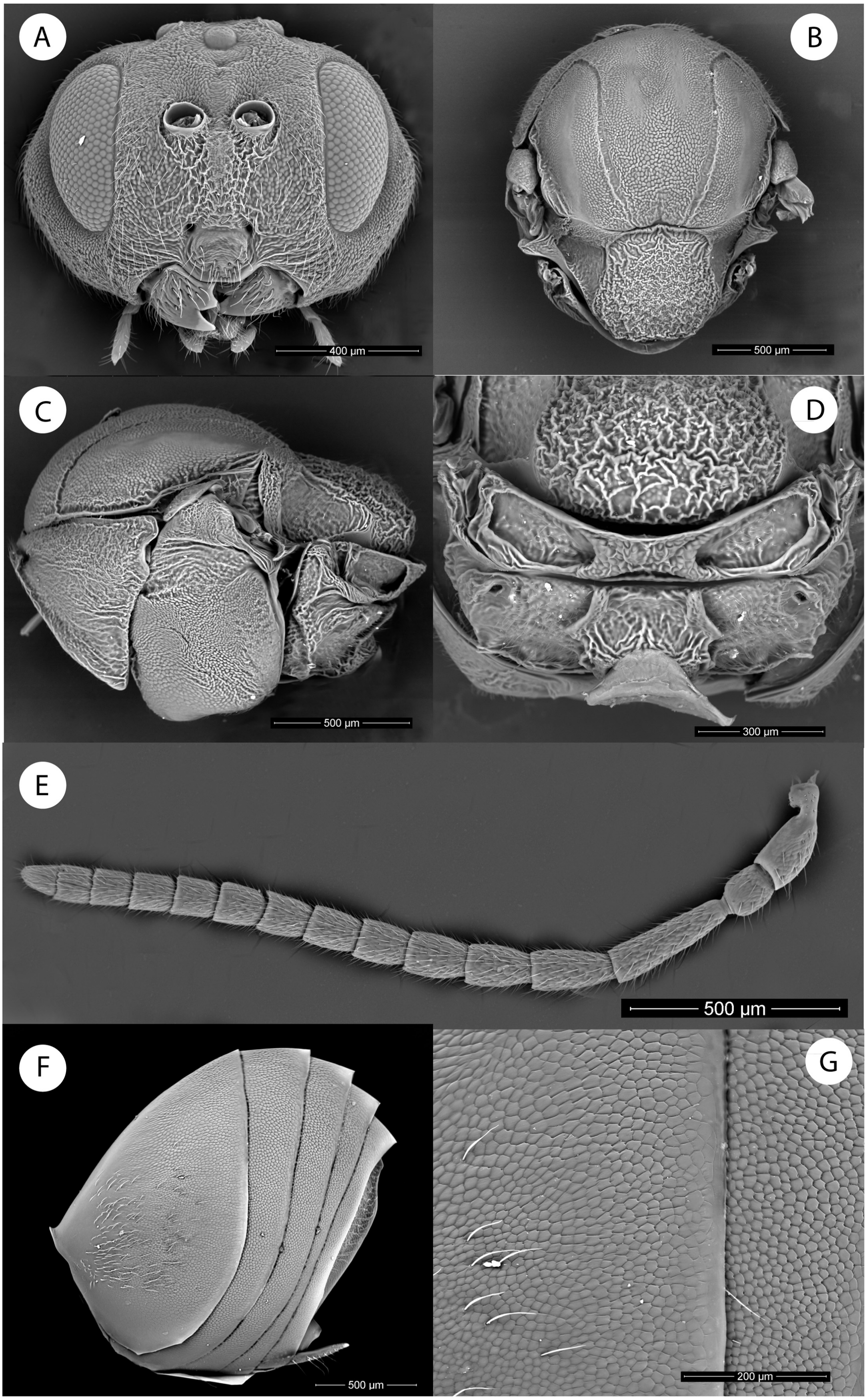

FIG. 5. *Kokkocynips doctorrosae* Pujade-Villar from Oaxaca (México), female, SEM pictures. (A) Head anterior view. (B) Mesosoma dorsal view. (C) Mesosoma lateral view (D) Propodeum posterior view. (E) Antenna. (F) Metasoma lateral view. (G) Detail of sculpture on terga.

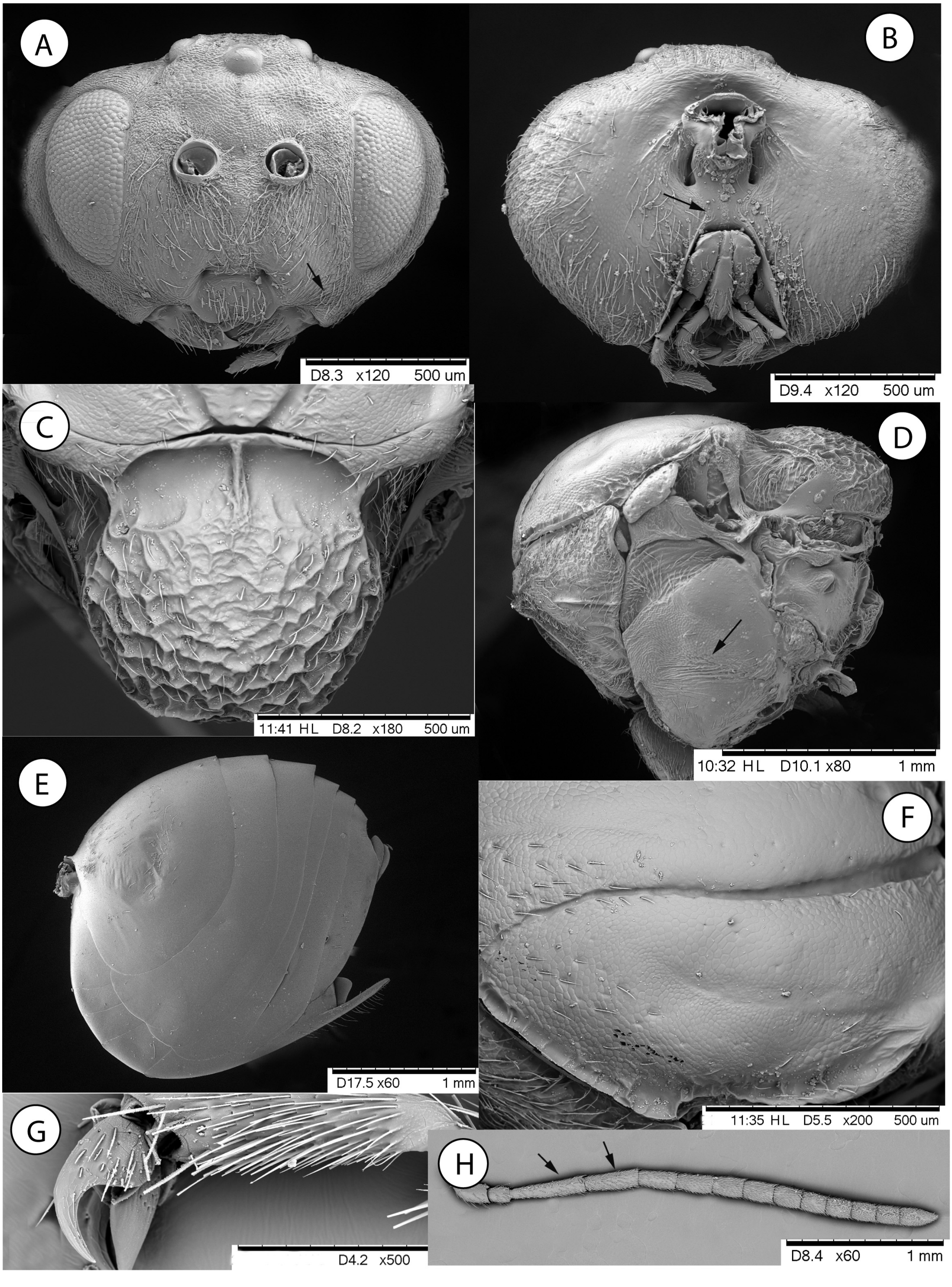

FIG. 6. *Kokkocynips imbricariae* (Ashmead), n. comb., female, SEM pictures. (A) Head anterior view. (B) Head posterior view. (C) Mesoscutellum (D) Mesosoma lateral view. (E) Metasoma lateral view. (F) Mesoscutum dorso-lateral view. (G) Metatarsal claw. (H) Antenna.

Gall: according to the original description (Ashmead 1896) the gall is globular, brownish and hard, 7-10 mm in diameter (Fig. 11B). The surface of the gall has a striped pattern, and is hence commonly known as the banded bullet gall. The galls typically grow in clusters from a fissure in twigs from the previous year's growth. The larval cell is nearly always closely cemented to the thick, hard, gall epidermis, but in a single instance there were a few fibers separating it.

Host plant: the species was described from galls collected on *Quercus imbricaria* and *Q. ilicifolia*. Weld (1926b) added *Quercus marilandica*, *Q. catesbaei*, *Q. texana* and *Q. laurifolia* to the host plant records, and later mentioned that it galled all eastern US red oak species (Weld 1959).

Biology: known only from an asexual generation. Adults emerge from galls from September to October. Galls collected in the autumn produced adults in the following year, but some emerged a year later after diapause (Ashmead 1896).

Distribution: USA and Canada; originally described from Missouri, and also recorded from many localities from Ontario southwards to Florida and westwards to Texas (Weld 1926b).

Remarks: this species shares the main diagnostic characters that define *Kokkocynips* as described herein, although it is readily distinguished from the type species and other *Kokkocynips* species by the characters given in the identification key. Moreover, our phylogenetic analyses also support transfer of this species to *Kokkocynips*, placing it sister to the type species (a placement reflected in the very similar gall morphology) and also closely allied to *K. difficilis* and *K. decidua*.

Kokkocynips coxii **(Bassett, 1881) n. comb. (Figs. 7, 10C, 11C)**

Cynips coxii Bassett, 1881. *Canad. Ent*., vol. 13, p.112. [Syn. by Kinsey, 1922: 123-125].
Andricus coxii (Bassett), Ashmead, 1885. *Trans. Amer. Ent. Soc*., vol. 12: 295.
Andricus coxi Bassett, 1900. *Trans. Amer. Ent. Soc*., vol. 26, p.320.
Andricus bassetianus Dalla Torre and Kieffer, 1902. in Wytsman *Gen. Ins. Hym. Cynipidae*, p.61. [Syn. by Kinsey, 1922: 123-125].
Plagiotrichus (sic.) *coxii* (Bassett), Kinsey, 1922. *Ind. Univ. Stud.* 53, pp.122-5.
Plagiotrochus coxii var *translatus* Kinsey, 1922: 126 **n. syn.**
Dryocosmus coxii (Bassett): Weld, 1926b. *Proc. U.S. Nat. Mus*., 68(10): 41.
Dryocosmus coxii var *translatus* (Kinsey) Weld, 1951: 646.

Material examined: *paratype*. Tucson, AZ. ET Cox, Type (red label), *Andricus coxii*, WB Bassett, Beut coll. rec'd 1935, *Dryocosmus coxii* (Bass). 1 female, USNMENT01525986 (USNM).

Other material examined: USA. Arizona. Hopkins 15639a. Oracle, AZ. 17 Dec. 1921, *Q. emoryi*, LH Weld. Wasps emerged between Jan-Sep 1922, most in January. 34 females. USNMENT01525950-USNMENT01525983 (USNM). California. Los Angeles, Coll. Ashmead, 1 female, USNMENT01525987 (USNM). Note on specimen: "Weld questions locality".

Gall: the galls (Fig. 11C) are elongate to globose twig swellings up to 20 mm. in diameter and 65 mm in length; on older twigs from previous years' growth. Multilocular, smooth surface covered with normal bark. Larval cells closely embedded in the less solid part of the tissue (Kinsey 1922).

Host plant: *Quercus emoryi* and *Quercus hypoleucoides* (=*hypoleuca* Engelm.).

Biology: only known from an asexual generation. The original source is somewhat imprecise about gall phenology, saying that the whole life cycle takes more than one year, as the insects emerge in midwinter and the young galls appear immediately.

Distribution: Arizona, New Mexico and possibly Texas (Kinsey 1922).

Remarks: Kinsey (1922) transferred this species described by Bassett to the genus *Plagiotrichus* (sic.) (=*Plagiotrochus* Mayr) under the mistaken belief that this genus, described from the Western Palaearctic, was also present in North America. In his account of this species Kinsey gave a short re-description, summarized the data on biology and distribution, and described two new varieties. Kinsey (1922) emphasized the particularity of this species as he had some doubts about its correct generic placement, but his placement was finally made based on the structure of the gall. Weld later transferred the species to *Dryocosmus*, on the basis that "the flies run to *Dryocosmus* in the Tierreich key" (a reference to the work by Dalla Torre and Kieffer (1910); Weld 1926b).

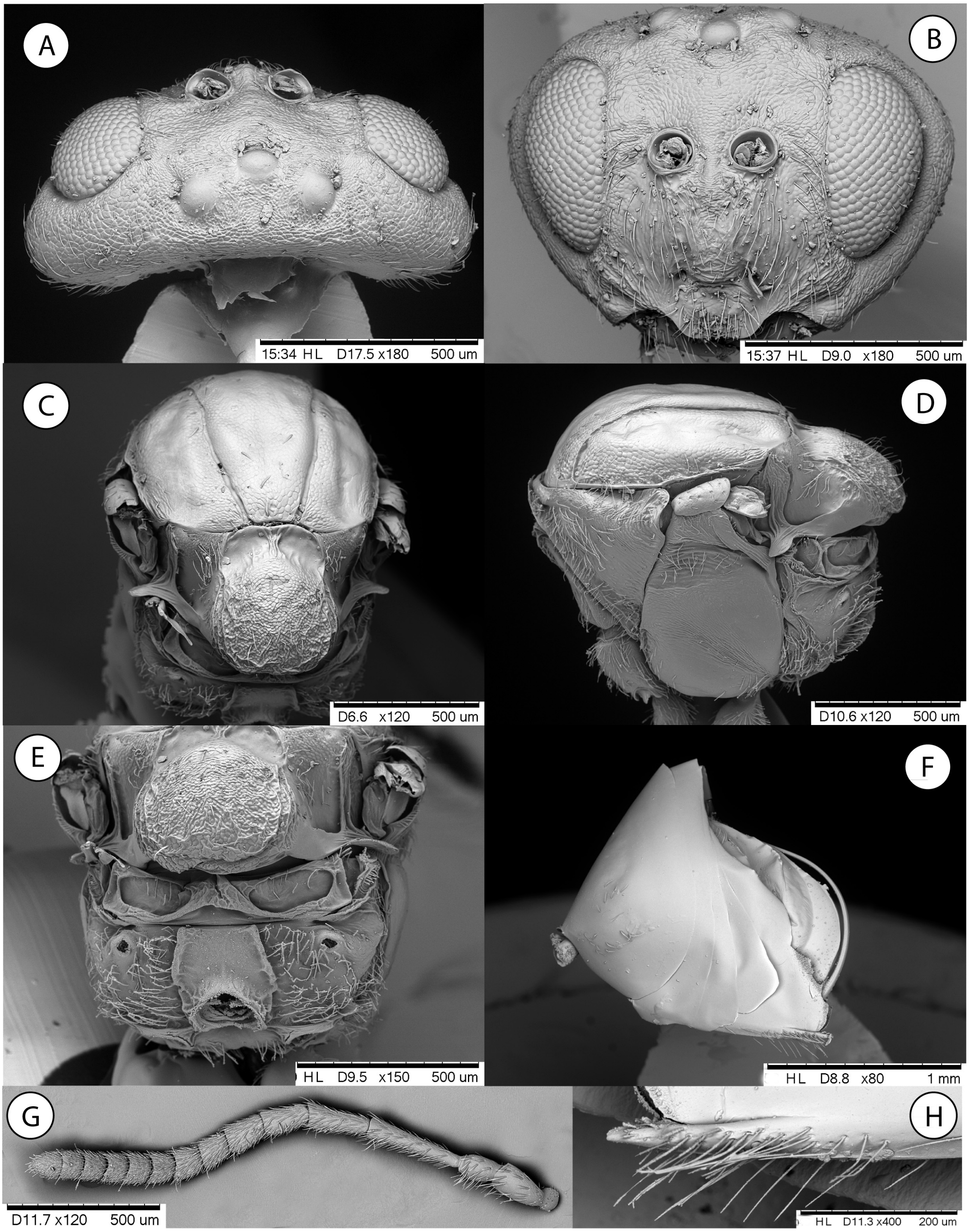

FIG. 7. *Kokkocynips coxii* (Bassett), n. comb., female, SEM pictures. (A) Head dorsal view. (B) Head anterior view. (C) Mesosoma dorsal view (D) Mesosoma lateral view. (E) Propodeum. (F) Metasoma lateral view. (G) Antenna. (H) Hypopygium.

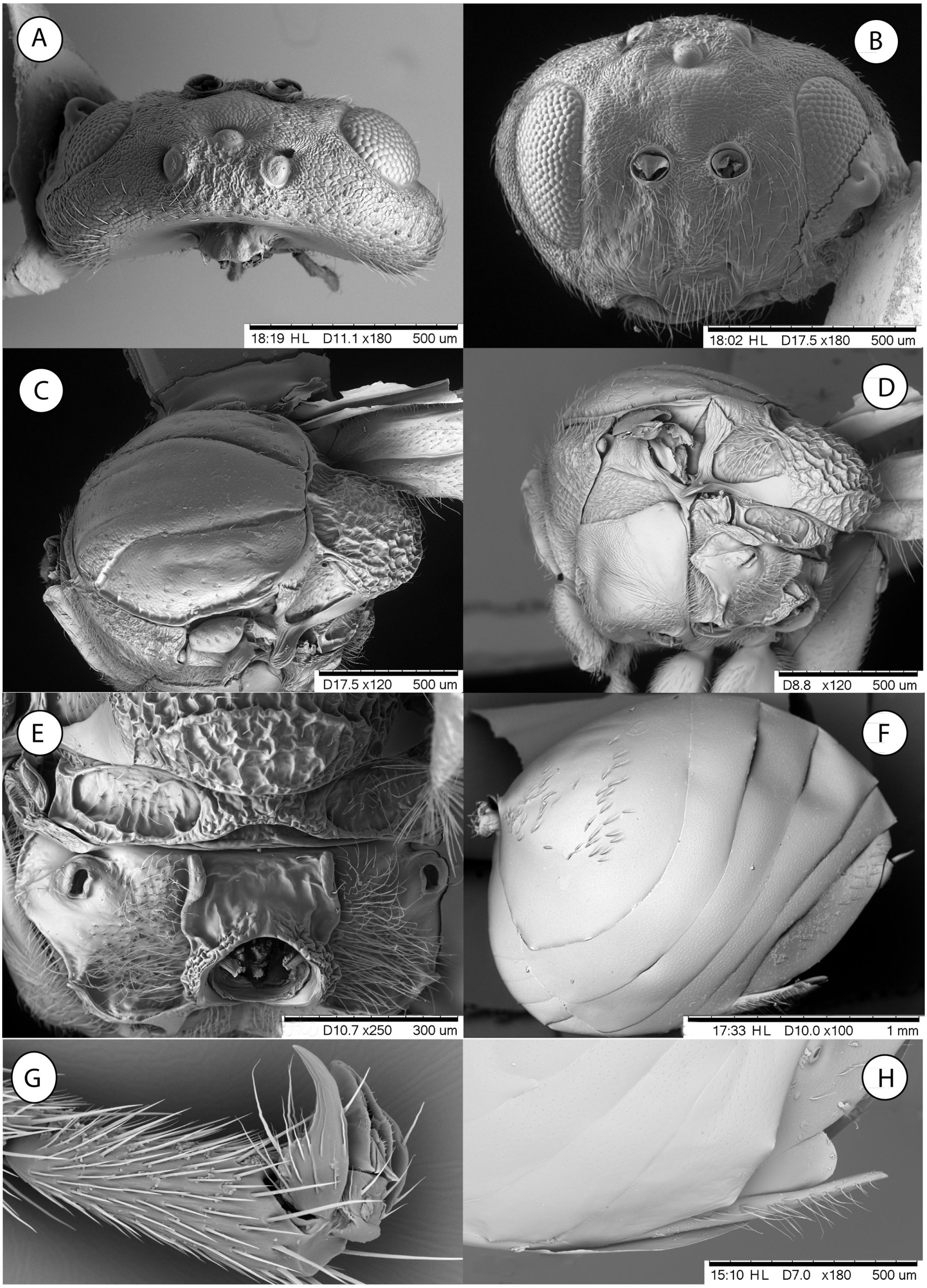

FIG. 8. *Kokkocynips rileyi* (Ashmead), n. comb., female, SEM pictures. (A) Head dorsal view. (B) Head anterior view. (C) Mesosoma dorsal view (D) Mesosoma lateral view. (E) Propodeum. (F) Metasoma lateral view. . (G) Metatarsal claw. (H) Hypopygium

The species is here transferred to the genus *Kokkocynips* based on molecular and morphological evidence. The species does not fit well morphologically into either of the above mentioned genera (see Fig. 7) as it has a malar sulcus that is complete but weakly impressed (Fig. 7B). It can be excluded from *Plagiotrochus* by the relative length of the hypopygial spine, antennae with F1 clearly longer as F2, the almost smooth and shiny mesoscutum, the absence of facial radiating striae from clypeus and by the different sculpture of the propodeum. It differs from *Dryocosmus* mainly in the spine of the hypopygium (much shorter in *Dryocosmus* and with setae reaching beyond apex of spine) and due to the presence of a longitudinal band of sculpture on the mesopleuron (which is absent in *Dryocosmus* species). The molecular phylogeny (Fig. 1) places *K. coxii* as sister to the new species *K. panamensis*, consistent with their similar gall morphologies.

Kokkocynips rileyi **(Ashmead, 1896) n. comb. (Figs. 8, 10D, 11F)**

Andricus rileyi Ashmead, 1896. *Proc. U.S. Nat. Mus*, vol. 19, p. 121.
Dryocosmus rileyi (Ashmead): Weld, 1926b. *Proc. U.S. Nat. Mus*., 68(10): 44.

Material examined: *holotype*. Through CV Riley, Type No. 3070, USNM, 710P. Iss. July 2/77, *Andricus Rileyi* Ashm, USNMENT00802310 (USNM).

Paratype. Type #3070, USNM. No. 710Q on red oak, St L. Mo, Oct 2, '81. Female, USNMENT01525998. USNM.

Other material examined: USA. New York. Woodlawn, X.9. NY, *Andricus rileyi* W.B. Ash, Beut Coll rec'd 1935, 1 female, USNMENT01525995 (USNM), Woodlawn, VIII.17. NY City, Beut Coll rec'd 1935, *Dryocosmus rileyi* (Ashm), 1 female, USNMENT01525996 (USNM), Woodlawn, IX.2.1915. NY City, W. Beutenmuller Collector, Beut Coll rec'd 1935, 1 female, USNMENT01525997 (USNM).

Gall: the main body of the gall is globular, small (around 3 mm.), with a detachable yellowish fleshy knob on the dorsal side of the gall (Fig. 11F). Galls are attached to the midrib or lateral veins of a leaf by a slender stalk. The young gall body is yellowish, and gradually turns brownish following maturation. The larval cell occupies the whole of the interior (Ashmead 1896).

Host plant: this species was originally described from galls collected on *Quercus rubra*. It has subsequently been found on all eastern US red oaks (Weld 1926b, Weld 1959).

Biology: known only from an asexual generation. Galls collected in the autumn produced adults in September and October of the following year; in other samples adults emerged from January to March next year.

Distribution: this species was originally described from Missouri. Weld (1926b) added many localities from New York to Florida and westwards to Missouri and Texas.

Remarks: as in the case of other species discussed here, Weld (1926b) transferred this species from its original placement in *Andricus* to the genus *Dryocosmus* on the basis of the following set of characters: "mesoscutum smooth, head sculptured, claws simple, no malar groove and third segment of antenna longer than fourth". We herewith transfer this species to *Kokkocynips* based on all these shared characters (with the exception of the ambiguous malar sulcus) and in addition based on the presence of the long hypopygium without long subapical setae, a sculptured band on the mesopleuron, the micropunctate metasomal tergites and the percurrent notauli (see Fig. 8), Our phylogenetic analysis placed *K. rileyi* as sister to the clade of detachable stem galling *Kokkocynips* species plus the other leaf galler *K. decidua*, although with poor support.

Kokkocynips difficilis **(Ashmead, 1887) n. comb. (Figs. 9, 10E, 11E)**

Andricus difficilis Ashmead, 1887. in: *Tr. Amer. Ent. Soc*, V. 14 p.143.
Callirhytis difficilis (Ashm.): Mayr, 1902. *Verh. Ges. Wien*, v. 52, 289.

Material examined: *syntype*. Jacksonville, Fla. Collection Ashmead. Type No. 2878, USNM, *Andricus difficilis* Ashm., USNMENT00802031 (USNM).

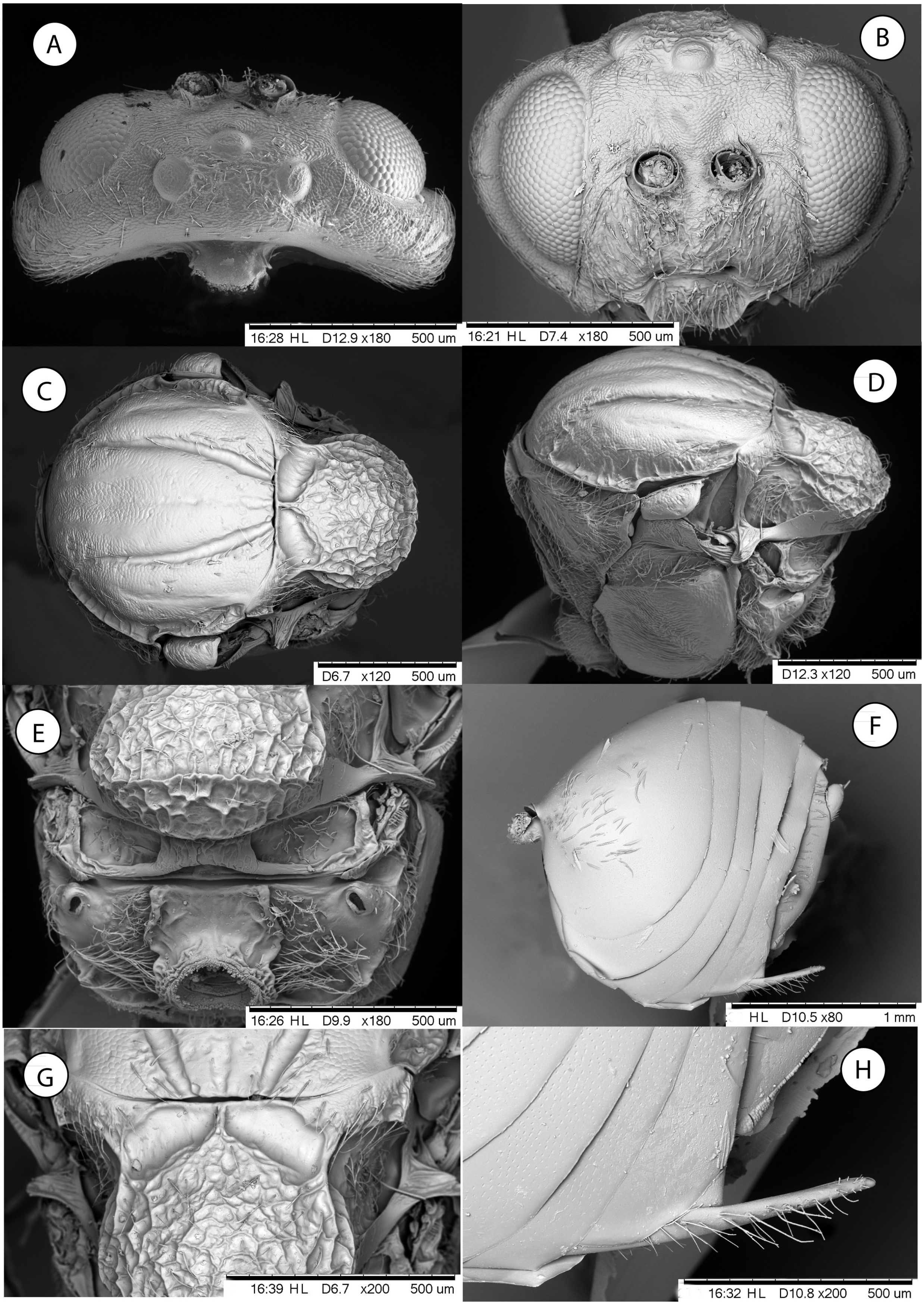

FIG. 9. *Kokkocynips difficilis* (Ashmead), n. comb., female, SEM pictures. (A) Head dorsal view. (B) Head anterior view. (C) Mesosoma dorsal view (D) Mesosoma lateral view. (E) Propodeum. (F) Metasoma lateral view. (G) Detail of mesoscutellar foveae. (H). Hypopygium.

Other material examined: USA. Florida. Jacksonville. Coll. Ashm. 2 females, USNMENT00892936 and USNMENT01525988 (USNM). Texas. Hoxie. IX.6/1918. LH Weld, ex *Q. phellos*, 7 females, USNMENT01525989-USNMENT01525994, USNMENT01525999.

Gall: small (12 X 15 mm), irregularly rounded, densely rugose, reddish when young and turns grayish following gall maturation, slightly flattened at sides, the rugosities arranged transversally in five to six rows. These galls occur in clusters, emerging in rows from fissures or slits in the terminal twigs (Fig. 11E); when mature fall to the ground (Ashmead 1887).

Host plant: *Quercus laurifolia*, *Q. cinerea, Q. catesbaei*, *Q. nigra*, *Q. myrtifolia* and *Q. phellos* (Weld 1959).

Biology: only known from the asexual generation. According to Ashmead (1887), the adults emerge from galls from August to September; Weld (1959) noted that adults also emerged later in the year up to December.

Distribution: South-eastern North America, from Maryland southwards to Florida and westwards to Texas (Burks 1979, pers. obs.).

Remarks: in the original description the following set of morphological characters was mentioned: "Thorax almost smooth shining, with distinct parapsidal grooves, a median groove, the mesopleura showing fine, short microscopical striae; scutellum rugose not pubescent; abdomen microscopically punctate; wings hyaline, areolet distinct cubital cell almost closed"; our examination of specimens confirms this set of characters. Additionally we observed that the spine of the hypopygium is long (almost 6 times as long as wide in lateral view), without long subapical setae and the antennae is 14 segmented; F1 about 1.4 times as long as F2 (Figs. 9H, 10E).

Both the finely coriaceous to smooth and shiny mesoscutum and the absence of striae radiating from the clypeus indicate that *C. difficilis* is very different from Palaearctic species of *Callirhytis* (the true *Callirhytis*), all of which have a transversely ridged mesoscutum and conspicuous facial radiating striae (Nieves-Aldrey 1992). Recently two new genera, *Zapatella* Pujade-Villar & Melika, 2012 and *Melikaiella* Pujade-Villar, 2014, were described to include some Nearctic and Neotropical species of *Callirhytis* that did not fit the diagnostic characters of Palaearctic *Callirhytis* sensu Förster (Pujade-Villar *et al*. 2012a; Pujade-Villar *et al*. 2014). However, *C. difficilis* differs from these two genera as well. It differs from *Zapatella* by the absence of a ring of dense white setae on the second metasomal tergite, R1 of forewing complete and relatively shorter ventral projection of the hypopygium (that is about 6 – 12 times as long as wide in *Zapatella*). This species does not possess either of the diagnostic characters of *Melikaiella*, namely the presence of areolate-reticulate sculpture on metasomal tergites (punctate in *C. difficilis*) and rugose sculpture of mesoscutum (finely and shiny coriaceous in *C. difficilis*).

The morphology suggests that this species falls into the clade of closely related species discussed in this study. The molecular results highlight the close relationship of this species to both *K. imbricariae* and *K. doctorrosae* (Fig.1, Table 1). Hence based on the morphological and molecular evidence the species is here transferred from *Callirhytis* to *Kokkocynips*.

Kokkocynips attractans **(Kinsey, 1922) n. comb.**

Andricus attractans Kinsey, 1922. in: *Bull. Amer. Mus. Nat. His.*, vol. 46 p.281.
Callirhytis uvellae Weld, 1944. in: *Proc. U. A. Nat. Mus.*, vol. 95 p.23 [Syn. in Dailey, 1969: 132].
Dryocosmus attractans (Kinsey): Weld, 1951: 644.
Callirhytis attractans (Kinsey): Dailey, 1969: 132

The molecular results placed one additional species, *Callirhytis attractans* (Kinsey 1922), within the same clade as species from *Kokkocynips* with 100% posterior probability support (Fig. 1). This is an interesting placement, as this species is known only from its sexual form, unlike other species in the genus. Accordingly, we transfer this species to *Kokkocynips* although we have not yet been able to study the type material. In the near future we hope to have the opportunity to re-describe this species.

Callirhytis uvellae Weld was synonymized with *Dryocosmus attractans* (Kinsey) by Dailey (1969) but Burks (1979) did not mention this synonymy, which we consider to be a mistake. The galls (Fig. 11G) are unilocular, about 2 mm in diameter and develop gregariously in spring on buds (Dailey 1969). The host oaks are of all the section Lobatae present in California, *Q. agrifolia*, *Q. kelloggii* and *Q. wislizeni*.

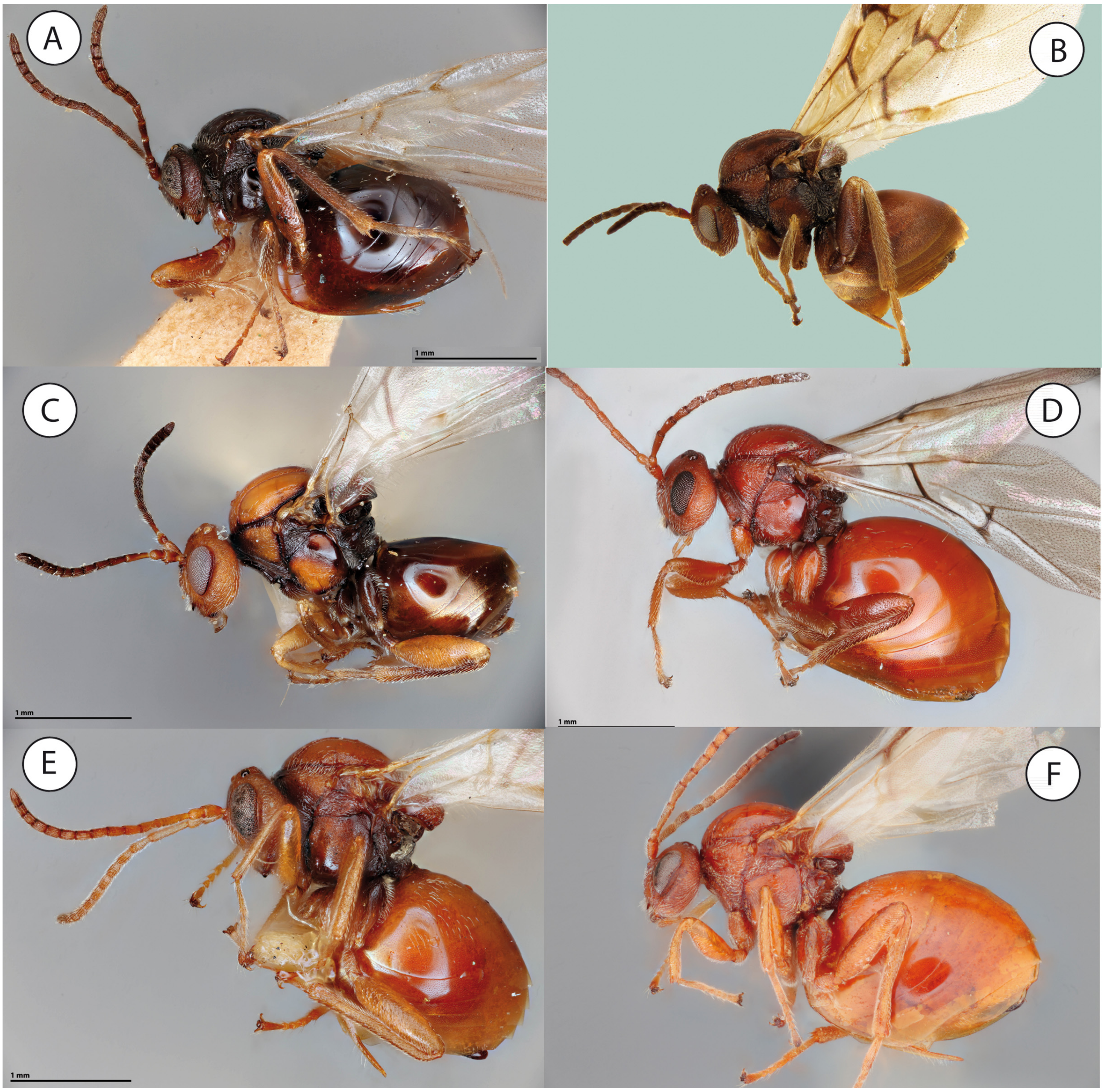

FIG. 10. Female habitus of species of *Kokkocynips.* (A) *Kokkocynips decidua* (Beutenmueller) n. comb. (B) *Kokkocynips doctorrosae* Pujade-Villar. (C) *Kokkocynips coxii* (Bassett) n. comb. (D) *Kokkocynips rileyi* (Ashmead) n. comb. (E) *Kokkocynips difficilis* (Ashmead) n. comb. (F) *Kokkocynips imbricariae* (Ashmead) n. comb.

DISCUSSION

Studies over the last decade have revealed new morphological diversity in Neotropical oak-associated cynipids; around 100 species of Nearctic and Neotropical Cynipidae have been described or revised, primarily associated with red oaks (*Quercus* section Lobatae) and white oaks (*Quercus* section Quercus; see for example Pujade-Villar *et al*. 2010, Pujade-Villar *et al*. 2012a, Pujade-Villar *et al*. 2012b, Pujade-Villar *et al*. 2013, Medianero & Nieves-Aldrey 2013, Pujade-Villar *et al*. 2014, Nicholls *et al*. 2018b, Cuesta-Porta *et al*. 2020). Incorporating this novel morphological diversity into the existing generic level classification has been a challenge because some taxa show combinations of characters otherwise diagnostic of different genera. The difficulty in defining generic limits within Cynipidae is in part historical, since much of the current generic level taxonomy still follows Weld (1952), and is based upon diagnostic characters that are sometimes inconsistent within genera (Nicholls *et al*. 2018b).

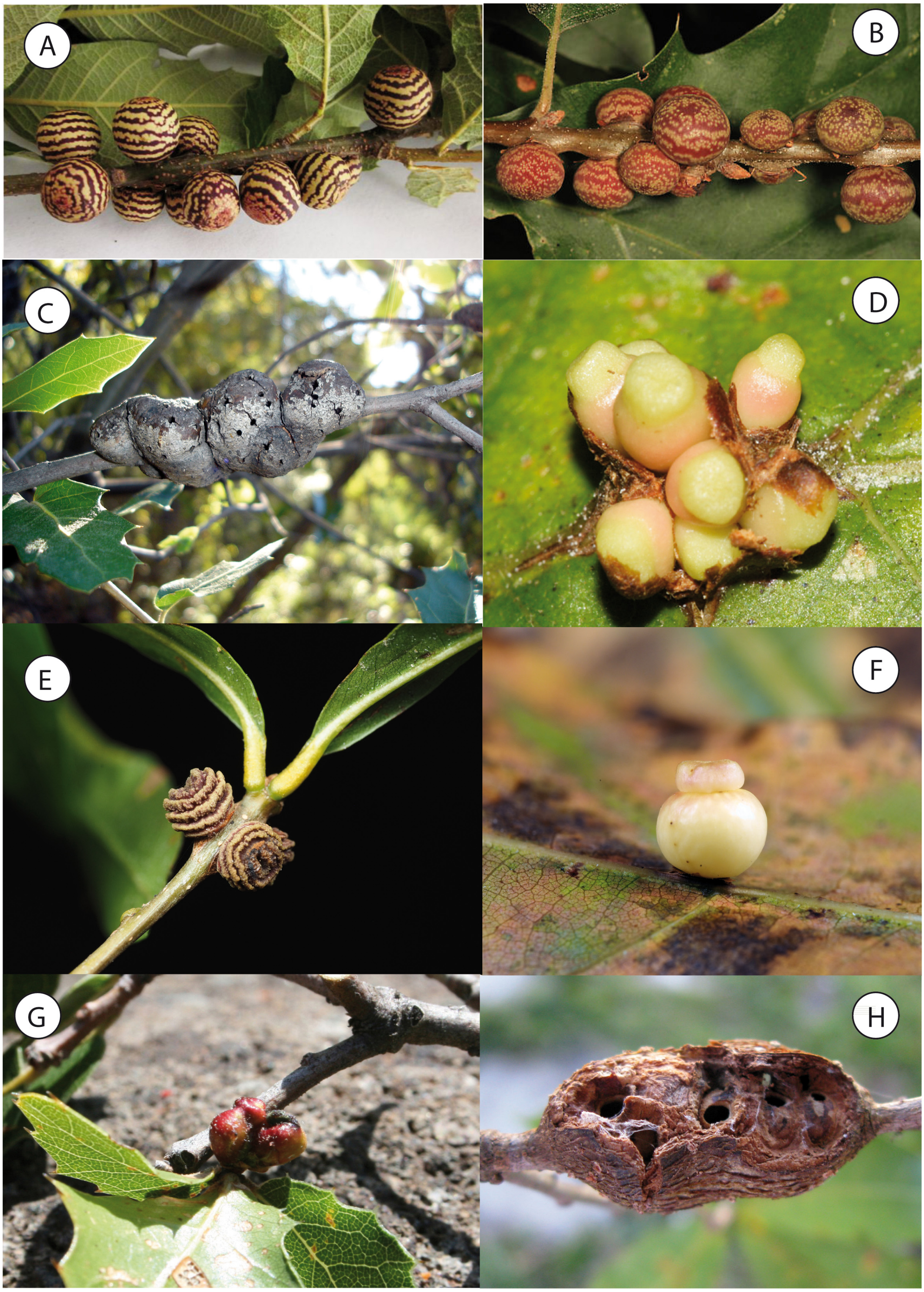

FIG. 11. Galls of species of *Kokkocynips*. (A) *K. doctorrosae* Pujade-Villar. (B) *Kokkocynips imbricariae* (Ashmead). (C) *Kokkocynips coxii* (Basset). (D) *Kokkocynips decidua* (Beutenmueller). (E) *Kokkocynips difficilis* (Ashmead). (F) *Kokkocynips rileyi* (Ashmead). (G) *Kokkocynips attractans* (Kinsey). (H) *Kokkocynips panamensis* n. sp.

This inconsistent morphology problem in Cynipini can be attributed to the high level of homoplasy that exists in many of the taxonomic characters used in this group (Pujade & Arnedo 1997; Liljeblad *et al*. 2008). Molecular data have also shown some genera as defined by Weld to be polyphyletic (Nicholls *et al*. 2018a). The nomenclatural history of the six species we have transferred to *Kokkocynips* illustrates this taxonomic instability; after original placement in the genus *Andricus* Hartig or *Cynips* L., these species were later transferred to other genera including *Dryocosmus* Giraud and *Callirhytis* Förster. To avoid propagating such taxonomic instability in Cynipini, taxonomic placement of newly discovered morphological diversity needs to proceed alongside the development of a solid generic framework supported by morphological, biological and molecular data, with associated revision of the nomenclature of known species. Our re-description and re-appraisal of the genus *Kokkocynips* is a step in this process. Ongoing additional studies, including sequencing of more species and genera from section Lobatae oaks, will shed more light on the phylogenetic relationships of *Kokkocynips* and allied taxa.

The biology of *Kokkocynips* species supports the hypothesis of high host plant specificity in oak gall wasps. The vast majority of individual oak gall wasp species induce galls on species from just a single section within the genus *Quercus* (Stone *et al*. 2009, Liljeblad *et al*. 2008, Melika *et al*. 2010, Tang *et al*. 2011, 2016, Pénzes *et al*. 2018). All known *Kokkocynips* species induce galls either on the leaves, twigs or buds of red oaks (*Quercus* section Lobatae), and this genus is nested within a larger clade of species all of which also induce their galls on red oaks. Other genera with distributions extending across both the Nearctic and Neotropical regions - including *Amphibolips* Reinhard, *Bassettia* Ashmead, *Loxaulus* Mayr, *Zapatella* Pujade-Villar & Melika, *Melikaiella* Pujade-Villar and the recently described *Striatoandricus* Pujade-Villar - are similarly specific to a single section of oaks.

While most *Kokkocynips* species are known only from their asexual generation, a single sexual-only species, *K. attractans* (Kinsey), has been recognized via molecular data and transferred to *Kokkocynips* pending study of the type material. This result should not be surprising since purely asexual reproduction has been conclusively demonstrated in the Cynipini in only a very few instances (Csóka *et al*. 2005). Both these facts imply that alternate matching generations await discovery for all of the described *Kokkocynips* species; for example Dailey (1969) notes that the currently unknown asexual generation of *K. attractans* may well induce a gall on leaves. Alternatively, molecular methods may allow pairing of currently unmatched sexual and asexual generations into a single species lifecycle (Stone *et al*. 2008, Nicholls *et al*. 2018a, Cerasa *et al*. 2020).

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