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**Re-establishment of the Nearctic oak cynipid gall wasp genus *Feron* Kinsey, 1937  
(Hymenoptera: Cynipidae: Cynipini), including the description of six new species**

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**Abstract**

The Nearctic cynipid oak gall wasp genus *Feron* Kinsey, **comb. rev.** is re-established with 34 species: *F. albicomus* (Weld, 1952), **comb. nov.**, *F. amphorus* (Weld, 1926), **comb. nov.**, *F. apiarium* (Weld, 1944), **comb. nov.**, *F. atrimentum* (Kinsey, 1922), **comb. nov.**, *F. bakkeri* (Lyon, 1984), **comb. nov.**, *F. caepula* (Weld, 1926), **comb. nov.**, *F. californicum* (Beutenmueller, 1911), **comb. nov.**, *F. clarkei* (Bassett, 1890), **comb. nov.**, *F. comatum* (Weld, 1952), **comb. nov.**, *F. crystallinum* (Bassett, 1900), **comb. nov.**, *F. cylindratum* (Kinsey, 1937), **comb. nov.**, *F. discale* (Weld, 1926), **comb. nov.**, *F. discularis* (Weld, 1926), **comb. nov.**, *F. dumosae* (Weld, 1957), **comb. nov.**, *F. gigas* (Kinsey, 1922), **comb. nov.**, *F. izabellae* Melika, Nicholls & Stone, **sp. nov.**, *F. kingi* (Bassett, 1900), **comb. nov.**, *F. parmula* (Bassett, 1900), **comb. nov.**, *F. pattersonae* (Fullaway, 1911), **comb. nov.**, *F.*

*roberti* Melika, Nicholls & Stone, **sp. nov.**, *F. rucklei* Melika, Nicholls & Stone, **sp. nov.**, *F. scutellum* (Weld, 1930), **comb. nov.**, *F. serranae* Pujade-Villar & Cuesta-Porta, **sp. nov.**, *F. splendens* (Weld, 1919), **comb. nov.**, *F. stellare* (Weld, 1926), **comb. nov.**, *F. stellulum* (Burnett, 1974), **comb. nov.**, *F. sulfureum* (Weld, 1926), **comb. nov.**, *F. syndicorum* Pujade-Villar & Cuesta-Porta, **sp. nov.**, *F. tecturnarum* (Kinsey, 1920), **comb. nov.**, *F. tetyanae* Melika, **sp. nov.**, *F. tibiale* Kinsey, 1937, **comb. rev.**, *F. tubifaciens* (Weld, 1926), **comb. nov.**, *F. verutum* Kinsey, 1937, **comb. rev.**, and *F. vitreum* Kinsey, 1937, **comb. rev.** Most species are known only from the asexual generation; *F. clarkei*, *F. comatum*, and *F. dumosae* are known only from the sexual generation while both generations are recognised for *F. atrimentum*, *F. crystallinum*, *F. gigas*, *F. kingi* and *F. pattersonae*. Matching of alternate sexual and asexual generations is established for the first time for *F. kingi* and *F. pattersonae* (= *Andricus pedicellatus* (Kinsey, 1922), **syn. nov.**) based on molecular data (both *cytb* and ITS2 sequences). Morphological descriptions, re-descriptions, diagnoses, and a key to species are given, as well as data on DNA sequences, biology, phenology, and distribution.

## Introduction

Cynipid gall wasps (Hymenoptera: Cynipidae) comprise approximately 1,400 species worldwide, predominantly occurring in temperate regions of the Holarctic (Ronquist *et al.* 2015). Within this family, the oak gall wasps (Cynipini) are by far the most species-rich group, with c. 1,000 species worldwide (Stone *et al.* 2002; Ronquist *et al.* 2015; Péntzes *et al.* 2018).

*Andricus* was established by Hartig (1840) to include some sexual forms of Cynipini. Rohwer & Fagan (1917) described a new genus, *Adleria*, for the large asexual females with dense setae that had been included in *Cynips* sensu Authors [not *Cynips* Linnaeus]. Benson (1953) closed the first *Adleria* alternating lifecycle, matching *Adleria kollari* (Hartig, 1843) with the sexual form corresponding to *Andricus circulans* Mayr, 1870 under the name *Andricus kollari*, and thus proposing *Adleria* to be a junior synonym of *Andricus*. The presence of alternating asexual and sexual generations in the genus *Andricus* creates considerable morphological variation among adults that markedly complicates the assessment of generic limits. Weld (1951) synonymized four American genera with *Andricus*: *Canobius* Kinsey, 1937, *Druon* Kinsey, 1937, *Femuros* Kinsey, 1937 and *Feron* Kinsey, 1937. Later, Melika & Abrahamson (2002) proposed further generic synonyms and considered *Dros* Kinsey, 1937, *Erythres* Kinsey, 1937, *Liodora* Foerster, 1869, *Parandricus* Kieffer, 1906 and *Trichoteras* Ashmead, 1897 as junior synonyms of *Andricus*. These nomenclatorial changes

turned *Andricus* into a chaotic macrogenus, which has repeatedly been reported as polyphyletic (for example, Nicholls *et al.* 2017, Blaimer *et al.* 2020, Melika *et al.* 2021, Cuesta-Porta *et al.* 2022). It currently includes more than 400 species (Stone *et al.* 2002) with many species from the Nearctic and Neotropics requiring revision as their generic affiliation is uncertain. Thus, the genus *Andricus* requires a major revision.

Recently, some of these previously synonymized genera have been re-established: *Erythres* Kinsey (Pujade-Villar & Melika, 2014), *Femuros* Kinsey (Pujade-Villar & Ferrer-Suay 2015), *Dros* Kinsey (Pujade-Villar *et al.* 2017), *Trichoteras* Ashmead (Zimmermann 2018), and *Druon* Kinsey (Cuesta-Porta *et al.* 2022). In addition, new genera for some species erroneously placed into *Andricus* have been established: *Protobalandricus* Melika, Nicholls & Stone, 2018 (Nicholls *et al.* 2018b), *Striatoandricus* Pujade-Villar, 2020 (Cuesta-Porta *et al.* 2020) and *Disholandricus* Melika, Pujade-Villar & Nicholls, 2021 (Melika *et al.* 2021). Regardless, many Nearctic and Neotropical species still have uncertain generic affiliations and must be revised. This study is a further taxonomic and phylogenetic contribution to clarify the contents of the genus *Andricus*. We present the formal re-establishment of the genus *Feron*, with an updated description, an identification key, and new descriptions of constituent species. All adults of *Feron* species share the characteristic morphological feature of the presence of two smooth or delicately alutaceous areas on the lower face between the clypeus and eye. *Feron* species have very variable gall morphology, but are all unilocular (although aggregated in some species) and usually on leaves. Sexual generation galls are integral to leaves, catkins, or buds and are typically small, thin-walled, and conical. Asexual generation galls are detachable leaf galls of very variable morphology; some are small spangles, others conical or cylindrical, and some in dense gregarious clusters; with a crystalline bristly, pubescent, or glabrous surface. We also provide molecular data supporting the limits of the re-established genus and phylogenetic placement of *Feron* within a broader sampling of the tribe Cynipini.

## Material and Methods

### *Specimen collection*

Fresh material was obtained from galls collected in the U.S.A. (from the Pacific slopes to the Atlantic Coast), Canada (British Columbia), and Mexico, with details under the material examined sections for each species. Galls were kept at ambient temperature in plastic

containers with mesh lids to ensure ventilation; emerged adults were preserved in 99% ethanol.

Types of established and newly described species are deposited at the American Museum of Natural History (AMNH) in New York City, U.S.A.; the U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, U.S.A.; the Essig Museum, University of California, Berkeley, the collection of Plant Health Diagnostic National Reference Laboratory (PHDNRL), National Food Chain Safety Office, Budapest, Hungary; and the University of Barcelona (UB, JP-V collection) and all were examined by GM.

#### *Morphological descriptions*

The terminology used to describe gall wasp morphology follows other recent cynipid studies (Liljeblad *et al.* 2008, Melika 2006, Melika *et al.* 2010). Abbreviations for fore wing venation follow Ronquist & Nordlander (1989), and cuticular surface terminology follows Harris (1979). Measurements and abbreviations used here include: F1–F12 for the 1st and subsequent flagellomeres; POL (post-ocellar length) for the distance between the inner margins of the posterior ocelli; OOL (ocellar-ocular length) for the distance from the outer edge of a posterior ocellus to the inner margin of the eye; and LOL (lateral-frontal ocelli length) for the distance between lateral and frontal ocelli. The width of the fore wing radial cell is measured from the margin of the wing to the Rs vein.

Bright field images of adults were produced with a digital Leica DC500 camera attached to a Leica DM2700M compound microscope using the LAS Store&Recall software, followed by processing in Adobe Photoshop 6.0. For all species mentioned in this paper, descriptions are provided according to the current morphological requirements as the original descriptions are superficial.

Species are listed in alphabetical order.

#### *Nomenclature of host plants*

Denk *et al.* (2017) reorganized the classification of *Quercus* and divided the genus into two subgenera (*Cerris* and *Quercus*). Subgenus *Cerris* includes three sections: *Cyclobalanopsis* (previously considered as a subgenus), and the sections *Ilex* and *Cerris* from Menitsky (1984). Subgenus *Quercus* includes five sections: *Lobatae* and *Protobalanus* as in Nixon (1993), with the old section *Quercus* divided into three new sections (*Quercus sensu stricto*, *Virentes*, and

*Ponticae*). Manos & Hipp (2021) further subdivided section *Quercus* s.s. into seven subsections, six of which naturally occur in North America and Mexico. The gall wasp species listed herein are associated with the following host plant species, all belonging to subgenus *Quercus*, section *Quercus*: *Q. alba* L. within subsection *Albae*; *Q. berberidifolia* Liebm., *Q. cornelius-mulleri* Nixon & K. P. Steele, *Q. douglasii* Hook. & Arn., *Q. dumosa* Nutt., *Q. gambelii* Nutt., *Q. garryana* Douglas ex Hook., *Q. lobata* Née within subsection *Dumosae*; *Q. arizonica* Sarg. (= *Q. sacame* Trel.), *Q. chihuahuensis* Trel., *Q. deserticola* Trel. (= *Q. texcocana* Trel.), *Q. engelmannii* Greene, *Q. glabrescens* Benth., *Q. glaucoides* Mart & Gal., *Q. grisea* Liebm., *Q. john-tuckeri* Nixon & C. H. Muller, *Q. magnoliifolia* Née, *Q. oblongifolia* Torr., *Q. obtusata* Bonpl., *Q. potosina* Trel., *Q. rugosa* Née (= *Q. rhodophlebia* Trel.), *Q. toumeyi* Sarg., *Q. turbinella* Greene (= *Q. subturbinella* Trel.) within section *Leucomexicana*; *Q. pungens* Liebm. within subsection *Polymorphae*; and *Q. stellata* Wangenh. in subsection *Stellatae*.

#### *Molecular phylogenetics*

The phylogenetic limits and placement of the re-established genus *Feron* **comb. rev.** were determined using a multi-gene dataset. One individual from 20 of the 34 recognised *Feron* species was sequenced for fragments of four genes (cytochrome *b* [cytb], the D2 loop of the 28S ribosomal RNA gene [D2], long-wavelength opsin [opsin] and wingless [wg]) using the protocols and primers presented in Stone *et al.* (2009) and Nicholls *et al.* (2018a), with phylogenetic context provided using new and previously published data from Nearctic Cynipini taxa (see also Nicholls *et al.* 2017, Nicholls *et al.* 2018a, Medianero *et al.* 2021, Melika & Nicholls 2021, Melika *et al.* 2021, Nieves-Aldrey *et al.* 2021, Cuesta-Porta *et al.* 2022; sample details and GenBank accession numbers in Supplementary Table 1). The type species of the genus *Andricus*, the Western Palearctic species *A. quercusradicis* (Fabricius, 1798), was also included to demonstrate the genetic distinctiveness between *Andricus* sensu stricto and the re-established *Feron*. The final dataset consisted of 60 Cynipini species, rooted using an *Aphelonyx* Mayr, 1881 species known to be placed in the sister clade to the sampled Nearctic taxa (see Nicholls *et al.* 2017). All new sequences generated for this study have been deposited in GenBank, accession numbers OQ446172–OQ446309, OQ448214–OQ448231, and OQ448237–OQ448248.

Alignments for each gene were constructed using MAFFT v7.471 (Katoh & Standley 2013) and checked by eye, at which stage an ambiguously aligned section of the opsin intron and two insertions present in only a single taxon (also from the opsin intron) were removed.

Final alignments contained 433bp (cytb), 571bp (D2), 492bp (opsin), and 377bp (wg). The four alignments were then concatenated into a single 1873bp dataset as the phylogenetic histories of these genes show no evidence of significant topological incongruence (Stone *et al.* 2009); within this alignment 648 positions were variable and 478 were parsimony informative. The data were initially partitioned by gene and if the gene was protein coding further partitioned into each codon position and intron regions. PartitionFinder v2.1.1 (Lanfear *et al.* 2017) was then used to determine both the optimal partition scheme and appropriate substitution models for those partitions. Final models used for the six resultant partitions were GTR+G for partition1 containing cytb 3rd codon positions, HKY+I+G for partition2 containing cytb 1st and 2nd codon positions, GTR+I+G for partition3 containing all of D2 and 1st codon positions from both opsin and wg, HKY+I for partition4 containing 2nd codon positions from opsin and wg, GTR+G for partition5 containing opsin 3rd codon positions and the opsin intron region, and HKY+G for partition6 containing wg 3rd codon positions. Phylogenetic relationships were estimated using MrBayes v3.2.7a (Ronquist *et al.* 2012) incorporating these substitution models, variable rates among partitions, and a strict molecular clock. Two independent runs were performed, each for 6 million generations sampled every 1000 generations; this provided effective sample sizes >100 for all model parameters. A majority-rule consensus tree was calculated using samples taken from the final 3 million generations of both runs.

A DNA-barcoding style approach was used to assess the degree of genetic variation between and within *Feron* species, by sequencing 433bp of the mitochondrial cytb gene from between one and 26 individuals of the same 20 *Feron* species used in the phylogenetic analysis (see Supplementary Table 1). Pairwise genetic distances using HKY corrections were calculated between all individuals in the software PAUP\* (Swofford 1998), then average distances for within- and among-species comparisons were determined. A more sophisticated barcoding approach, utilising both cytb and the nuclear ITS2 region (see details in Nicholls *et al.* 2022), was also used to confirm the matching of alternate generations within *Feron* species and the conspecific status of variable morphotypes within one *Feron* species. Both these genes are useful for determining species boundaries in oak gall wasps, with variation within a species typically being less than about 1.5% for cytb and less than 0.85% for ITS2; instances of insertions/deletions of single bases or short repeat units can also occasionally be observed among conspecific ITS2 sequences (Nicholls *et al.* 2018a,b, 2022).

## Results

The multi-gene phylogenetic analysis supports the re-establishment of *Feron* as a valid genus independent from *Andricus*. This genus constitutes a monophyletic lineage with 100% posterior probability support that is clearly different from the clade of true *Andricus* species that contains the type species of that genus (Fig. 514). *Feron* forms one of multiple lineages within a larger well-supported clade containing other leaf-galling Nearctic and Neotropical Cynipini genera, being allied to *Dros*, *Prokius* Nieves Aldrey, Medianero & Nicholls, 2021 and *Phylloteris* Ashmead, 1897. Even though species within *Feron* and other recently re-established or described genera (*Disholandricus*, *Dros*, *Druon*, *Striatoandricus*, and *Trichoteris*) have been split from *Andricus*, the latter genus remains a polyphyletic entity requiring further revision.

Cytochrome *b* distances among *Feron* species were on average 7.8% (range from 2.2 - 12.1%), while average within-species distances were typically less than 1% (range 0 - 1.7%, see Table 1). These values are comparable with distances reported among congeneric species and within-species respectively in other Cynipini taxa (e.g., Nicholls *et al.* 2018b, Medianero *et al.* 2021, Melika & Nicholls 2021, Cuesta-Porta *et al.* 2022). In cases where our sampling encompassed multiple host plants and collection locations, within-species genetic variation did not show any correlation with host plant species, sampling location or adult morphology (see also Supplementary Figure 1).

Below we present a comprehensive morphological re-description and diagnosis of the re-established genus *Feron*. We also provide descriptions of the 34 constituent species within *Feron*, as well as a key to all known sexual and asexual forms.

### ***Feron* Kinsey, 1937**

#### **Figs 1–513**

**Etymology.** Kinsey (1937) did not indicate the etymology of this genus name in the original description. The name *Feron* could come from either the Greek φέρω (phérō) or Latin *fero*, both of which are verbs meaning “to carry” in which case its gender would be neuter; it could alternatively come from Φηρῶν which is a mythological name of a centaur, in which case it would be masculine. The suffixes in the epithets of the original species described under the name *Feron*, correspond to a neuter word, thus it must refer to a verb and not to a noun. Here, all species names’ terminals have been changed to neuter when applicable.

**Type species:** *Feron verutum* Kinsey, 1937 (according to the original description).

Kinsey (1937) described this genus with six new Mexican species, *Feron tibiale*, *F. tostum*, *F. uterinum*, *F. validum*, *F. verutum* and *F. vitreum*, which induce crystalline galls on leaves of



white oaks in the subgenus *Quercus* (section *Quercus*, subsection *Leucomexicana*; Denk *et al.* 2017, Manos & Hipp 2021). Kinsey (1937: 70) commented that *Feron* should include numerous species that had previously been assigned to *Andricus* and other Western Palearctic genera; in addition, two other genera, *Dros* and *Druon*, were described in the same paper and Kinsey mentioned that the limits of all three genera would be determined in a monographic revision of the entire group. However, this revision was never published. Moreover, Kinsey constantly compared his new *Feron* species with *Andricus tecturnarum* but never transferred that species to *Feron*; our phylogenetic study shows that *A. tecturnarum* falls within the genus *Feron*. According to Weld (1951; 1952a), morphologically *Feron* closely resembles *Andricus*, and Weld (1951: 632) synonymized both genera. However, the original description of *Feron* does not mention several important characters that differentiate it from *Andricus* so for this reason, *Feron* is re-described below.

**Diagnosis.** *Feron* has the lower face with two smooth or almost smooth areas between the clypeus and eye, the malar sulcus absent; gena broadened or not behind the eye in frontal view, toruli usually located in the upper half of the head, the antenna always with 11–12 flagellomeres, the notaulus is usually complete, the mesopleuron is smooth or with a few vertical carinae on the most posterodorsal part of the speculum or with weak longitudinal carinae anteriorly; the transscutal articulation is present; lateral propodeal carinae bent outwards, sometimes strongly; the prominent part of the ventral spine of the hypopygium relatively long, usually around 4.0–6.0× as long as broad. According to these characters, *Feron* is similar to some sexual *Andricus* species. *Andricus* do not exhibit smooth areas on the lower face, toruli are always located at mid-height of the head, and the prominent part of the ventral spine of the hypopygium is usually shorter (around 2.0–3.5× as long as broad). Exceptionally, *Andricus* with longer ventral spines of the hypopygium have lateral propodeal carinae subparallel or bent slightly outwards and the mesoscutum is completely smooth or partially delicately alutaceous; even in some sexual female *Andricus* the antenna has 13 flagellomeres. Biologically, an important character to differentiate *Feron* from *Andricus* is the galls: one group of *Feron* species induces pubescent, crystalline or conical galls with rigid extensions on leaves, while the galls of *Andricus* never form gregarious pubescent masses on leaves; also, other lineages of *Feron* species induce disc-shaped, often star-like, spangle galls on leaves, a morphology that never occurs in *Andricus*. A few sexual-generation *Andricus* species, for example, the Western Palearctic *A. quercusramuli* (Linnaeus, 1761), induce *Feron*-like pubescent galls but only on catkins; in addition, those sexual females differ from *Feron* in the absence of smooth areas on the lower face, the mesopleuron is uniformly and

very delicately transversally striate and the prominent part of the ventral spine of the hypopygium is usually short. The galls of some *Feron* species are similar to those induced by *Druon* species, but in *Druon* galls are covered in softer, more wool-like pubescent compared to the more crystalline hairs on *Feron* galls. The adults of *Druon* differ from *Feron* by the mesopleuron striate, and the lower face is entirely sculptured without smooth areas. Finally, some species of *Feron* can resemble *Dros*, but in *Dros* the frons is completely smooth (always sculptured in *Feron*) and the galls are significantly different.

**Re-description. Females.** Body yellowish to light brown, chestnut brown or dark brown, legs always lighter; antenna light brown to dark brown, with scape, pedicel and flagellomeres from F1 until F4 lighter than subsequent flagellomeres.

Head trapezoid, rounded, slightly ovate or semiquadrangular, with sparse white setae, denser on lower face, 1.1–1.2× as broad as high, slightly broader than mesosoma in small specimens in frontal view; 1.6–2.3× as broad as long in dorsal view. Gena alutaceous-reticulate, not broadened or very slightly broadened behind eye in frontal view, narrower than the transverse diameter of the eye in lateral view. Malar space alutaceous-reticulate, with striae radiating from clypeus sometimes reaching the eye, malar sulcus absent; eye 1.7–6.1× as high as the length of malar space. Inner margins of eyes parallel, converging, or slightly divergent. POL 1.3–3.0× as long as OOL (longer in males), OOL 1.0–3.3× as long as the diameter of lateral ocellus and slightly shorter to 2.0× as long as LOL, all ocelli ovate, of the same size. Transfacial distance longer or slightly shorter than the height of eye (shorter in some sexual forms); toruli usually located in the upper half of head and then frons shorter than lower face, the diameter of antennal torulus 1.0–2.0× as long as the distance between them, distance between torulus and eye around 1.0–1.5× as long as diameter of torulus; lower face smooth or slightly alutaceous between clypeus and eye, glabrous or with sparse white setae; slightly elevated median area alutaceous to smooth, with a few setae. Clypeus trapezoid, rectangular or quadrangular, smooth, or delicately coriaceous or striate, glabrous or with a few long setae scattered all over; ventrally rounded, emarginate, with or without median incision; anterior tentorial pit small, rounded, indistinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons alutaceous-reticulate or imbricate; interocellar area and vertex alutaceous-reticulate, without striae or setae; area under central ocellus impressed, alutaceous; occiput, postocciput and postgena alutaceous-reticulate, with few setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal

sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 11–12 flagellomeres (13 in males); pedicel longer than broad; F1 1.5–2.6× as long as pedicel and from equal with to 1.4× as long as F2; F2 equal to or longer than F3; all subsequent flagellomeres shorter, sometimes thicker; placodeal sensilla from F2 to F5 in females (in all flagellomeres in males); F1 in males with a variable shape, sometimes 1.6× as long as F2.

Mesosoma as long as high, with a few white setae along propleura. Pronotum smooth, glabrous or more or less pubescent laterally, foveolate or not along propleuron, laterally smooth or with delicate parallel striae in anteroposterior part; propleuron smooth, glabrous or setose. Mesoscutum as long as broad or slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae), uniformly delicately coriaceous or alutaceous to rugose-reticulate, sometimes with smooth areas and punctures (smooth in some sexual forms). Notaulus complete or not, deep or shallow, posteriorly converging and usually broader than anteriorly, bottom smooth, glabrous; in most posterior section the distance between notauli shorter than distance between notaulus and side of mesoscutum. Anterior parallel line indistinct or distinct, impressed, smooth, glabrous, reaching at most 1/2 length of mesoscutum; parapsidal line indistinct or marked with broad smooth, glabrous stripe; median mesoscutal line absent or in the form of a short triangle; parascutal carina broad, reaching notaulus. Mesoscutellum ovate or trapezoid, longer than broad, broader at posterior end; disc of mesoscutellum uniformly rugoso-coriaceous, reticulate or smooth in central part, rugose in most posterior section and along sides, with some longitudinal rugae, overhanging metanotum. Mesoscutellar foveae present, divided by a rugose elevated central area or fused in the form of an anterior transverse impression, with smooth, glabrous bottom. Mesopleuron entirely smooth or with a few vertical carinae in most posterodorsal section, glabrous or with setae only along ventral edge; mesopleural triangle delicately coriaceous, glabrous or with white setae; dorsal and lateral axillar areas smooth, with or without dense setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, triangular, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, in some species slightly higher or lower, lower part of sulcus delimiting broad triangular coriaceous area; upper part of sulcus either distinct, separating smooth, glabrous area or indistinct. Metascutellum coriaceous or smooth, glabrous, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, glabrous or with short setae; central propodeal area lyre-shaped, smooth, without or with only a few strong short

longitudinal rugae; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral propodeal area smooth, rarely alutaceous, glabrous or with long white setae, each seta with piliferous point at the base. Nucha with parallel longitudinal sulci dorsally and laterally or with a net of short irregular rugae. Tarsal claws with basal lobe.

Fore wing longer than body, except in brachypterous forms, hyaline, with dense cilia on margin, veins brown, radial cell open, 3.5–5.2× as long as broad; Rs and R1 not or nearly reaching wing margin; areolet triangular, enclosed by distinct veins. Rs+M distinct along entire length or along 1/3 to 2/3 of distance between areolet and basalis, its projection reaching basalis at half of its height.

Metasoma longer than head+mesosoma; 2nd metasomal tergum extending to 1/3–5/6 length of metasoma in dorsal view, with patch of dense white setae anterolaterally, with or without micropunctures; all subsequent terga and hypopygium with or without micropunctures; prominent part of ventral spine of hypopygium variable, 2.0–8.0× as long as broad in ventral view, with or without a few short white setae ventrally.

Body length 0.9–3.1 mm.

**Gall.** The asexual generation's galls are always found on leaves but have a wide range of morphologies that can mainly be divided into two subgroups: One with pubescent masses, crystalline (resembling mineral crystalline structures, usually erected tubular structures with short rigid and brittle filaments radiating from it) or conical galls with rigid extensions on leaves; and a second with disc-shaped, often star-like, spangle galls (disc-shaped with a central round protrusion). The sexual generation's gall

**Biology.** Adults galling on oaks from Section *Quercus*. The galls of the asexual generation mature during autumn, and adults overwinter in the galls and emerge between late January and May. The sexual generation occurs in late spring. The galls maturation and emergence of adults spans between April and May.

**Distribution.** Southern Canada, USA, and Mexico.

Descriptions of the sexual females and males are given in the species section below.

Thirty-four species are currently recognized within *Feron*:

*F. albicomus* (Weld, 1952), **comb. nov.**, *F. amphorus* (Weld, 1926), **comb. nov.**, *F. apiarium* (Weld, 1944), **comb. nov.**, *F. atrimentum* (Kinsey, 1922), **comb. nov.**, *F. bakkeri* (Lyon, 1984), **comb. nov.**, *F. caepula* (Weld, 1926), **comb. nov.**, *F. californicum* (Beutenmueller, 1911), **comb. nov.**, *F. clarkei* (Bassett, 1890), **comb. nov.**, *F. comatum* (Weld, 1952), **comb. nov.**, *F. crystallinum* (Bassett, 1900), **comb. nov.**, *F. cylindratum* (Kinsey, 1937), **comb. nov.**, *F. discale* (Weld, 1926), **comb. nov.**, *F. discularis* (Weld, 1926), **comb. nov.**, *F.*

*dumosae* (Weld, 1957), **comb. nov.**, *F. gigas* (Kinsey, 1922), **comb. nov.**, *F. izabellae* Melika, Nicholls & Stone, **sp. nov.**, *F. kingi* (Bassett, 1900), **comb. nov.**, *F. parmula* (Bassett, 1900), **comb. nov.**, *F. pattersonae* (Fullaway, 1911), **comb. nov.** (= *Andricus pedicellatus* (Kinsey, 1922), **syn. nov.**), *F. roberti* Melika, Nicholls & Stone, **sp. nov.**, *F. rucklei* Melika, Nicholls & Stone, **sp. nov.**, *F. scutellum* (Weld, 1930), **comb. nov.**, *F. serranae* Pujade-Villar & Cuesta-Porta, **sp. nov.**, *F. splendens* (Weld, 1919), **comb. nov.**, *F. stellare* (Weld, 1926), **comb. nov.**, *F. stellulum* (Burnett, 1974), **comb. nov.**, *F. sulfureum* (Weld, 1926), **comb. nov.**, *F. syndicorum* Pujade-Villar & Cuesta-Porta, **sp. nov.**, *F. tecturnarum* (Kinsey, 1920), **comb. nov.**, *F. tetyanae* Melika, **sp. nov.**, *F. tibiale* Kinsey, 1937, **comb. rev.** (= *F. tostum* Kinsey, 1937, **syn. nov.**, *Feron uterinum* Kinsey, 1937, **syn. nov.**), *F. tubifaciens* (Weld, 1926), **comb. nov.**, *F. verutum* Kinsey, 1937, **comb. rev.** and *F. vitreum* Kinsey, 1937, **comb. rev.** (= *F. validum* Kinsey, 1937, **syn. nov.**).

#### Key to *Feron* species

1. Males (Figs 62–67, 110–115, 146–147, 245–249, 288–292)..... 2
  - Females (Figs 1–11, 51–61, 68, 116–120)..... 9
2. Ocelli strongly elevated above frons in frontal view (Fig. 62), OOL shorter than diameter of lateral ocellus and inner margins of eyes subparallel (Figs 62–63); mesoscutum uniformly reticulate between notauli in anterior half and laterad to notauli, smooth between notauli in posterior half..... *atrimentum* **comb. nov.**
  - Ocelli moderately or not elevated above frons; if not then inner margins of eyes strongly converging laterally and/or OOL longer (Figs 110–111, 146, 245, 247, 288–289); mesoscutum smooth or partially alutaceous only anteriorly..... 3
3. Notaulus narrow, distinct only posteriorly, fragmented or absent anteriorly where mesoscutum delicately coriaceous..... *gigas* **comb. nov.**
  - Notaulus distinct, complete, reaching pronotum ..... 4
4. Inner margins of eyes slightly diverging ventrally (Fig. 146); mesoscutellar foveae absent, present in the form of a transverse smooth anterior impression, continuing into smooth mesoscutellar disc (Fig. 146); body yellowish to amber (Figs 146–147) *crystallinum* **comb. nov.**
  - Inner margins of eyes parallel or slightly converging ventrally (Figs 110, 245, 288); mesoscutellar foveae present, delimited posteriorly and delimited or not medially; mesoscutellar disc sometimes smooth; body brown to black (Figs 110–115, 245–248, 288–292)..... 5

5. Mesoscutellum with irregular rugae at least in lateral and posterior part; sometimes dorsocentral part smooth, shining, without piliferous points..... 6
- mesoscutellum uniformly alutaceous, with numerous setae on piliferous points; body brown or chestnut (Fig. 115); body black (Fig. 116) ..... 7
6. F1 1.6× as long as F2; transfacial distance as long as or slightly shorter than height of eye ..... *dumosae* **comb. nov.**
- F1 1.3× as long as F2; transfacial distance longer than height of eye ..... *clarkei* **comb. nov.**
7. F1 equal in length to scape+pedicel, 1.45× as long as F2, slightly broadened and curved, flagellomeres lighter than scape and pedicel ..... *comatum* **comb. nov.**
- F1 longer than scape+pedicel, 1.3× as long as F2, straight, not broadened and curved, flagellomeres, scape and pedicel uniformly coloured..... 8
8. Head ovate in frontal view; internal margin of eyes parallel; space between central elevated area of lower space to lateral margin of eye sculptured; OOL shorter than diameter of lateral ocellus ..... *kingi* **comb. nov.**
- Head triangular in frontal view (Fig. 288); inner margin of eyes converging ventrally; space between central elevated area of lower face to lateral margin of eye smooth (Fig. 288); OOL as long as diameter of lateral ocellus (Fig. 289) ..... *pattersonae* **comb. nov.**
9. Fore wing rudimentary, as long as head+mesosoma but not reaching the mid-length of metasoma, with indistinct veins (Fig. 94)..... *californicum* **comb. nov.** (asex.)
- Fore wing longer than length of body with distinct veins (Figs 184–185) ..... 10
10. Mesoscutum smooth or partially finely alutaceous anteriorly; always glabrous (Figs 20–21, 32–33, 104–105, 118, 120, 143–144, 156–157, 169–170, 196–197, 251–252, 295–296) ..... 11
- Mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, sometimes with small smooth areas and piliferous points; glabrous or pubescent (Figs 8–9, 44–45, 70, 131, 210–211, 305, 436) ..... 21
11. Mesoscutellum uniformly reticulate (Fig. 157)..... *cylindratum* **comb. nov.** (asex.)
- Mesoscutellum with different sculpture (Figs 21, 105, 118, 120, 170, 277) ..... 12
12. Frons bulging in frontal view (Fig. 162); inner margins of eyes strongly converging ventrally (Fig. 162); mesoscutellum in central part smooth, glabrous, posteriorly and laterally rugose (Figs 170–171); body yellowish to reddish brown (Figs 162–172)..... *discale* **comb. nov.** (asex.)

–Frons flat, not or only slightly bulging in frontal view (Fig. 121); inner margins of eyes parallel or only slightly converging ventrally; mesoscutellum rugose and/or with piliferous points (Figs 116, 118, 120); darker specimens (Figs 13–23, 25–35, 97–106, 116–121, 241–243, 250–253, 254, 293–299) ..... 13

13.; mesoscutellum uniformly alutaceous with numerous setae on piliferous points (Figs 33, 120, 252, 296); body black (Figs 25–35, 116–121, 241–243, 250–253, 254, 293–299)..... 14

–Mesoscutellum with irregular rugae at least in lateral and posterior parts, sometimes central part smooth, shining, without piliferous points (Figs 21, 105, 144, 197); body light brown to chestnut brown, rarely darker (Figs 13–23, 97–106, 136–145, 189–198)..... 18

14. Notaulus narrow, distinct only posteriorly, discontinuous or absent and finely coriaceous in anterior part; mesopleuron smooth, with transverse striae in central part .....  
..... *gigas* **comb. nov.** (sex)

– Notaulus distinct, complete, reaching pronotum (Figs 32, 116, 118, 251, 295); mesopleuron entirely smooth, without transverse striae in central part (Figs 31, 117–119, 250, 294)..... 15

15. Toruli at half the height of head (Fig. 121); scape, pedicel, F1–F2 yellowish (Fig. 116); legs including hind coxa yellowish (Fig. 117); prominent part of ventral spine of hypopygium without setae ventrally ..... *comatum* **comb. nov.** (sex)

– Toruli in the upper half of head (Figs 25, 241, 284; scape, pedicel, F1–F2 dark brown, sometimes light brown but never yellowish (Figs 29, 244, 287); legs reddish brown, at least hind coxa darker; prominent part of ventral spine of hypopygium with setae ventrally ..... 16

16. Eyes parallel; eye 1.7× as high as length of malar space (Fig. 25); antennomeres with long and erect setae (Fig. 29); OOL only slightly longer than diameter of lateral ocellus (Fig. 26); notaulus complete, deep (Fig. 32); prominent part of ventral spine of hypopygium with long dense white setae ventrally (Fig. 35) ..... *apiarium* **comb. nov.** (asex)

– Eyes converging ventrally; eye at least 4.0× as high as length of malar space (Figs 241, 284); antennomeres with short setae (Figs 244, 287); OOL 1.5× as long as diameter of lateral ocellus (Figs 242, 286); notaulus complete, sometimes weakly impressed anteriorly (Figs 251, 295); prominent part of ventral spine of hypopygium with few short setae ventrally (Figs 255, 299)..... 17

17. Antenna with 11 flagellomeres; F1 subequal to F2 and at most 2.0× as long as pedicel (Fig. 244); head distinctly narrower than mesosoma and genae broadened in frontal view (Fig. 241); mesoscutellar foveae separated by narrow elevated coriaceous central carina; areolet inconspicuous (Figs 251–252) ..... *kingi* **comb. nov.** (sex)

- Antenna with 12 flagellomeres; F1 1.2× as long as F2 and more than 2.0× as long as pedicel (Fig. 287); head only slightly narrower than mesosoma and genae not broadened (Fig. 284); mesoscutellar foveae fused in the form of a narrow, semi-lunar depression (Figs 296–297); areolet triangular (Fig. 298) ..... *pattersonae* **comb. nov.** (sex)
18. Transfacial distance as long as or slightly shorter than height of eye; eye more than 3.6× as high as length of malar space (Figs 136, 189) ; pronotum laterally with short carinae only along posterior margin (Figs 142, 195)..... 19
- Transfacial distance longer than height of eye; eye less than 3.0× as high as length of malar space (Figs 13, 97); pronotum with carinae going across entire lateral surface (Figs 19, 103) ..... 20
19. Eyes converging ventrally (Fig. 189); F1 longer than F2 (Fig. 193); mesopleuron smooth, shining, with delicate transverse subparallel striae in central part (Fig. 195); prominent part of ventral spine of hypopygium slightly longer than broad, without setae (Fig. 200); brown coloured (Figs 189–198, 200) ..... *dumosae* **comb. nov.** (sex)
- Eyes parallel or only slightly converging posteriorly (Fig. 136); F1= F2; mesopleuron completely smooth, without striae (Fig. 139); ventral spine of hypopygium 3.7× as long as broad, with short white setae ventrally (Fig. 145; dark-coloured body (Figs 136–138, 142–145) ..... *crystallinum* **comb. nov.** (sex)
20. Gena not broadened behind eye in frontal view (Fig. 13); mesoscutellar foveae in the form of an anterior transverse impression, posteriorly not defined, continuing into disc of mesoscutellum (Fig. 21); mesopleuron completely smooth; metapleural sulcus reaching mesopleuron at half of its height (Fig. 19); 2nd metasomal tergum with setae anteriorly (Fig. 23); body light brown (Figs 13–23) ..... *amphorus* **comb. nov.** (asex)
- Gena slightly broadened behind eye in frontal view (Fig. 97); mesoscutellar foveae well-delimited by a carina posteriorly, separated medially (Fig. 105); mesopleuron with delicate indistinct transverse subparallel striae in anterodorsal part at mid height; metapleural sulcus reaching mesopleuron above half of its height (Fig. 103); 2nd metasomal tergum without setae (Fig. 108); body dark brown to chestnut brown (Figs 97–106, 108) ..... *clarkei* **comb. nov.** (sex)
21. Pronotum laterally smooth to coriaceous, without carinae (Figs 7, 43, 130, 222, 275, 378) ..... 22
- Pronotum with longitudinal carinae laterally (Figs 57, 68, 78, 209, 304, 360, 401, 470) .... 27



22. Frons bulging in frontal view (Figs 1, 216); ocelli not elevated above head; transfacial distance 1.4× longer than height of eye (Figs 1, 216); eyes slightly converging ventrally, metapleural sulcus reaching mesopleuron on upper 2/3 of its height (Figs 7, 222) ..... 23
- Frons not bulging in frontal view, ocelli sometimes elevated above head; transfacial distance subequal or 1.2× longer than height of eye (Figs 37, 124, 269, 372); metapleural sulcus reaching mesopleuron at half of its height (Figs 43, 130, 275, 378) ..... 24
23. Median mesoscutal line in the form of a short smooth, shining triangle (Fig. 8); mesoscutellar foveae divided by a thin carina (Fig. 9); ventral spine of hypopygium 11.0× longer than broad in ventral view (Fig. 11); head and mesosoma uniformly reddish brown (Figs 1–10).....*albicomus* **comb. nov.** (asex)
- Median mesoscutal line absent (Figs 223–224); mesoscutellar foveae divided by an elevated coriaceous triangle (Fig. 224); ventral spine of hypopygium 8.0× as long as broad in ventral view (Fig. 226); head and mesosoma amber (Figs 216–225).....*izabellae* **sp. nov.** (asex)
24. Pronotum smooth, with sparse setae and piliferous points along dorsal edge (Fig. 43); mesoscutum longer than broad, scarcely pubescent, without black stripes, alutaceous-reticulate between notauli in anterior 2/3 length and lateral to notauli, smooth between notauli in posterior 1/3; anterior parallel line indistinct, parapsidal line absent (Figs 44–45) .....*atrimentum* **comb. nov.** (asex)
- Pronotum coriaceous, if smooth then with dense setae and piliferous points (Figs 130, 275, 378); mesoscutum only slightly longer than broad (subequal), pubescent (Figs 131, 276, 379); mesoscutum dark brown in between notauli in anterior 1/3 length of mesoscutum and along parapsidal line, with other surface sculpture; anterior parallel line and parapsidal line present (Figs 131, 276, 379) ..... 25
25. Head ovate in frontal view (Fig. 269); pronotum smooth with dense setae and piliferous points (Fig. 275); mesoscutellar foveae fused (Fig. 277); 2nd metasomal tergum extending to 1/3 the length of metasoma in dorsal view (Fig. 280) .....*pattersonae* **comb. nov.** (asex)
- Head trapezoid in frontal view (Figs 124, 372); pronotum coriaceous, if smooth then with dense setae and without piliferous points (Figs 130, 378); mesoscutellar foveae divided by median elevated narrow triangular area or carina (Figs 132, 379); 2nd metasomal tergum smooth, extending at least to 5/6 length of metasoma in dorsal view (Figs 134, 382)..... 26
26. Pronotum coriaceous in posterolateral area, with piliferous points (Fig. 130); mesoscutum rugose-reticulate between notauli and laterad to notaulus in anterior half, alutaceous glabrous between notauli in posterior half (Fig. 131); eye 2.7× as high as length of malar

space (Fig. 124); distal flagellomeres broader than basal ones, F1 shorter than scape+pedicel (Fig. 128); prominent part of ventral spine of hypopygium 6.5x as long as broad in ventral view (Fig. 134).....*crystallinum* **comb. nov.** (asex)

– Pronotum smooth, without piliferous points (Fig. 378); mesoscutum uniformly delicately coriaceous (Fig. 379); eye 3.7x as high as length of mala space (Fig. 372); all flagellomeres uniformly broad, F1 longer than scape+pedicel (Fig. 376); prominent part of ventral spine of hypopygium more than 5.5x as long a broad in ventral view (Fig. 382).....*sulfureum* **comb. nov.** (asex)

27. Mesoscutum with distinct and deep piliferous points (Figs 235–236, 471)..... 28

– Mesoscutum without piliferous points or shallow almost inconspicuous points (Figs 58, 70, 79, 210, 305, 361, 390, 402–403, 420, 436) ..... 30

28. Frons bulging in frontal view, ocelli not elevated above head (Fig. 186); toruli at mid-height of head (Fig. 186); median mesoscutal line in the form of a short triangle; entire body black (Figs 184–186) .....*discularis* **comb. nov.** (asex)

– Frons not bulging in frontal view, ocelli not elevated above head; toruli in upper half of head (Figs 228, 464); median mesoscutal line absent (Figs 235, 471); head and mesosoma never black (Figs 228–238, 464–472, 474) ..... 29

29. Gena broadened behind eye in frontal view (Fig. 228); clypeus smooth; eye 2.9x as high as length of malar space (Fig. 228); metapleural sulcus reaching mesopleuron at half of its height (Fig. 234); fore wing longer than body ; metasomal terga 6 and 7 with micropunctures; prominent part of ventral spine of hypopygium around 8.0x as long as broad in ventral view (Fig. 238); light specimens, rusty brown and rarely uniformly dark brown (Figs 228–238).....*kingi* **comb. nov.** (asex)

– Head not broadened behind eye in frontal view; clypeus with short interrupted delicate transverse striae; eye 1.9x as high as length of malar space (Fig. 464); metapleural sulcus reaching mesopleuron at upper 1/3 of its height (Fig. 470); fore wing only slightly longer than length of body (Fig. 473); all metasomal terga smooth, without micropunctures; prominent part of ventral spine of hypopygium around 5.0x as long as broad (Fig. 474); dark specimens, head dark brown to black, mesosoma reddish brown with some darker tints (Figs 464–472, 474) ..... *tubifaciens* **comb. nov.** (asex)

30. Eyes strongly converging ventrally; transfacial distance shorter than height of eye; antennal toruli located at half or slightly above height of eyes; eye around 6.0x as high as length of malar space (Fig. 51); body black (Figs 51–61)..... *atrimentum* **comb. nov.** (sex)

–Eyes parallel or very slightly converging ventrally; transfacial distance equal to or longer than height of eye; toruli located above mid-height of eyes; eye less than 3.0× as high as length of malar space (Figs 69, 72, 300, 329, 342, 476, 489, 502); body yellowish, reddish brown, brown to chestnut brown (Figs 68–70, 72–82, 203–212, 256–265, 324–327, 329–338, 354–363) .....	31
31. Head quadrangular or ovate in frontal view, with ocelli always elevated above frons (Figs 342, 476, 489, 502); lateral ocelli large, OOL subequal or at most 1.7× as long as diameter of ocellus (Figs 344, 477, 490, 503) .....	32
– Head rounded or trapezoid to triangular in frontal view, ocelli usually not elevated above frons (Figs 69, 72, 203, 256, 300, 354, 384, 395, 429); lateral ocelli smaller, OOL at least 2.5× as long as diameter of ocellus, if shorter then head and mesosoma are not yellowish or light brown (Figs 73, 204, 257, 302, 356, 386, 397, 430) .....	34
32. F1 distinctly longer than scape+pedicel (Fig. 493); transfacial distance equal to or slightly shorter than height of eye (Fig. 489).....	<i>vitreum</i> <b>comb. rev.</b> (asex)
– F1 subequal to or slightly longer than scape+pedicel (Figs 346, 480, 506); transfacial distance longer than height of eye (Figs 342, 476, 502).....	33
33. Mesoscutum with some delicate transverse striae in anterior part between notauli; anterior parallel lines indistinct (Figs 349–350); mesoscutellar foveae transverse, ovate, separated by a broad carina, posteriorly delimited by a carina (Fig. 350).....	<i>splendens</i> <b>comb. nov.</b> (asex)
– Mesoscutum without striae, anterior parallel line in the form of a bare, smooth stripe, extending to 1/3 length of mesoscutum (Figs 483–484); foveae quadrangular, separated by a thin carina, posteriorly not delimited by a carina (Fig. 484) .....	<i>verutum</i> <b>comb. rev.</b> (asex)
34. Mesopleuron with transverse reticulate-carinate band at mid-height (Figs 209, 262, 370, 389, 435) .....	35
– Mesopleuron entirely smooth or slightly sculptured on anterior margin (Figs 68, 78, 304, 317, 327, 335, 360, 401, 419, 435) .....	39
35. Gena broadened behind eye in frontal view (Figs 384, 429); 2nd metasomal tergum without micropunctures posteriorly and subsequent terga with or without micropunctures (Figs 393, 439) .....	36
– Gena not broadened behind eye in frontal view (Figs 203, 256, 369); 2nd metasomal tergum with a band of micropunctures posteriorly and all subsequent terga with micropunctures (Figs 214, 267, 368).....	37

36. Mesoscutum coarsely reticulated; notaulus complete, notaular furrow smooth and deep along its length or alutaceous on anterior 1/4 (Fig. 436); mesoscutellar disk flat in lateral view, following curvature of mesoscutum (Fig. 437); subaxillular bar reaching half-length of mesoscutellum in lateral view (Fig. 435)..... *tibiale* **comb. rev.** (asex), part
- Mesoscutum finely alutaceous; notaulus complete, but indistinct and shallow at least on anterior 3/4 of its length (Fig. 390); mesoscutellar disk strongly curved in lateral view; mesoscutum and mesoscutellum forming two independent lobes in lateral view (Fig. 391); subaxillular bar reaching 1/3 of height of mesoscutellum (Fig. 389).....  
.....*syndicorum* **sp. nov.** (asex)
37. Malar space without striae (Fig. 256); notaulus complete, indistinct in anterior 1/4 of mesoscutum (Fig. 263); mesoscutellar foveae absent or slightly impressed (Fig. 264); veins of fore wing pale (Fig. 266); prominent part of ventral spine of hypopygium 7.0× as long as broad in ventral view (Fig. 267) ..... *parmula* **comb. nov.** (asex)
- Malar space with a few delicate striae radiating from clypeus (Figs 203, 369); notaulus complete, distinct through all its length (Figs 210, 367); mesoscutellar foveae defined (Figs 211, 367); veins of fore wing light brown to brown (Figs 213, 367); prominent part of ventral spine around 4.5× as long as broad in ventral view (Figs 214, 368) ..... 38
38. Antenna with 11 flagellomeres (Figs 368–370); eye 2.7× as high as length of malar space (Fig. 369); veins of fore wing brown; areolet present (Fig. 367); central propodeal area with rugae..... *stellulum* **comb. nov.** (asex)
- Antenna with 12 flagellomeres (Fig. 207); eye 2.2× as high as length of malar space (Fig. 203); veins of fore wing lighter; areolet absent (Fig. 213); central propodeal area without rugae (Fig. 212)..... *gigas* **comb. nov.** (asex)
39. Head trapezoid (Fig. 300); gena not broadened behind eye; transfacial distance equal to height of eye (Fig. 300); antenna with 11 flagellomeres; F1=F2; mesoscutellar disc reticulate (Fig. 303); metapleural sulcus reaching mesopleuron in lower 1/3 of its height (Fig. 304); 2nd metasomal tergum extending to 3/4 of metasoma length in dorsal view (Fig. 309).....  
..... *roberti* **sp. nov.** (asex)
- Head rounded or ovate (Figs 69, 72, 311, 324, 329, 354, 395, 409, 429); gena at least slightly broadened behind eyes; transfacial distance longer than height of eye (Figs 69, 72, 311, 324, 329, 354, 395, 409, 429); antenna with 12 flagellomeres, sometimes suture between F11 and F12 incomplete; F1 longer than F2; distal flagellomeres broader than basal ones (Figs 76, 315, 326, 333, 358, 399, 413, 418, 433); mesoscutellar disc smooth or with a

different sculpture; metapleural sulcus reaching mesopleuron at least at 1/2 of its height (Figs 70, 80, 319, 325, 337, 362, 403, 420, 424, 437); 2nd metasomal tergum extending to 1/2–2/3 length of metasoma in dorsal view (Figs 68, 82, 321, 327, 340, 365, 406, 426–427, 439) ..... 40

40. Head transversely ovate in frontal view (Figs 329, 395, 409, 429); slightly elevated median area of lower face alutaceous to delicately coriaceous, matte (Figs 329, 395, 409, 429); lateral sides of pronotum longitudinally striated at least on posterior half, rest of pronotum alutaceous, matte (Figs 335, 401, 419, 435); mesoscutum coarsely reticulated, each individual cell formed by the reticula bulging (Figs 336, 402, 420, 436); mesopleuron finely striated to alutaceous on anterior margin (Figs 335, 401, 419, 435) ..... 41

– Head rounded (Figs 69, 72, 311, 324, 354); slightly elevated median area of lower face smooth, shining (Figs 69, 72, 311, 324, 354); lateral sides of pronotum with fine longitudinal striations on posterior margin, never reaching half the length of pronotum, rest of the pronotum shining, smooth with piliferous points on dorsal margin (Figs 68, 78, 317, 327, 360); mesoscutum finely reticulated, the cells formed by the reticula flat (Figs 70, 79, 318, 325, 361), mesopleuron completely smooth (Figs 68, 78, 317, 327, 360) ..... 44

41. Mesoscutellum 1.3× longer than broad and margined posteriorly by a strong circumscutellar carina (Fig. 337) ..... *serranoae* **sp. nov.** (asex)

– Mesoscutellum slightly longer than broad and circumscutellar carina absent (Figs 403, 420, 424, 437) ..... 42

42. Frons bulging in frontal view (Fig. 429); POL subequal to OOL (Fig. 430); gena broadened behind eye in frontal view (Fig. 429); mesoscutum uniformly reticulate-coriaceous (Fig. 436); central mesoscutellar disk coriaceous (Fig. 437); radial cell around 4.8× as long as broad; third and subsequent metasomal terga with sparse micropunctures (Fig. 439); body yellowish to light brown (Figs 429–439)..... *tibiale* **comb. rev.** (asex), part

– Frons not bulging in frontal view (Figs 395, 409, 414), POL at least 1.4× longer than OOL (Figs 397, 410, 415); gena not or slightly broadened behind eye in frontal view (Figs 395, 409, 414); mesoscutum alutaceous to reticulate (Figs 402, 420, 424); center of mesoscutellar disk smooth or finely rugose (Figs 403, 420, 424); radial cell around 3.7× as long as broad (Figs 405, 422); all metasomal terga without micropunctures (Figs 406, 426–427); body chestnut brown or rusty brown (Figs 395–406, 409–427, 429–439)..... 43

43. Mesoscutum sometimes with dark brown areas around anterior parallel lines and parapsidal lines (Figs 420, 424); frons coarsely coriaceous (Figs 409–410); mesoscutellar

foveae divided by a fine carina (Fig. 420); chestnut brown, head always darker than mesosoma (Figs 409–427) ..... *tetyanae* **sp. nov.** (asex)

–Frons finely alutaceous (Fig. 395); mesoscutellar foveae divided by a triangular elevated coriaceous central carina (Fig. 403); rusty brown to light brown, head and mesosoma of the same colour and without dark areas (Figs 395–404, 406) ..... *tecturnarum* **comb. nov.** (asex)

44. Frons bulging in frontal view; eyes strongly converging ventrally; eye 3.0× as high as length of malar space (Fig. 72); central part of mesoscutellum smooth (Fig. 80); prominent part of ventral spine of hypopygium around 3.8× as long as broad in ventral view (Fig. 82); yellowish to light brown (Figs 72–82)..... *caepula* **comb. nov.** (asex)

–Head rounded; eyes parallel or very slightly converging ventrally; height of eye less than 2.6× as high as length of malar space (Figs 69, 311, 324, 354); central part of mesoscutellum coriaceous to rugose (Figs 70, 319, 325, 362); prominent part of ventral spine of hypopygium at least 5.5× as long as broad in ventral view (Figs 68, 321, 327, 365); brown, sometimes with darker marks (Figs 68–70, 311–315, 317–321, 324–327, 354–363, 365)... 45

45. Mesoscutellar foveae absent, only slightly impressed on anterior part, with the bottom finely rugose like the rest of the disk, without central carina (Fig. 70); metasoma longer than high in lateral view (Fig. 68)..... *bakkeri*, **comb. nov.** (asex)

– Mesoscutellar foveae conspicuous and bottom smooth, fused or divided by a central carina or a triangular elevated area (Figs 319, 325, 362); metasoma as high as long or higher in lateral view (Figs 321, 327, 365) ..... 46

46. Mesoscutellum disk faintly reticulate, with an elevated central area; mesoscutellar foveae not delimited posteriorly (Fig. 325)..... *scutellum* **comb. nov.** (asex)

– Mesoscutellar disk coarsely rugose, without elevated area; mesoscutellar fovea completely delimited by rugose sculpture or by a carina (Figs 319, 362)..... 47

47. Notaulus incomplete (Fig. 361); mesoscutellar foveae delimited all around by strong black carina; mesoscutellum rugose-coriaceous (Fig. 362); all metasomal terga without micropunctures (Fig. 365); first flagellomeres lighter than subsequent (Fig. 358) ..... *stellare* **comb. nov.** (asex)

–Notaulus complete (Fig. 318); mesoscutellar foveae separated by triangular elevated coriaceous central carina; mesoscutellum rugose (Fig. 319); third and subsequent terga with sparse micropunctures (Fig. 321); all flagellomeres dark (Fig. 315)..... *rucklei* **sp. nov.** (asex)

*Feron albicomus* (Weld, 1952), **comb. nov.**

## Figs 1–12

*Andricus albicomus* Weld, 1952b: 328, female, gall.

**Types examined.** HOLOTYPE: Asexual female “Caves Jn, Ore, IV-1-50”, red label “Holotype 60114 USNM”, white label “*Q. garryana*”. PARATYPE (1 asexual female) “Caves Jn, Ore, IV-1-50”, red label “Paratype 60114 USNM”, white label “*Q. garryana*”. All types examined by GM. Specimen data and images available at <http://n2t.net/ark:/65665/3e7f08a02-77fe-4b33-a2d9-6c7eff63e6af>

**Diagnosis.** The asexual form of this species belongs to the *Feron* group in which the pronotum is laterally smooth to coriaceous, without carinae, and the mesoscutum is alutaceous to coriaceous, rugose-reticulate, or reticulate, sometimes with smooth areas and piliferous points, glabrous or pubescent as in *F. atrimentum* (asex), *F. crystallinum* (asex), *F. izabellae* (asex), *F. pattersonae* (asex), and *F. sulfureum* (asex). It differs from *F. atrimentum* (asex), *F. crystallinum* (asex), *F. pattersonae* (asex), and *F. sulfureum* (asex) in the following combination of characters: the frons is bulging in frontal view; ocelli are not elevated above the head, the transfacial distance is 1.4× as long as the height of eye, the eyes slightly convergent ventrally, and the metapleural sulcus reaching the mesopleuron on the upper 2/3 of its height. The most similar species is *F. izabellae* (asex) from which *F. albicomus* differs in having the head and mesosoma reddish brown, the median mesoscutal line in the form of a short smooth, shining triangle, mesoscutellar foveae divided by a carina, and ventral spine of hypopygium 11.0× as long as broad in ventral view.

**Re-description.** Asexual female (Figs 1–11). Body, antenna, legs rusty brown.

Head alutaceous, with sparse setae on lower face, postgena, 1.2× as broad as high and slightly narrower than mesosoma in frontal view; 2.3× as broad as long in dorsal view. Gena alutaceous-reticulate, only slightly broadened behind eye in frontal view; gena in lateral view narrower than transverse diameter of eye in the dorsal part of eye and as broad as transverse diameter of eye in ventral part. Malar space alutaceous, with striae radiating from clypeus and reaching eye; eye 2.4× as high as length of malar space; malar sulcus absent. Inner margins of eyes very slightly converging ventrally. POL 1.5× as long as OOL, OOL 3.3× as long as diameter of lateral ocellus and 1.5× as long as LOL, all ocelli ovate, central ocellus slightly larger than lateral ocellus. Antennal toruli located above mid-height of eyes. Transfacial distance 1.4x as long as height of eye; diameter of antennal torulus 1.75× as long as distance between them, distance between torulus and eye 1.3× as long as diameter of torulus; lower face smooth, shining, with white setae, ventral area along malar space alutaceous; slightly

elevated median area and area between toruli alutaceous, without setae. Clypeus impressed, rectangular, broader than high, delicately coriaceous, with a few setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit large, rounded, deep, epistomal sulcus broad and deep, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex uniformly reticulate, without striae and setae; area under central ocellus impressed, smooth, glabrous; occiput alutaceous, with dense setae; postocciput glabrous, with numerous delicate longitudinal interrupted parallel striae; postgena smooth, with few setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal sulci which diverge until half the height of postgenal bridge, further sulci parallel and running alongside foramen until 1/3 of its height. Antenna as long as body, with 12 flagellomeres (suture between F11 and F12 indistinct), pedicel longer than broad, F1 slightly shorter than length of scape+pedicel, 1.25× as long as F2, F2 slightly longer than F3, F3=F4, subsequent flagellomeres shorter and nearly equal in length, F12 shorter than F11; placodeal sensilla on F3–F12.

Mesosoma longer than high, with white setae, setae denser on pronotum laterally, mesopleural triangle, mesoscutellum and lateral area of propodeum. Pronotum smooth without striae, with setae only in dorsal and posterior edges, piliferous points along dorsal edge; anterolateral edge of pronotum smooth, glabrous, without foveae; propleuron smooth, with sparse white setae. Mesoscutum longer than broad (greatest width measured across mesoscutum level with base of tegulae), uniformly alutaceous-reticulate. Notaulus complete, deep, posteriorly converging and broader than anteriorly, with smooth, glabrous bottom; at most posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line indistinct, hardly traceable; parapsidal line marked with narrow, smooth elevated stripe; median mesoscutal line in the form of a short smooth, glabrous, impressed triangle; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid, longer than broad, broadest part in posterior 1/3; center part of mesoscutellum disc rugoso-coriaceous, with stronger rugae posteriorly and laterally, overhanging metanotum, with long setae. Mesoscutellar foveae rounded, as broad as high, with smooth, glabrous bottom, divided by a narrow, elevated carina. Mesopleuron entirely smooth, with setae only along ventral edge; mesopleural triangle smooth, with dense white setae and piliferous points; dorsal and lateral axillar areas smooth, with setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, triangular, posteriorly slightly higher than height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, lower part



delimiting smooth area with few setae, upper part of sulcus indistinct. Metascutellum coriaceous, top as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with a few setae; central propodeal area lyre-shaped, smooth, glabrous; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral propodeal area smooth, with long white setae. Nucha with longitudinal sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins light brown, radial cell open, 4.4× as long as broad; Rs and R1 nearly reaching wing margin; areolet small, triangular, closed, indistinct. Rs+M lightly pigmented, hardly traceable, visible on 1/3 of distance from areolet to basalis, its projection reaching basalis slightly below half of its height.

Metasoma longer than head+mesosoma, longer than high in lateral view; all metasomal terga smooth, glabrous, 2nd metasomal tergum extending to 2/3 length of metasoma in dorsal view, with white setae anterolaterally, without micropunctures; all subsequent terga with rare, weak, very delicate micropunctures. Hypopygium with micropunctures, prominent part of ventral spine of hypopygium 6.3× as long as broad in ventral view.

Body length 2.0 mm (n = 53) (Weld 1952b).

**Gall** (Fig. 12). The asexual monolocular, round, bristly pubescent galls are mostly on the underside and, sometimes, the dorsal surface of leaves. Galls are covered with short, stellate white hairs. Galls occur singly or in scattered groups along the edges of the leaves or near the midrib. Galls are 4 mm high and wide (Russo 2006, 2021; Weld 1952b, 1957).

**Biology.** The asexual generation is only known, which induces galls on *Q. garryana* (section *Quercus*, subsection *Dumosae*), the gall matures by October; adults emerge in April.

**Distribution.** USA: north California (Russo 2006, 2021; authors), Oregon (Burks 1979).

***Feron amphorus* (Weld, 1926) comb. nov.**

**Figs 13–24**

*Diplolepis amphora* Weld, 1926: 17, female, gall.

*Dros amphora* (Weld): Weld, 1951: 629.

*Andricus amphorus* (Weld): Melika & Abrahamson 2002: 162.

**Types examined.** HOLOTYPE: Asexual female “Tijeras, N.M.”, “Cut out Nov. 1.21”, red label” Type No. 27186 USNM”, “*Diplolepis amphora* Weld” deposited in USNM, examined by GM. Specimen data and images available at <http://n2t.net/ark:/65665/302837515-1e1c->

4243-9b94-f5fc71dc5d68. PARATYPE (2 females, and 2 galls) “Tijeras N.M.”, “*Quercus pungens*”, red label “Paratype No. 27186 USNM”, “*Diplolepis amphora* Weld”. Another seven paratypes are deposited in other institutions according to the original description.

**Additional material examined.** One female “USA, Arizona, 25 miles S of Flagstaff on I17, AZ246, galltype 71, *Q. turbinella*; leg. J.A. Nicholls, 2007.10.31”.

**Diagnosis.** Asexual females belong to the group of *Feron* species that are brown to chestnut brown, rarely darker; inner margins of eyes parallel or only slightly converging ventrally; the frons is flat, not or only slightly bulging in frontal view; the mesoscutum is smooth or partially alutaceous anteriorly and glabrous; the mesoscutellum with irregular rugae at least in the lateral and posterior parts, sometimes the dorsocentral part is smooth, shining, without piliferous points; as in *F. clarkei* (sex), *F. crystallinum* (sex) and *F. dumosae* (sex). Differs from *F. crystallinum* and *F. dumosae* in the transfacial distance which is longer than the height of eye, the eye is less than 3.0× as high as length of the malar space and the pronotum with carinae going across entire lateral surface; and differs from *F. clarkei* in characters mentioned at couplet 20 of the key.

**Re-description.** Asexual female (Figs 13–23). Body uniformly light brown, legs light brown; scape, pedicel, F1 and F2 light brown, all subsequent flagellomeres uniformly dark brown; mesoscutum with narrow yellowish stripe along notaulus.

Head with sparse white short setae on lower face, 1.2× as broad as high and slightly broader than mesosoma in frontal view; 2.1× as broad as long in dorsal view. Gena alutaceous, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, with a few striae radiating from clypeus, some of which reach eye; eye 2.5× as high as length of malar space; malar sulcus absent. Inner margins of eyes parallel. POL 1.7× as long as OOL, OOL 1.9× as long as diameter of lateral ocellus and slightly longer than LOL, all ocelli ovate, of same size. Transfacial distance slightly longer than height of eye; toruli located in the upper half of head and frons shorter than lower face, diameter of antennal torulus nearly 2.0× as long as distance between them, distance between torulus and eye 1.4× as long as diameter of torulus; lower face smooth, with sparse white setae; slightly elevated median area alutaceous, with a few setae. Clypeus trapezoid, slightly broader than high, delicately coriaceous, with a few long setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit small, rounded, indistinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex uniformly alutaceous, without striae and setae; area under central

ocellus impressed, alutaceous; occiput and postocciput, postgena alutaceous, with few setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal sulci which strongly diverge toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres; pedicel 1.6× as long as broad; F1 1.7× as long as pedicel and slightly longer than F2; F2 1.2× as long as F3; F3 to F6 equal in length, F7 to F11 shorter and all equal in length, F12 as long as F11; placodeal sensilla on F3–F12.

Mesosoma as long as high, with a few white setae along propleura. Pronotum smooth, glabrous, foveolate along propleuron, laterally smooth to coriaceous, sometimes with delicate parallel striae in anteroposterior part; propleuron smooth, glabrous. Mesoscutum slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae), weakly alutaceous between notauli in anterior half and laterad to notauli, smooth and glabrous in between notauli in posterior half. Notaulus complete, deep, posteriorly converging and broader than anteriorly, bottom smooth, glabrous; at most posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line indistinct, impressed, smooth, glabrous, reaching to 1/5 length of mesoscutum; parapsidal line invisible; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid, longer than broad, with subparallel sides, broader at posterior end; disc of mesoscutellum smooth glabrous in central part, rugose in most posterior part and along sides, with some longitudinal rugae, overhanging metanotum; circumscutellar carina present. Mesoscutellar foveae in the form of an anterior transverse, smooth, glabrous impressed area, well-delimited anteriorly and smoothly continuing into disc of mesoscutellum. Mesopleuron entirely smooth, glabrous, without setae, setae present only along ventral edge; mesopleural triangle delicately coriaceous, with sparse short white setae; dorsal and lateral axillar areas smooth, glabrous, without setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, triangular, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, lower part of sulcus delimiting broad triangular coriaceous area; upper part of sulcus also distinct, separating smooth, glabrous area. Metascutellum smooth, glabrous, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with a few short setae; central propodeal area lyre-shaped, smooth, glabrous, without rugae; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral propodeal area smooth, with long white setae, each seta

with rounded bump at the base. Nucha with parallel longitudinal sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with dense cilia on margin, veins brown, radial cell open, 3.9× as long as broad; Rs and R1 nearly reaching wing margin; areolet triangular, enclosed by distinct veins. Rs+M indistinct, visible on 1/3 of distance between areolet and basalis, its projection reaching basalis at half of its height.

Metasoma longer than head+mesosoma, rounded, higher than long in lateral view; 2nd metasomal tergum smooth, extending to 2/3 length of metasoma in dorsal view, with patch of dense white setae anterolaterally, without micropunctures; all subsequent terga and hypopygium smooth, without micropunctures; prominent part of ventral spine of hypopygium 5.2× as long as broad in ventral view, with a few short white setae ventrally.

Body length 1.4–2.2 mm (n = 31) (Weld 1926).

**Gall** (Fig. 24). The gall is on the underside of leaf, either side of midrib but not on it, red, reddish-purple or brownish, with pale brown apical dimple, 3 mm in diameter, 4–5 mm height, the hole at apex about 1 mm in diameter, surface with very short pilosity. A hollow cylinder, with a short petiole at the base, swollen more or less in the middle and tapering to the apex at which there is a small hole leading into a deep cavity at the bottom of which is the thin-walled larval cell (Weld 1926).

**Biology.** Only the asexual generation is known which induces galls on *Q. arizonica*, *Q. oblongifolia* and *Q. turbinella* (section *Quercus*, subsection *Leucomexicana*), and *Q. pungens* (section *Quercus*, subsection *Polymorphae*). Galls mature in autumn, drop with leaves.

**Distribution.** USA: Arizona, New Mexico.

***Feron apiarium* (Weld, 1944), comb. nov.**

**Figs 25–36**

*Liodora apiarium* Weld, 1944: 6, female, gall.

*Andricus apiarum* (Weld): Melika & Abrahamson, 2002: 162 [misspelling]

**Types examined.** HOLOTYPE: Asexual female No. 56376. Five paratypes are deposited in the USNM and were examined by GM. Specimen data and images available at <http://n2t.net/ark:/65665/355e5568d-b757-4f7c-8e96-a0ef983d8d67>. Paratypes were deposited also in the American and Chicago Museums, Museum of Comparative Zoology, Academy of Natural Sciences of Philadelphia, and California Academy of Sciences. One paratype female and one gall on one pin “E. Falls Church, Va, mar. 7’42”, “*Quercus alba*”, “648”, red label “Paratype 56376”.

**Diagnosis.** This asexual form belongs to the group of species with a black body, the scape, pedicel, F1, F2 are dark brown (sometimes light brown but never yellowish), legs are reddish brown with at least hind coxae darker; the frons is flat, not or only slightly bulging in frontal view; toruli are located in the upper half of the head, inner margins of eyes never strongly converging ventrally; the mesoscutum smooth or partially alutaceous anteriorly and glabrous, notaulus complete, the mesopleuron entirely smooth without transverse striae in central part, the mesoscutellum is uniformly alutaceous with numerous setae on piliferous points and the prominent part of the ventral spine of the hypopygium with setae; similar to *F. kingi* (sex) and *F. pattersonae* (sex). *Feron apiarium* differs from these two species in the eyes which are parallel and 1.7× as high as length of the malar space, antennomeres have long and erect setae, OOL only slightly longer than the diameter of lateral ocellus, the notaulus is deep and the prominent part of the ventral spine of the hypopygium has long dense white setae ventrally.

**Re-description.** Asexual female. Head, antenna, mesosoma, black; legs, metasoma slightly lighter, reddish brown.

Head alutaceous, with sparse white setae on lower face, 1.2× as broad as high and as broad as mesosoma in frontal view, 2.0× as broad as long in dorsal view. Gena alutaceous, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, shining, with delicate striae radiating from clypeus and nearly reaching eye, malar sulcus absent; eye 1.7× as high as length of malar space. Eyes slightly converging ventrally. POL 1.6× as long as OOL, OOL slightly longer than diameter of lateral ocellus and 1.8× as long as LOL, all ocelli ovate, of same size. Transfacial distance 1.2× as long as height of eye; toruli located at half height of head; diameter of antennal torulus as long as distance between them, distance between torulus and eye slightly shorter than diameter of torulus; lower face alutaceous, with white setae, without striae; slightly elevated median area alutaceous, glabrous, without setae. Clypeus rectangular, nearly 2.0× as broad as high, smooth, with long setae; ventrally rounded, not emarginate and without median incision; anterior tentorial pit large, rounded, indistinct, epistomal sulcus distinct, clypeo-pleurostomal line inconspicuous. Frons, interocellar area, vertex, occiput uniformly alutaceous, without striae and setae, with some piliferous points; postocciput alutaceous, smooth, glabrous along occipital foramen; postgena for the most part reticulate, smooth and glabrous along occipital foramen, postgenal bridge and hypostomata; posterior tentorial pit large, ovate, area below impressed; occipital foramen higher than height of postgenal bridge; hypostomal carina

emarginate, continuing into postgenal sulci which strongly diverge toward occipital foramen, postgenal bridge anteriorly as broad as occipital foramen. Antenna as long as head+mesosoma, antennomeres with long setae, with 12 flagellomeres, pedicel slightly longer than broad, flagellomeres slightly broadened towards apex; F1 2.0× as long as pedicel and 1.2× as long as F2; F2 1.2× as long as F3; F3=F4, F5=F6=F7, subsequent flagellomeres nearly equal in length; placodeal sensilla on F4–F12.

Mesosoma slightly longer than high, with sparse white setae, denser on lateral propodeal area. Pronotum alutaceous, with sparse dense setae, with a few delicate striae anteroventrally; propleuron smooth, glabrous, shining on ventral invaginated broad half, delicately coriaceous in the dorsal narrowed part. Mesoscutum alutaceous, with a few setae anteriorly, along notaulus and parascutal carina, with denser setae along anterior edge, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, narrow, deep, with smooth bottom, posteriorly converging; anterior parallel line, parapsidal line not marked, invisible; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum rounded, slightly longer than broad, uniformly alutaceous, with numerous setae on piliferous points, with net of strong irregular rugae posteriorly, overhanging metanotum; circumscutellar carina complete. Mesoscutellar foveae separated by narrow elevated coriaceous central carina, ovate, with smooth, glabrous bottom. Mesopleuron and speculum uniformly smooth, shining; mesopleural triangle smooth, glabrous, with some delicate striae and sparse white setae; dorsal and lateral axillar areas delicately coriaceous, with a few white setae; subaxillular bar smooth, glabrous, with parallel sides, as high as height of metanotal trough, slightly higher at posterior end; metapleural sulcus reaching mesopleuron slightly above half of its height, delimiting coriaceous area, upper part of sulcus distinct. Metascutellum coriaceous, glabrous, slightly shorter than height of smooth, glabrous ventral impressed area; metanotal trough smooth, glabrous, without setae; central propodeal area smooth, glabrous, with a few irregular rugae; lateral propodeal carinae bent slightly outwards at mid-height; lateral propodeal area smooth, with dense white setae. Nucha with sulci dorsally and laterally. Tarsal claws toothed, with acute basal lobes.

Fore wing longer than body, hyaline, with cilia on margin, veins brown, distinct, radial cell open, narrow, 4.4× as long as broad; R1 and Rs nearly reaching wing margin; areolet distinct. Rs+M distinct on 2/3 of distance between areolet and basalis, its projection reaching basalis at its mid height.

Metasoma longer than head+mesosoma, longer than high in lateral view; 2nd metasomal tergum extending to 1/3 length of metasoma in dorsal view, with setae on anterodorsal part and a row of a few setae laterally at mid height, without micropunctures; subsequent terga smooth, glabrous, without micropunctures. Hypopygium without micropunctures, prominent part of ventral spine of hypopygium short, slightly longer than broad in ventral view, with long dense white setae ventrally.

Body length 1.7–2.6 mm (n = 21) (Weld 1944).

**Gall** (Fig. 36). Solitary, sessile, on underside of leaf close to edge, shaped like an old-fashioned straw beehive, white or pinkish, up to 4.6 mm broad by 4.0 mm high. Inside is a large cavity with a transverse larval cell at the very base. During the winter on the ground the outer fleshy layer shrivels and the gall becomes more cylindrical (Weld 1944).

**Biology.** Only females are known. Leaf galls on *Q. alba* (section *Quercus*, subsection *Albae*). Mature galls in October; adults emerge next year, in February-March.

**Distribution.** USA: Washington DC, VA (Burks 1979).

### ***Feron atrimentum* (Kinsey, 1922)**

#### **Figs 37–67**

*Andricus atrimentus* Kinsey, 1922: 279, female, male, gall.

*Dros atrimentum* (Kinsey): Weld, 1951: 629.

**Types examined.** HOLOTYPE: sexual female “Three Rivers Cal., gall 3.23.20.’, ‘*Q. douglasii*, Kinsey coll.’, red ‘*And. atrimentus* Holo- ♂TYPE” deposited in AMNH, NYC, examined by GM. PARATYPES (2 sexual females) in the general collection in AMNH also examined by GM.

**Additional material.** Asexual females: 27 females label as “USA: CA, Dye Creek Preserve, CA1170, galltype 137; *Q. douglasii*; leg. J.A. Nicholls, 2001.09.27”; 2 females “USA: CA, Del Puerto Canyon, *Q. douglasii*; leg. R. Challis, 2004.10.21”; 4 females “USA: CA, Clearlake, CA941, galltype 137; *Q. douglasii*; leg. J.A. Nicholls, 2007.11.03”. Sexual generation: 3 females “USA: CA, Quail Ridge Reserve, CA1044, galltype 231, *Q. douglasii*; leg. J.A. Nicholls, 2008.04.04”; 55 females and 37 males “USA: CA, Dye Creek Preserve, CA1048, 1049, galltype 231; *Q. douglasii*; leg. J.A. Nicholls, 2008.03.30”.

**Diagnosis.** Asexual females belong to the group of *Feron* species with the pronotum laterally smooth to coriaceous, without carinae; the mesoscutum is alutaceous to coriaceous, rugose-reticulate, reticulate, sometimes with smooth areas and piliferous points, glabrous or pubescent as occurs in *F. albicomus* (asex.), *F. crystallinum* (asex), *F. izabellae* (asex), *F.*

*pattersonae* (asex) and *F. sulfureum* (asex). *Feron atrimentum* differs from *F. albicomus* and *F. izabellae* in having the ocelli elevated above the head and the pronotum laterally with setae on the entire lateral surface; differs from *F. crystallinum*, *F. pattersonae* and *F. sulfureum* in the pronotum which is smooth (coriaceous in the other three species); the mesoscutum is longer than broad, scarcely pubescent, without black stripes and the anterior parallel line is indistinct. For other characters consult couplet 24 in the key. Sexual females belong to the group of *Feron* species in which the mesoscutum is alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points and the pronotum laterally with longitudinal carinae as in *F. splendens* (asex), *F. vitreum* (asex) and *F. verutum* (asex); nevertheless, it differs from these asexual forms by having a black body, eyes are strongly converging ventrally, the transfacial distance shorter than the height of eye, antennal toruli located slightly above half the eyes' height and the eye around 6.0× as high as length of the malar space. Males differs from all known *Feron* males in having strongly elevated ocelli above the frons in frontal view, OOL shorter than the diameter of lateral ocellus and inner margins of eyes subparallel, the mesoscutum is uniformly reticulate between notauli in anterior half and laterad to the notaulus but smooth between notauli in the posterior half.

**Re-description.** Asexual female (Figs 37–48). Body uniformly brown, with darker propodeum.

Head with sparse setae on lower face, gena and posteriorly, 1.2× as broad as high and slightly narrower than mesosoma in frontal view; 1.9× as broad as long in dorsal view. Gena alutaceous-reticulate, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, shining, with short striae radiating from clypeus reaching to 1/3 of malar space length; eye 3.0× as high as length of malar space; malar sulcus absent. Inner margins of eyes parallel. POL 2.6× as long as OOL, OOL 1.7× as long as diameter of lateral ocellus and slightly shorter than LOL, all ocelli ovate, of same size. Antennal toruli located above mid-height of eyes. Transfacial distance 1.2× as long as height of eye; diameter of antennal torulus slightly longer than distance between them, distance between torulus and eye as long as diameter of torulus; lower face smooth with white setae; slightly elevated median area smooth, without setae. Clypeus impressed, rectangular, 1.75× as broad as high, delicately coriaceous, with a few setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit large, rounded, deep, epistomal sulcus broad and deep, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex uniformly reticulate, without striae and setae; area under central ocellus impressed,



smooth, glabrous; occiput alutaceous, with dense setae; postocciput glabrous, with numerous delicate longitudinal interrupted parallel striae; postgena smooth, with a few setae; posterior tentorial pit large, elongated, area below impressed; occipital carina black, well-visible alongside occipital foramen; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal sulci which diverge until half height of postgenal bridge, further sulci parallel and running alongside foramen until 1/3 of its height. Antenna slightly longer than head+mesosoma, with 12 flagellomeres; flagellomeres gradually broadened towards apex; F1–F3 with sparse white setae, F4–F12 with dense setae; pedicel 1.7× as long as broad; F1 2.2× as long as pedicel and 1.4× as long as F2; F2=F3=F4; F5=F6 and shorter than previous; all subsequent flagellomeres shorter and equal in length; F12 as long as F11, suture between F11 and F12 distinct; placodeal sensilla on F4–F12.

Mesosoma longer than high, with white setae, setae denser on pronotum laterally, mesopleural triangle and mesoscutellum. Pronotum smooth without striae, with sparse setae, piliferous points along dorsal edge; propleuron smooth, with sparse white setae. Mesoscutum longer than broad (greatest width measured across mesoscutum level with base of tegulae), alutaceous-reticulate between notauli in anterior 2/3 of length and laterad to notauli, smooth, glabrous in between notauli in posterior half. Notaulus complete, deep, posteriorly strongly converging and broader than anteriorly, with smooth, glabrous bottom; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line indistinct; parapsidal line absent, not marked; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid, longer than broad, broadest part in posterior 1/3; center part of mesoscutellum disc rugoso-coriaceous, with stronger rugae posteriorly and laterally, overhanging metanotum, with long setae. Mesoscutellar foveae ovate, broader than high, with smooth, glabrous bottom, divided by a elevated narrow carina. Mesopleuron entirely smooth, with setae only along ventral edge; mesopleural triangle smooth, with dense white setae and piliferous points; dorsal and lateral axillar areas smooth, with setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with subparallel sides, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, lower part delimiting smooth area with a few setae, upper part of sulcus absent. Metascutellum coriaceous, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with few setae; central propodeal area lyre-shaped, smooth, glabrous; lateral propodeal carinae strong, bent outwards in posterior 1/3; lateral propodeal area smooth, with long white setae. Nucha with longitudinal sulci dorsally and laterally. Tarsal claws with acute basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins brown, radial cell open, 4.2× as long as broad; Rs and R1 nearly reaching wing margin; areolet absent. Rs+M indistinct, visible on 2/3 of distance between areolet and basalis, its projection reaching basalis at half of its height.

Metasoma longer than head+mesosoma, higher than long in lateral view; 2nd metasomal tergum extending nearly to half-length of metasoma in dorsal view, with patch of dense white setae anterolaterally, without micropunctures; all subsequent terga and hypopygium with fine micropunctures; prominent part of ventral spine of hypopygium 6.7× as long as broad in ventral view, with a few short white setae ventrally.

Body length 1.7–1.9 mm (n = 2).

Sexual female (Figs 51–61). Head, mesosoma, metasoma black; antenna dark brown, except yellowish scape, pedicel and F1; metasoma chestnut, hypopygium light brown; legs yellow with dark brown to black coxae.

Head with sparse setae, denser on lower face and postgena, 1.2× as broad as high and slightly broader than mesosoma in frontal view; 2.1× as broad as long in dorsal view. Gena alutaceous, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, without striae; eye 6.1× as high as length of malar space; malar sulcus absent. Inner margins of eyes strongly converging ventrally. POL 2.4× as long as OOL, OOL 1.2× as long as diameter of lateral ocellus and equal in length to LOL, all ocelli ovate, of same size. Transfacial distance shorter than height of eye; toruli located at half of eyes height, frons shorter than lower face, diameter of antennal torulus 1.3× as long as distance between them, distance between torulus and eye as long as diameter of torulus; lower face smooth with white setae, alutaceous in most ventral part above malar space; slightly elevated median area and area between toruli alutaceous. Clypeus trapezoid, as broad as high, delicately coriaceous, with a few long setae along ventral edge; ventrally emarginate, with median incision; anterior tentorial pit large, ovate, epistomal sulcus distinct, deep, clypeo-pleurostomal line well impressed, deep. Frons, interocellar area, vertex uniformly reticulate, without striae and setae; area under central ocellus impressed, alutaceous; occiput and postgena alutaceous; postocciput with numerous delicate interrupted parallel striae dorsally and laterally of occipital foramen; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna slightly

longer than head+mesosoma, with 12 flagellomeres; F1–F3 with rare setae, subsequent flagellomeres with denser setae; scape, pedicel, F1 yellowish brown, all subsequent flagellomeres dark brown; pedicel only slightly longer than broad; F1 2.5× as long as pedicel and slightly longer than F2; F2 1.2× as long as F3, F3=F4, all subsequent flagellomeres nearly equal in length, F12 longer than F11; placodeal sensilla on F3–F12.

Mesosoma longer than high, with a few white setae, denser on mesoscutellum and lateral propodeal area. Pronotum delicately coriaceous, with sparse setae and delicate parallel striae laterally; propleuron alutaceous. Mesoscutum slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae), uniformly reticulate between notauli in anterior half and laterad to notauli, smooth and glabrous in between notauli in posterior half. Notaulus complete, shallow, posteriorly converging and broader than anteriorly, bottom smooth, glabrous; in most posterior part distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line distinct, smooth, glabrous, reaching to 1/3 length of mesoscutum; parapsidal line marked with broad smooth, glabrous stripe; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid, longer than broad, broadest part in posterior 1/3, uniformly rugoso-coriaceous, overhanging metanotum, with sparse long setae. Mesoscutellar foveae quadrangular, as broad as high, with smooth, glabrous bottom, divided by a rugose elevated triangular area. Mesopleuron entirely smooth, with setae only along ventral edge; mesopleural triangle smooth, with dense white setae; dorsal and lateral axillar areas smooth, glabrous, without setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with parallel sides, posteriorly shorter than height of smooth, glabrous metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus indistinct, lower part of sulcus delimiting smooth, glabrous area, with few setae. Metascutellum coriaceous, slightly higher than height of smooth, glabrous ventral impressed area; metanotal trough smooth, with few setae and few rugae; central propodeal area smooth, glabrous, with a few strong short longitudinal rugae posteriorly; lateral propodeal carinae strong, broad and high, bent strongly outwards at mid-height; lateral propodeal area smooth, with long white setae, each seta with piliferous point at the base. Nucha with numerous irregular rugae. Tarsal claws with small basal lobe.

Fore wing longer than body, hyaline, with short cilia on margin, veins brown, radial cell open, 4.3× as long as broad; Rs and R1 reaching wing margin; areolet distinct, triangular. Rs+M distinct, reaching basalis slightly below half of its height.

Metasoma slightly longer than head+mesosoma, longer than high in lateral view; 2nd metasomal tergum extending to 1/3 length of metasoma in dorsal view, with patch of white setae anterolaterally, without micropunctures; all subsequent terga and hypopygium without micropunctures; prominent part of ventral spine of hypopygium 4.5× as long as broad in ventral view, with short white setae ventrally.

Body length 2.7–3.1 mm (n = 10).

**Male** (Figs 62–67). Like female but antenna longer than body, with 13 flagellomeres, F1 with longitudinal yellow stripe on the inner side, placodeal sensilla on all flagellomeres, F13 slightly shorter than F12. Eye and ocelli larger than in female; POL 3.0× as long as OOL, OOL slightly longer than diameter of ocellus and slightly shorter than LOL; transfacial distance shorter than height of eye, height of eye 6.0× as long as length of malar space.

Body length 2.2–2.7 mm (n = 10).

**Gall.** The sexual gall (Fig. 49) is monolocular, spherical, 3–5 mm in diameter, smooth, green when growing, becoming paler later, mature galls when dried are yellow-brown; larval cell is blue-black and sometimes visible through outer layers of the gall. Walls of the gall are thin, the larval chamber is also thin-walled, 1.5 mm in diameter and connected with the outside wall by a tangle of dense fibers. The gall is in the leaf tissue, projecting equally on both sides. Asexual galls (Fig. 50) are monolocular, conical, flat-based, detachable, on lower leaf margin. Sides nearly straight, flaring slightly at base. Red and yellow striped when fresh, turning to brown and yellow with age. Basal larval cell oval from lateral view, 1.6 mm in diameter, 0.8 mm high, pubescent. Upper surface of larval cell coriaceous with sparse pubescence; brown, darker towards center. Gall height 3.6–4.6 mm, width 3.0–4.6 mm.

**Biology.** Matching of generations was first presented in Dailey & Sprenger (1973b). Alternate sexual and asexual generations are also confirmed herein using DNA data, with four individuals (three asexual females, one sexual female) sequenced for cytb. Cytb sequences were on average 0.35% divergent between individuals (range 0–0.70%; GenBank accessions OK041496, OQ446191–OQ446193).

*Feron atrimentum* is associated with *Q. douglasii*, *Q. dumosa*, *Q. john-tuckeri* and *Q. lobata* (section *Quercus*, subsection *Dumosae*). The sexual generation females emerge throughout April and usually oviposit in the lower leaf surface near the margin. Asexual galls develop over the following three months. Pupation occurs during late October to November; asexual females emerge in late winter and oviposit in leaf buds. Sexual generation galls usually reach full size by mid-March (Dailey & Sprenger 1973b).

**Distribution.** USA: California.

***Feron bakkeri* (Lyon, 1984), comb. nov.**

**Figs 68–71**

*Andricus bakkeri* Lyon, 1984: 292, female, gall.

**Type material.** HOLOTYPE: Asexual female “Los Angeles, Calif., II.9.58”, “*Q. dumosa*”, “R.J. Lyon Collection”, “*Andricus bakkeri* Lyon”, red label “Holotype”. PARATYPES (6 asexual females) with the same data as the holotype. The female holotype and the six paratypes are in the collection of the USNM, examined by VC-P. The type was examined based on photos taken by M. Buffington, USNM. Information and pictures of the holotype can be consulted here:

<http://n2t.net/ark:/65665/32562b378-0160-44b1-94a5-4136889a738e>.

**Diagnosis.** Asexual females belong to the group of *Feron* species in which the body is reddish brown; the head is rounded in frontal view, ocelli are not elevated above the frons; inner margins of eyes slightly converging ventrally, the transfacial distance is longer than the height of eye; toruli are located above mid-height of eyes; the eye is less than 3.0× as high as length of the malar space as in *F. scutellum* (asex), *F. stellare* (asex), and *F. rucklei* (asex). However, *F. bakkeri* has inconspicuous mesoscutellar foveae with faintly rugose bottoms like the rest of the mesoscutellar disk; the metasoma is distinctly longer than high; while in the asexual forms of the other species the mesoscutellar foveae are conspicuous, with the bottom smooth, and the metasoma is almost as high as long. The gall is reminiscent of the gall of *F. scutellum* but is somewhat smaller (Lyon 1984).

**Re-description.** Asexual female (Figs 68–70). Head, antenna, mesosoma, legs, metasoma uniformly reddish brown, except dark brown posterior tergum.

Head alutaceous-reticulate, with sparse setae on lower face, slightly broader than high and as broad as mesosoma in frontal view; 2.6× as broad as long in dorsal view. Gena alutaceous-reticulate, not broadened behind eye in frontal view; gena in lateral view 2.0× narrower than transverse diameter of eye in dorsal part and as broad as eye in ventral part. Malar space delicately coriaceous, with delicate striae, malar sulcus absent; eye 2.6× as high as length of malar space. Inner margins of eyes converging ventrally. POL 1.4× as long as OOL, OOL 3.6× as long as diameter of lateral ocellus and slightly shorter than LOL, all ocelli ovate, of same size. Antennal toruli located above mid-height of eyes. Transfacial distance 1.3× as long as height of eye; frons shorter than height of lower face, diameter of antennal

torulus 1.7× as long as distance between them, distance between torulus and eye slightly longer than diameter of torulus; lower face delicately coriaceous, with dense white setae; slightly elevated median area and area between toruli delicately coriaceous, with a few setae. Clypeus impressed, flat, rectangular, broader than high, delicately coriaceous, with a few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, small; epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex and occiput uniformly alutaceous-reticulate, without striae and setae. Antenna shorter than body, with 12 flagellomeres, pedicel subglobose, slightly longer than broad; F1 1.2× as long as F2 and 1.6× as long as pedicel; F2>F3, F4-F7 subequal in length, F8-F11 slightly shorter, subequal and wider; F12 slightly shorter than F11; placodeal sensilla on F3-F12.

Mesosoma nearly as long as high, with setae. Pronotum glabrous, with delicate short parallel striae along posterior edge, with piliferous points. Mesoscutum uniformly reticulate, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, distinctly impressed along entire length; posteriorly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line indistinct; parapsidal line marked with indistinct, narrow smooth, impressed area; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum slightly longer than broad, with subparallel sides; disk of mesoscutellum rugose, overhanging metanotum, with sparse setae. Mesoscutellar foveae inconspicuous, faintly rugose bottom, like the rest of the mesoscutellar disk, smoother anteriorly, without central carina. Mesopleuron smooth, alutaceous only on most anterior part; speculum smooth, glabrous, with transverse striae in most anterior part; mesopleural triangle smooth, with a few white setae; dorsal and lateral axillar areas smooth, with white setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with subparallel sides, posteriorly shorter than height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height; upper part of sulcus indistinct; lower part of sulcus delimiting smooth area with dense long white setae. Metascutellum smooth, glabrous, shorter than height of smooth, glabrous ventral impressed area; metanotal trough smooth, with sparse setae; central propodeal area lyre-shaped, smooth, glabrous, without rugae; lateral propodeal carinae distinct, bent outwards in posterior 1/3 of its height; lateral propodeal area smooth, and with long dense white setae with impressed setae points. Nucha with numerous sulci laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with cilia on margin, veins brown, radial cell open, 3.0× as long as broad; Rs and R1 nearly reaching wing margin; areolet indistinct. Rs+M indistinct, not reaching basalis.

Metasoma longer than head+mesosoma, slightly longer than high in lateral view; 2nd metasomal tergum extending to 2/3 length of metasoma in dorsal view, with numerous white setae anterolaterally, with rare micropunctures posteriorly; all subsequent terga with micropunctures. Hypopygium with micropunctures, prominent part of ventral spine of hypopygium 7.5× as long as broad in ventral view, with long setae ventrally.

Body length 1.3–2.0 mm (n = 3).

**Gall** (Fig. 71). A monolocular, cup-shaped leaf spangle gall, 3–3.5 mm in height. The larval cell occupies the base of the cup whose margins are collapsed at maturity (Lyon 1984).

**Biology.** Only the asexual generation is known, which induces galls on *Q. dumosa* (section *Quercus*, subsection *Dumosae*). The galls appear on the leaves during the early summer until August. At this time the galls are red and contain small larvae. Pupation occurs in late October and early November; adults can be cut out in early December; however, normal emergence takes place in February–March, or even later.

**Distribution.** USA: California (Lyon 1984).

***Feron caepula* (Weld, 1926), comb. nov.**

**Figs 72–83**

*Diplolepis caepula* Weld, 1926: 19, female, gall.

*Andricus caepula* (Weld): Weld, 1951: 632.

**Type examined.** HOLOTYPE: Asexual female “Hillsboro, N.M., April 25”, “*Quercus pungens*”, red label “Type No. 27187 USNM”, “*Diplolepis caepula* Weld” deposited in USNM, examined by GM. Specimen data and images available at <http://n2t.net/ark:/65665/3157da14c-7171-49c8-a07e-672605fcd699>.

**Additional material.** Five females labelled as “USA, Arizona, 25miles S of Flagstaff on I17, *Q. turbinella*; Code AZ798, galltype 95, leg. J.A. Nicholls, 2007.10.31.”

**Diagnosis.** Asexual females; as with *F. bakkeri* (asex), *F. rucklei* (asex) and *F. stellare* (asex) the body is never black, the head is rounded in frontal view, slightly elevated median area of the lower face smooth, shining; the gena at least slightly broadened behind the eye; ocelli are not elevated above the frons; the transfacial distance is longer than the height of eye; the antenna with 12 flagellomeres, sometimes suture between F11 and F12 incomplete; toruli are

located above the mid-height of the eye; the eye is less than 3.0× as high as length of the malar space; lateral ocelli smaller, OOL at least 2.5× as long as the diameter of ocellus if shorter, then the head and mesosoma are not yellowish or light brown; the pronotum laterally with longitudinal carinae; the mesoscutum is alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points; mesoscutellar foveae divided by a central carina; and the mesopleuron is entirely smooth. Nevertheless, *F. caepula* differs from those species in its yellowish to light brown body, eyes strongly converging ventrally; eye 3.0× as high as length of malar space; central part of mesoscutellum smooth; prominent part of ventral spine of hypopygium around 3.8× as long as broad in ventral view.

**Re-description.** Asexual female (Figs 72–82). Head, mesosoma, mandibles, mouthparts, antennae, legs and metasoma uniformly light brown; head with dark brown small spots near ocelli; central propodeal area and last terga dark brown to black; legs slightly lighter than body.

Head alutaceous, with sparse setae on lower face and postgena; 1.1× as broad as high and slightly narrower than mesosoma in frontal view; 1.9× as broad as long in dorsal view. Broadest part of head in frontal view at mid-height of lower face. Gena alutaceous-reticulate, only slightly broadened behind eye in frontal view, narrower than transverse diameter of eye; gena in lateral view at least 2.0× narrower than transverse diameter of eye in the dorsal part of eye; ventral part of gena 2.0× as broad as dorsal part. Malar space alutaceous, with striae radiating from clypeus and reaching to half-length of malar space; eye 3.0× as high as length of malar space; malar sulcus absent. Inner margins of eyes strongly converging ventrally. POL 1.7× as long as OOL, OOL 2.7× as long as diameter of lateral ocellus and slightly longer than LOL, all ocelli ovate, of the same size. Antennal toruli located above mid-height of eyes. Transfacial distance 1.25× as long as height of eye; diameter of antennal torulus 1.8× as great as distance between them, distance between torulus and eye 1.5× as long as diameter of torulus; lower face smooth with white setae; slightly elevated median area and area between toruli smooth and shining, without setae. Clypeus impressed, trapezoid, broader than high, delicately coriaceous, with a few setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit large, rounded, deep, epistomal sulcus broad and deep, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex uniformly reticulate, without striae and setae; area under central ocellus impressed, smooth, glabrous; occiput alutaceous, with dense setae; postocciput glabrous, with numerous delicate longitudinal interrupted parallel striae; postgena smooth, with few setae; posterior tentorial pit



large, elongated, area below impressed; occipital foramen slightly shorter than height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal sulci which diverge until occipital foramen, ending in posterior tentorial pit. Antenna nearly as long as body, with 12 flagellomeres (suture between F11 and F12 indistinct), pedicel longer than broad, F1 shorter than length of scape+pedicel, 1.3× as long as F2, F2 slightly longer than F3, F3=F4, subsequent flagellomeres shorter and nearly equal in length, F12 slightly longer than F11; placodeal sensilla on F5–F12.

Mesosoma longer than high, with sparse setae on pronotum laterally, on mesopleural triangle, mesoscutellum and lateral area of propodeum. Pronotum smooth, with setae laterally, piliferous points along dorsal edge; anterolateral edge of pronotum smooth, glabrous, without foveae; propleuron smooth, with sparse white setae. Mesoscutum longer than broad (greatest width measured across mesoscutum level with base of tegulae), uniformly alutaceous-reticulate. Notaulus complete, deep, posteriorly strongly converging and broader than anteriorly, with smooth, glabrous bottom; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line indistinct, hardly traceable; parapsidal line marked with impressed stripe; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid, longer than broad, broadest part in posterior 1/3; center part of mesoscutellum smooth, glabrous, rugose posteriorly and laterally, overhanging metanotum, with a few long setae. Mesoscutellar foveae transverse, broader than high, with smooth, glabrous bottom, divided by a narrow stripe. Mesopleuron entirely smooth, with setae only along ventral edge; mesopleural triangle smooth, with dense white setae and piliferous points; dorsal and lateral axillar areas smooth, with setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with nearly parallel sides, posteriorly slightly shorter than height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, lower part delimiting smooth area with few setae, upper part of sulcus indistinct. Metascutellum rugose, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with few setae; central propodeal area lyre-shaped, smooth, glabrous, with net of strong rugae in most posterior part; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral propodeal area smooth, with long white setae and piliferous points. Nucha with longitudinal sulci dorsally and laterally and a net of irregular rugae. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins distinct, radial cell open, 4.1× as long as broad; Rs and R1 nearly reaching wing margin; areolet small,

triangular, closed, distinct. Rs+M light pigmented, hardly traceable, visible on 1/2 of distance from areolet to basalis, its projection reaching basalis at half of its height.

Metasoma longer than head+mesosoma, longer than high in lateral view; 2nd metasomal tergum extending to 2/3 length of metasoma in dorsal view, with white setae anterolaterally, without micropunctures; all subsequent terga with rare, weak, very delicate micropunctures. Hypopygium with micropunctures, prominent part of ventral spine of hypopygium 3.8–4.0× as long as broad in ventral view with some sparse setae ventrally.

Body length 1.7–1.9 mm (n = 5).

**Gall** (Fig. 83). Small leaf galls on underside of leaf, 3 mm in diameter with small point in centre of gall, shaped rather like an onion or garlic bulb, pinkish to reddish-brown.

**Biology.** Only the asexual generation is known, which induces galls on *Q. pungens* (section *Quercus*, subsection *Polymorphae*) and the section *Quercus*, subsection *Leucomexicana* oaks: *Q. arizonica*, *Q. oblongifolia*, *Q. turbinella* (Burks 1979). The asexual galls mature by October–November, and adults emerge by April.

**Distribution.** USA: Arizona, New Mexico (Burks 1979).

***Feron californicum* (Beutenmueller, 1911), comb. nov.**

**Figs 84–96**

*Philonix californica* Beutenmueller, 1911: 69, female, gall.

*Biorhiza californica* (Beutenmueller): Fullaway, 1911: 334.

*Trichoteris californicum* (Beutenmueller): Weld, 1951: 625.

*Andricus californicum* (Beutenmueller): Melika & Abrahamson, 2002.

**Type examined.** HOLOTYPE: Asexual female “5541...”, “Kern Co. I.XI.92. Cala”, “Coquilletti coll.”, red label, “Type No. 13722 USNM”, handwriting label “*Philonix californica* Beutnm.” deposited in USNM, examined by GM.

**Additional material.** One female labeled as “Sta Barbara Nat. For. Cal., Liebre Sum-t.”, “*Q. dumosa*”, “cut out Novem. 10”, Weld’s handwriting label “*Trichoteris californicum* (Beutm.)”.

**Diagnosis.** The only *Feron* species with rudimentary fore wings and indistinct veins.

**Re-description.** Asexual female (Figs 84–95). Head, antennae, mesosoma, metasoma uniformly rusty brown; legs slightly lighter.

Head delicately coriaceous, frons rugoso-coriaceous, with sparse setae on lower face and postgena, slightly higher than broad and slightly broader than mesosoma in frontal view; 1.9× as broad as long in dorsal view. Broadest part of head in frontal view at mid-height of

head. Gena alutaceous-reticulate, not broadened behind eye in frontal view, narrower than transverse diameter of eye; gena in lateral view at least 2.0× narrower than transverse diameter of eye at the dorsal part of eye; ventral part of gena 2.0× broader than dorsal part. Malar space alutaceous, with striae radiating from clypeus and reaching eye; eye 2.2× as high as length of malar space; malar sulcus absent. Inner margins of eyes only slightly converging ventrally. POL 2.5× as long as OOL, OOL 3.2× as long as diameter of lateral ocellus and nearly equal to LOL, lateral ocelli small, black, central ocellus light brown, at least 2.0× as large as lateral ocellus. Antennal toruli located above mid-height of eyes. Transfacial distance 1.4× as long as height of eye; diameter of antennal torulus equal to distance between them, distance between torulus and eye 1.3× as long as diameter of torulus; lower face alutaceous to delicately coriaceous, with white setae; slightly elevated median area delicately coriaceous, glabrous, without setae; area between torulus and eye with delicate striae. Clypeus impressed, quadrangular, as broad as high, delicately coriaceous, with a few setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit large, rounded, deep, epistomal sulcus broad and deep, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex, occiput uniformly reticulate, with a few delicate striae and setae; area under central ocellus impressed, smooth, glabrous; postocciput glabrous, with numerous delicate longitudinal interrupted parallel striae; postgena smooth, with few setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen slightly shorter than height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge until occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres (suture between F11 and F12 indistinct), flagellomeres gradually broadened towards apex, pedicel longer than broad, F1 as long as scape+pedicel, 1.3× as long as F2, F2 slightly longer than F3, F3=F4, F5 slightly shorter than F4, subsequent flagellomeres gradually shorter, F12 slightly shorter than F11; placodeal sensilla on F5–F12.

Mesosoma higher than long, with rare setae. Pronotum delicately coriaceous, with some striae laterally, with sparse setae; propleuron coriaceous, with sparse, scattered setae. Mesoscutum longer than broad (greatest width measured across mesoscutum level with base of tegulae), uniformly coriaceous-reticulate. Notaulus complete, deep, posteriorly strongly converging and broader than anteriorly, with smooth, glabrous bottom; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line and parapsidal line indistinct, hardly traceable; median mesoscutal line narrow but distinct; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid,

longer than broad, broadest part in posterior 1/3; disc of mesoscutellum uniformly rugose, only just overhanging metanotum, with a few long setae. Mesoscutellar foveae only slightly broader than high, with smooth, glabrous bottom, well-delimited all around by strong carina, divided by an elevated narrow carina. Mesopleuron delicately coriaceous, with transverse delicate striae at mid height, with setae only along ventral edge; mesopleural triangle smooth, with dense white setae and piliferous points; dorsal and lateral axillar areas smooth, with setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, triangular, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron in upper 1/3 of mesopleuron height, lower part delimiting delicately coriaceous area with a few setae, upper part of sulcus indistinct. Metascutellum rugose-coriaceous, glabrous ventral impressed area; metanotal trough smooth, glabrous; central propodeal area lyre-shaped, smooth, glabrous, without rugae; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral propodeal area alutaceous to smooth, with long white setae and piliferous points. Nucha with irregular short rugae dorsally and laterally. Tarsal claws with small basal lobe.

Fore wing rudimentary, as long as head+mesosoma but not reaching the middle of the metasoma, with indistinct veins.

Metasoma longer than head+mesosoma, more than 2.0× as high as mesosoma in lateral view; all metasomal tergites smooth, glabrous, 2nd metasomal tergum extending to half-length of metasoma in dorsal view, with white setae anterolaterally, sparse micropunctures only dorsally; all subsequent terga and hypopygium without micropunctures, prominent part of ventral spine of hypopygium 5.8× as long as broad in ventral view.

Body length 2.1 mm (n = 1).

**Gall** (Fig. 96). The monolocular spangle leaf gall is on the upper surface of the leaves, rounded, flattened disc-like, slightly elevated toward the middle, pinkish or purplish, with the apex sometimes yellowish. Sides of the gall are flat and very thin; the larval chamber is in the central elevated part; the diameter of the gall is 3–4 mm, height 1 mm (Beutenmueller 1911).

**Biology.** Only the asexual generation is known, which induces galls on *Q. cornelius-mulleri*, *Q. douglasii* and *Q. dumosa* (section *Quercus*, subsection *Dumosae*). The gall matures by November and the adult emerges in January.

**Distribution.** USA: California.

***Feron clarkei* (Bassett, 1890), comb. nov.**

**Figs 97–115**

*Dryophanta clarkei* Bassett, 1890: 69, female, male, gall.

*Dryophanta vesiculoides* Ashmead, 1896: 114, female, male, gall. Synonymized in Weld (1951: 629).

*Liodora clarkei* (Ashmead): Weld, 1951: 629.

*Andricus clarkei* (Ashmead): Melika & Abrahamson 2002: 162.

**Types examined.** One sexual female “Boston. V.31. Mass. C.H. Clarke”, “Beut. Coll. rec’d 1939”, “*D. clarkei* Beut.”; three pins with 2 sexual females and four males “Wtby”, “*Q. alba* Phila Acad.”, red label “*D. clarkei* Paratype”. Nine pins with red label “Type”, “Massach.”, “H. F. Bassett Coll.”; one pin with Bassett handwriting label “*Callirhytis clarkei* Bass. Type” deposited in AMNH, NYC, examined by GM.

**Diagnosis.** As in *F. amphorus* (asex), *F. crystallinum* (sex) and *F. dumosae* (sex), sexual females have a brown to chestnut brown body, rarely darker; inner margins of eyes are parallel or only slightly converging ventrally; the frons is flat, not or only slightly bulging in frontal view; the mesoscutum is smooth or partially alutaceous anteriorly and glabrous; the mesoscutellum with irregular rugae at least in lateral and posterior parts, sometimes the dorsocentral part is smooth, shining, without piliferous points. Differs from *F. crystallinum* and *F. dumosae* in the transfacial distance which is longer than height of the eye, the eye is less than 3.0× as high as length of the malar space and the pronotum with carinae going across entire lateral surface. Differs from *F. amphorus* in the characters mentioned at couplet 20 in the key. Males are characterised by brown or chestnut body, notaulus reaching the pronotum, the mesoscutellum with irregular rugae at least in lateral and posterior parts, without piliferous points; as in *F. dumosae*. However, *F. clarkei* has F1 1.3× as long as F2 (1.6× as long as F2 in *F. dumosae*) and the transfacial distance is longer than height of the eye (as long as or slightly shorter than height of eye in *F. dumosae*).

**Re-description.** Sexual female (Figs 97–108). Head and mesosoma brown to chestnut, smooth, shining, antenna and legs light brown.

Head alutaceous, with sparse white setae on lower face, 1.2× as broad as high and slightly broader than mesosoma in frontal view, 2.0× as broad as long in dorsal view. Gena alutaceous, slightly broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, shining, with delicate striae radiating from clypeus and nearly reaching eye, malar sulcus absent; eye 2.8× as high as length of malar space. Eyes slightly converging ventrally. POL 1.3× as long as OOL, OOL 2.8× as long as diameter of lateral ocellus and 1.5× as long as LOL, all ocelli ovate, of same size. Transfacial

distance 1.3× as long as height of eye; diameter of antennal torulus slightly longer than distance between them, distance between torulus and eye slightly longer than diameter of torulus; lower face alutaceous, with a few white setae, without striae; slightly elevated median area alutaceous, glabrous, without setae. Clypeus rectangular, nearly 2.0× as broad as high, smooth, with long setae; ventrally rounded, not emarginate and without median incision; anterior tentorial pit large, rounded, indistinct, epistomal sulcus distinct, clypeo-pleurostomal line narrow, inconspicuous. Frons uniformly reticulate, without striae and setae, interocellar area reticulate. Frons, interocellar area uniformly alutaceous, without striae and setae. Vertex and occiput alutaceous, without striate and without white setae; postocciput smooth, glabrous; postgena in most part alutaceous, smooth, glabrous along occipital foramen, postgenal bridge and hypostomal; posterior tentorial pit large, ovate, area below impressed; occipital foramen higher than height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which strongly diverge toward occipital foramen, postgenal bridge anteriorly as broad as occipital foramen. Antenna longer than head+mesosoma, extending to half-length of metasoma, with 12 flagellomeres, pedicel slightly longer than broad, flagellomeres slightly broadened towards apex; F1 2.0× as long as pedicel and slightly longer than F2; F2 1.3× as long as F3; F3 shorter than F4, F4 longer F5, F5=F6, subsequent flagellomeres nearly equal in length; placodeal sensilla on F4–F11.

Mesosoma slightly longer than high, with sparse white setae, denser on lateral propodeal area. Pronotum laterally smooth, shining, with numerous delicate striae radiating from posterior end and extending to half-length of pronotum; propleuron smooth, with few setae. Mesoscutum smooth shining, alutaceous only along anterior 1/5, with sparse white setae, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, deep, broad, with smooth bottom, posteriorly broader and slightly converging; anterior parallel line indistinct, marked with smooth line, extending to 1/3 of mesoscutum length; parapsidal line indistinct, invisible; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid, slightly longer than broad, glabrous, with net of strong irregular rugae, posteriorly rounded, overhanging metanotum; disc of mesoscutellum in dorsocentral part smooth, shining. Mesoscutellar foveae well defined, separated by narrow elevated coriaceous central carina, ovate, with smooth, glabrous bottom. Mesopleuron smooth, shining, with some delicate transverse subparallel striae; speculum smooth, shining; mesopleural triangle smooth, glabrous, with some delicate striae and sparse white setae; dorsal and lateral axillar areas delicately coriaceous, with a few

white setae; subaxillary bar smooth, glabrous, with parallel sides, as high as height of metanotal trough, slightly higher in posterior end; metapleural sulcus reaching mesopleuron slightly above half of its height, delimiting coriaceous area, upper part of sulcus distinct. Metascutellum smooth, glabrous, slightly shorter than height of smooth, glabrous ventral impressed area; metanotal trough smooth, glabrous, without setae; central propodeal area smooth, glabrous, with irregular rugae; lateral propodeal carinae bent slightly outwards at mid-height; lateral propodeal area smooth, with dense white setae and piliferous points. Nucha with numerous sulci dorsally and laterally. Tarsal claws toothed, with basal lobe.

Fore wing longer than body, hyaline, with cilia on margin, veins light brown, hardly visible, radial cell open, 3.5× as long as broad; R1 and Rs reaching wing margin; areolet indistinct. Rs+M narrow, inconspicuous, its projection reaching basalis at its mid height.

Metasoma as long as head+mesosoma, longer than high in lateral view; 2nd metasomal tergum extending to half-length of metasoma in dorsal view, without setae and micropunctures; all terga smooth, glabrous, without micropunctures. Hypopygium without micropunctures, prominent part of ventral spine of hypopygium 3.0× as long as broad in ventral view, without setae ventrally.

Body length 1.4–2.1 mm (n = 4).

**Male** (Figs 110–115). Similar to female but darker, transfacial distance subequal to height of eye, ocelli slightly bigger, POL 2.0× as long as OOL, OOL 1.5× as long as diameter of lateral ocellus and as long as LOL, antenna with 13 flagellomeres, pedicel globular, F1 slightly curved and incised, placodeal sensilla on all flagellomeres; legs lighter than in female; metasoma shorter than head+mesosoma; body size as in female.

**Gall** (Fig. 109). Galls in terminal and axillary buds, many-celled, smooth, bare, often hidden by bud scales.

**Biology.** Only the sexual generation is known, inducing bud galls on *Q. alba* (section *Quercus*, subsection *Albae*) and *Q. stellata* (section *Quercus*, subsection *Stellatae*). Adults emerge in early spring until May (Ashmead 1896).

**Distribution.** USA: MA, MO (Burks 1979).

***Feron comatum* (Weld, 1952), comb. nov.**

**Figs 116–123**

*Liodora comata* Weld, 1952b: 325, female, male, gall.

*Andricus comata* (Weld): Melika & Abrahamson 2002: 162.

**Type material.** HOLOTYPE: Sexual female USNM No. 60112, PARATYPES (6 females) at the USNM. Specimen data and images available at <http://n2t.net/ark:/65665/3d8f99bbb-ffa6-4c06-a237-1da4ed776fc3>. Paratypes are deposited also in AMNH, CMNH, ANSP, CAS and MCZ.

**Diagnosis.** Sexual females are similar to *F. apiarium* (asex), *F. kingi* (sex) and *F. pattersonae* (sex) and are characterised by a black body, frons is flat, not or only slightly bulging in frontal view, inner margins of eyes never strongly converging ventrally, the mesoscutum is smooth, glabrous or partially alutaceous anteriorly; the notaulus is complete reaching the pronotum; the mesopleuron is entirely smooth without transverse striae in central part; the mesoscutellum is uniformly alutaceous with numerous setae on piliferous points. Nevertheless, *F. comatum* differs from these species in the torulus which is located halfway up the head; scape, pedicel, F1–F2 are yellowish; legs including hind coxa are yellowish and the prominent part of the ventral spine of the hypopygium without setae ventrally. Males are similar to *F. kingi* and *F. pattersonae* and are characterised by a black body, ocelli are moderately or not elevated above the frons, notaulus reaching the pronotum and the mesoscutellum is uniformly alutaceous with numerous setae on piliferous points. In *F. comatum* F1 equal in length to scape+pedicel, slightly broadened and curved, flagellomeres lighter than scape and pedicel (F1 longer than scape+pedicel, straight not broadened and curved, flagellomeres, scape and pedicel uniformly coloured in *F. kingi* and *F. pattersonae*).

**Re-description.** After Weld (1952b), with modifications.

Sexual female (Figs 116–121). Body black; mandibles, palpi, base of antenna and legs yellowish-white. Head transverse in dorsal view, as broad as mesosoma; gena not broadened behind eye, broader than high in frontal view; inner margins of eyes converging ventrally; length of malar space around 3.0× shorter than height of eye, malar sulcus absent. Antenna with 12 flagellomeres, F1 shorter than scape+pedicel and shorter than F2+F3. Pronotum, mesoscutum, mesopleuron smooth, glabrous, shining. Notaulus narrow, complete. Mesoscutellar foveae smooth, shallow; mesoscutellar disk smooth, punctate and pubescent behind, overhanging propodeum. Lateral propodeal carinae bent slightly outwards. Fore wing pubescent, ciliate on margin; radial cell opened, 5.0× as long as broad, veins brown, areolet small. Tarsal claws toothed, with strong basal lobe. Metasoma as high as long, all terga smooth, visible on dorsal margin. Prominent part of ventral spine of hypopygium stout, 2.0× as long as broad in ventral view, without setae.

Body length 1.45–2.15 mm (n = 6) (Weld 1952b).



**Male.** Like the female, head broader than mesosoma. Antennae with 13 flagellomeres, F1 equal in length to scape+pedicel, 1.45× as long as F2, slightly excavated and curved, lighter than scape and pedicel. Metasoma with short petiole. Body length 1.45–1.8 mm.

**Gall** (Figs 122-123). Conical, 3.0 by 1.4 mm, tan when mature, thin walled, covered with crinkly white matted hairs. Produced singly at edge of leaf. The gall is difficult to distinguish from the sexual galls of *F. crystallinum*, *F. dumosae* and *F. kingi*, although this species has an eastern distribution rather than Pacific slope (but see also diagnosis to species above).

**Biology.** Only the sexual generation is known, inducing galls on *Q. alba* (section *Quercus*, subsection *Albae*). Galls mature in early spring; adults emerge in late April-May.

**Distribution.** USA: VA (Weld 1952b).

***Feron crystallinum* (Bassett, 1900) comb. nov.**

**Figs 124–149**

*Andricus crystallinus* Bassett, 1900: 319, female, gall.

**Type examined.** Asexual female. A type female No. 10488 is deposited in the Entomology Type Collection at the Academy of Natural Sciences of Philadelphia, not examined by the authors. We have examined several pictures from several sexual specimens (females coded 1332063, and 1332065; males coded 1132047, and 1132055) made by Peter T. Oboyski.

**Additional material.** Three asexual females “USA, CA, Salt Springs, ex *Q. douglasii*, coll. 2004.02.29., leg. K. Schick”; 2 asexual females “USA, CA, Diablo, ex *Q. douglasii*, 1925.10.15, leg. A. Kinsey”; 2 asexual females “USA, CA, 30km SW of Williams, CA2, galltype165, ex *Q. douglasii*, 2007.11.02., leg. J.A. Nicholls”; 2 asexual females “USA, CA, Copperopolis, CA969, galltype165, ex *Q. douglasii*, 2007.11.06., leg. J.A. Nicholls”; 1 sexual female “USA, CA, Dye Creek Preserve, CA1042, spCA16\_1, ex *Q. douglasii*, coll. 2008.03.30., leg. J.A. Nicholls”. In the general collection of the USNM there are specimens with Bassett handwriting labels (not type material) and our asexual females are conspecific with those of Bassett.

**Diagnosis.** Asexual females belong to the *Feron* species group in which the pronotum is without carinae, with dense setae and piliferous points; the mesoscutum is dark brown between notauli in anterior 1/3 length of the mesoscutum; as in *F. pattersonae* (asex) and *F. sulfureum* (asex). Differs from *F. pattersonae* in the trapezoid head in frontal view (ovate in *F. pattersonae*) and the mesoscutellar foveae divided by a central carina (fused in *F. pattersonae*). Morphologically most similar is *F. sulfureum* but in *F. crystallinum* the pronotum is coriaceous, with piliferous points and distal flagellomeres broader than basal; for

other characters see couplet 26 in the key. Sexual females are brown to chestnut brown, rarely darker; inner margins of eyes are parallel or only slightly converging ventrally, the frons is flat, not or only slightly bulging in frontal view; the mesoscutum is smooth, glabrous or alutaceous anteriorly; the mesoscutellum with irregular rugae at least in lateral and posterior parts, sometimes dorsocentral part is smooth, shining, without piliferous points; these characters are shared with *F. amphorus* (asex), *F. clarkei* (sex) and *F. dumosae* (sex). Differs from *F. amphorus* and *F. clarkei* in the transfacial distance which is as long as or slightly shorter than the height of the eye, the eye more than 3.6× as high as length of the malar space; the pronotum laterally with short carinae only along posterior margin. Differs from *F. dumosae* by characters mentioned at couplet 19 in the key. Males are different from all other *Feron* males in the inner margins of eyes which are slightly diverging ventrally, the notaulus is complete, mesoscutellar foveae absent, present in the form of a transverse smooth anterior impression, continuing into smooth mesoscutellar disc.

**Re-description.** Asexual female (Figs 124–134). Head chestnut brown, posteriorly darker, clypeus darker, mandibles and palpi chestnut brown, antenna chestnut brown, with darker F4–F12; mesosoma predominantly brown; pronotum brown with darker anterolateral part, propleuron dark brown; mesoscutum brown with black marks between notauli in anterior half and next to lateral lines; mesoscutellum uniformly brown; mesopleuron brown, ventrally dark brown to black; propodeum dark brown to black; metasoma uniformly dark brown; legs chestnut brown, with darker coxae.

Head with sparse setae, denser on lower face, 1.2× as broad as high and slightly broader than mesosoma in frontal view; 2.1× as broad as long in dorsal view. Gena reticulated, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space reticulate, with striae radiating from clypeus and not reaching eye; eye 2.7× as high as length of malar space; malar sulcus absent. Inner margins of eyes parallel. POL 1.7× as long as OOL, OOL 1.9× as long as diameter of lateral ocellus and slightly longer than LOL, all ocelli ovate, of same size. Transfacial distance slightly longer than height of eye; toruli located in the upper half of head and frons definitely shorter than lower face, diameter of antennal torulus 1.3× as long as distance between them, distance between torulus and eye 1.2× as long as diameter of torulus; lower face smooth with white setae; slightly elevated median area coriaceous, with few setae. Clypeus quadrangular, slightly broader than high, smooth, with a few long setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit small, rounded, distinct, epistomal

sulcus distinct, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex uniformly reticulate, without striae and setae; area under central ocellus impressed, smooth, glabrous; occiput and postocciput alutaceous; postgena reticulate, with a few setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal sulci which strongly diverge toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres; F6–F12 about 2.0× broader than F1–F5; pedicel 1.7× as long as broad; F1 1.8× as long as pedicel and slightly longer than F2; F2 slightly longer than F3; all subsequent flagellomeres shorter, F12 as long as F11; placodeal sensilla on F5–F12.

Mesosoma as long as high, with a few white setae, denser along propleura and on lateral propodeal area. Pronotum coriaceous in posterolateral area, with dense setae laterally with piliferous points; propleuron smooth, glabrous. Mesoscutum slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae), rugose-reticulate between notauli in anterior half and laterad to notauli, smooth and glabrous in between notauli in posterior half; entirely and uniformly with dense long white setae and some distinct piliferous points. Notaulus complete, shallow, posteriorly converging and broader than anteriorly, with smooth, glabrous bottom; in most posterior part distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line distinct, elevated or impressed, smooth, glabrous, reaching to half-length of mesoscutum; parapsidal line marked with broad smooth, glabrous stripe; median mesoscutal line indistinct, very short, present at the most posterior end; parascutal carina broad, reaching notaulus. Mesoscutellum ovate, slightly longer than broad, broadest part posteriorly, circumscutellar carina complete; uniformly rugoso-coriaceous, overhanging metanotum, with sparse long setae. Mesoscutellar foveae quadrangular, as broad as high, with smooth, glabrous bottom, divided by a rugose elevated triangular area. Mesopleuron entirely smooth, with setae only along ventral edge; mesopleural triangle coriaceous, with dense white setae; dorsal and lateral axillar areas smooth, glabrous, without setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, triangular, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height; lower part separating smooth, glabrous area, with dense setae, upper part of sulcus also distinct. Metascutellum coriaceous, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with few setae; central propodeal area lyre-shaped, smooth, with a few strong short longitudinal rugae; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral

propodeal area smooth, with long white setae, each seta with piliferous point at the base. Nucha with numerous irregular rugae. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins brown, radial cell open, 3.8× as long as broad; Rs and R1 not reaching wing margin; areolet small, triangular, closed and distinct. Rs+M distinct in 2/3 of its length, its projection reaching basalis at half of its height.

Metasoma longer than head+mesosoma, longer than high in lateral view; 2nd metasomal tergum smooth, extending to 5/6 length of metasoma in dorsal view, with patch of dense white setae anterolaterally, without micropunctures; all subsequent terga and hypopygium smooth, with fine micropunctures; prominent part of ventral spine of hypopygium 6.8× as long as broad in ventral view, with short white setae ventrally, which do not extend beyond apex of spine.

Body length 2.1–2.3 mm (n = 3).

Sexual generation. According to Doult (1960), specimens used for the description of the sexual females and males were housed in the University of California, Albany. Currently they are deposited in the Essig Museum (University of California, Berkeley, Peter T. Oboyski *pers. comm.*). These specimens were not examined by the authors; however, photos were taken from females and males by Peter T. Oboyski and sent to authors. For material examined by the authors, see above in Additional material.

Sexual female (Figs 136–145). Head, mesosoma dark brown to black; scape, pedicel and F1 light brown, all subsequent flagellomeres uniformly dark brown; legs yellowish-brown, except dark brown to black coxae; metasoma chestnut brown.

Head slightly transverse, with sparse setae, denser on lower face and along inner margins of eyes, 1.2× as broad as high and as broad as mesosoma in frontal view; 2.1× as broad as long in dorsal view. Gena reticulated, not broadened behind eye in frontal view, 2.7× narrower than transverse diameter of eye in lateral view. Malar space alutaceous, with striae radiating from clypeus and reaching eye; malar sulcus absent; eye 3.8× as high as length of malar space. Inner margins of eyes parallel or very slightly converging ventrally. POL 2.2× as long as OOL, OOL 1.5× as long as diameter of lateral ocellus and slightly shorter than LOL, all ocelli ovate, of same size. Transfacial distance as long as height of eye or slightly longer; toruli located in the upper half of head and frons definitely shorter than lower face, diameter of antennal torulus 1.6× as long as distance between them, distance between torulus and eye 1.2× as long as diameter of torulus; lower face coriaceous with white setae, above malar space

smooth and glabrous; slightly elevated median area coriaceous, with few setae. Clypeus rectangular, around 1.6× as broad as high, coriaceous, with long setae along ventral edge; ventrally rounded, emarginate, without median incision; anterior tentorial pit small, rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex uniformly alutaceous, without striae and setae; area under central ocellus impressed, smooth, glabrous; occiput and postocciput alutaceous, postgena alutaceous, with few setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres; all flagellomeres nearly equal in width, F1 narrower than F2; pedicel longer than broad; F1 1.4× as long as pedicel, shorter than scape+pedicel and nearly equal in length to F2; F2 longer than F3, F3 longer than F4; all subsequent flagellomeres shorter and nearly equal in length; F12 slightly longer than F11; placodeal sensilla on F2–F12.

Mesosoma slightly longer than high, with a few white setae along propleura and on lateral propodeal area. Pronotum smooth with sparse setae laterally, with parallel short delicate wrinkles along posterior edge; propleuron smooth, with scattered white setae. Mesoscutum slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae), entirely smooth and glabrous without setae. Notaulus complete, deep, posteriorly converging, with smooth, glabrous bottom; at posterior end the distance between notauli just shorter than distance between notaulus and side of mesoscutum; anterior parallel line impressed, smooth, glabrous, extending to 1/3 length of mesoscutum; parapsidal line marked with impressed smooth, glabrous stripe; median mesoscutal line absent; parascutal carina broad, complete. Mesoscutellum trapezoid, slightly longer than broad, broadest part posteriorly, uniformly rugoso-coriaceous, overhanging metanotum, with sparse long setae. Mesoscutellar foveae ovate, broader than high, with smooth, glabrous bottom, divided by a smooth elevated triangular area. Mesopleuron entirely smooth, with setae only along ventral edge; mesopleural triangle rugose, with dense white setae; dorsal and lateral axillar areas smooth, with some sparse setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, triangular, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron in lower 1/3 of its height; lower part separating smooth, glabrous area with dense setae, upper part of sulcus indistinct. Metascutellum smooth, glabrous, slightly higher than height of smooth, glabrous ventral impressed area; metanotal trough smooth, glabrous, without setae, with some irregular rugae; central

propodeal area smooth, glabrous, without rugae; lateral propodeal carinae strong, broad and high, bent outwards in mid-height of propodeum; lateral propodeal area smooth, with long white setae, each seta with piliferous point at the base. Nucha with some irregular rugae. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins brown, radial cell open, 4.1× as long as broad; Rs and R1 not reaching wing margin; areolet small, triangular, closed and distinct. Rs+M distinct in 1/3 of its length, its projection reaching basalis at half of its height.

Metasoma longer than head+mesosoma, higher than long in lateral view; 2nd metasomal tergum smooth, extending to half-length of metasoma in dorsal view, with patch of dense white setae anterolaterally, without micropunctures; all subsequent terga and hypopygium smooth without micropunctures; prominent part of ventral spine of hypopygium 3.7× as long as broad in ventral view, with short white setae ventrally, which do not extend beyond apex of spine.

Body length 1.9 mm (n = 1).

**Male** (Figs 146–147). Body yellowish to amber; eyes bigger, transfacial distance much shorter than height of eye; height of eye 4.3× as high as length of malar space; ocelli much bigger, POL 6.0× as long as OOL, OOL 0.5× as long as diameter of lateral ocellus and much shorter than LOL, all ocelli ovate, of same size; antenna with 13 flagellomeres, longer than body, F1 slightly curved, not excavated laterally; placodeal sensilla on all flagellomeres; mesoscutum glabrous, scarcely pubescent on pronotum, along notaulus, along ventral edge of mesopleuron, mesopleural triangle and side of propodeum; mesosoma smooth and shiny, pronotum laterally and anterior part of mesoscutum alutaceous; mesoscutellar foveae absent; metasoma with long petiole, shorter than mesosoma.

**Gall.** Asexual galls (Fig. 135). Bristly-haired gall masses 35 mm long by 25 mm wide on the underside of leaves composed of small, individual, elliptical or spherical, monothalamous galls, 12–14 mm high, 7 mm in diameter. Each gall usually with a slightly curved beak at the apex and a sparse coating of crystalline white, rose pink, red, or brown hairs (Russo 2021). Sexual galls (Fig. 148-149) monolocular, they are mostly on the upper surface of leaves, singly or in small groups, green with straw coloured apex, conical, slightly curved. The gall has numerous long cottony, white hairs projecting laterally, which are longer than the greatest width of the gall. The gall is 2.5 mm in length, with the base 1.0 mm tapering to the tip. The position of the gall is indicated on the opposite (usually lower) side of leaf by a pale coloured

elliptical swelling (Doutt 1960). The gall is difficult to distinguish from other similar sexual galls such as *F. comatum*, *F. dumosae* and *F. kingi*.

**Biology.** Alternate asexual and sexual generations were matched by Doutt (1960). Alternate sexual and asexual generations are also confirmed herein using DNA data, with four individuals (three asexual females, one sexual female) sequenced for *cytb* and three individuals (two asexual females, one sexual female) sequenced for *cytb*. *Cytb* sequences grouped into two haplotypes that were 0.23% divergent (GenBank accessions KX683596, MZ030743, OQ446195–OQ446196) and ITS2 sequences were identical among the three individuals (GenBank accessions OQ448237–OQ448239).

Asexual galls in autumn on leaves, adults emerge in January-February; sexual galls in spring, adults emerge in March. Both generations develop on oaks from section *Quercus*, subsection *Dumosae*: *Q. douglasii*, *Q. dumosa* and *Q. garryana*.

**Distribution.** USA: California.

**Comments.** The sexual males and females from the experimental material deposited in the Essig Museum by Doutt all have an amber body colour which differs from the chestnut brown sexual females collected by JN and examined by GM, and also from the colour Doutt described for sexual generation adults. We consider this simply to represent within-species chromatic variation (as is known for other *Feron* species) since the remainder of the diagnostic characters, host plant, and distribution are consistent with Doutt's description.

***Feron cylindratum* (Kinsey, 1937), comb. nov.**

**Figs 150–161**

*Xystoteras cylindratum* Kinsey 1937a: 77, female, gall.

*Liodora cylindratum* (Kinsey): Melika & Abrahamson 2002: 160 (synonymized *Liodora* with *Andricus*); Pujade-Villar 2003: 234 (mentioned this combination).

*Andricus cylindratum* (Kinsey): Pujade-Villar 2003: 234.

**Types examined.** HOLOTYPE: Asexual female "Mex (City) 25E D.F. 7000", Mex. Gall 1-2-32, very many fms. 3-15-32", "*Q. texocana*, Kinsey coll." red "*Xystoteras cylindratum*, Holotype", deposited in AMNH, NYC, examined by GM. PARATYPES (around 600 asexual females) deposited in the general collection in AMNH, part of them also examined by GM.

**Additional material.** Four asexual females with the following label: "MEX-542, UNSIS, Mihauatlán de Porfirio Díaz, Oaxaca, México, ex *Q. obtusata*, (10.xi.2018) 05.ii.2019: 4 females, leg. R. Clark".

**Diagnosis.** The only *Feron* species with the mesoscutum smooth, partially alutaceous anteriorly, glabrous and with the mesoscutellum uniformly reticulate.

**Re-description.** Asexual female (Figs 150–160). Body dark brown; antenna and legs yellow to yellowish-brown.

Head alutaceous, with sparse white setae on lower face, 1.2× as broad as high and slightly broader than mesosoma in frontal view, 1.8× as broad as long in dorsal view. Gena alutaceous, slightly broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, shining, with delicate striae radiating from clypeus, some of which reaching eye, malar sulcus absent; eye 3.2× as high as length of malar space. Eyes slightly converging ventrally. POL 2.1× as long as OOL, OOL 1.6× as long as diameter of lateral ocellus and slightly longer than LOL, all ocelli ovate, of same size. Transfacial distance slightly longer than height of eye; diameter of antennal torulus 1.8× as long as distance between them, distance between torulus and eye 1.2× as long as diameter of torulus; lower face alutaceous, glabrous, without setae, without striae; slightly elevated median area alutaceous, glabrous, without setae. Clypeus rectangular, nearly 2.0× as broad as high, smooth, glabrous, without setae; ventrally rounded, not emarginate and without median incision; anterior tentorial pit large, rounded, indistinct, epistomal sulcus distinct, broad, clypeo-pleurostomal line narrow, distinct. Frons, interocellar area uniformly alutaceous, without striae and setae. Vertex and occiput alutaceous, with a few white setae; postocciput smooth, glabrous; postgena in most part alutaceous, smooth glabrous along occipital foramen; posterior tentorial pit large, ovate, area below impressed; occipital foramen higher than height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly as broad as occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres (suture between F12 and F11 indistinct), pedicel 2.0× as long as broad, flagellomeres not broadened towards apex; F1 1.5× as long as pedicel and 1.3× as long as F2; F2=F3=F4; F4 slightly longer than F5, all subsequent flagellomeres nearly equal in length; placodeal sensilla on F4–F12.

Mesosoma slightly higher than long, with a few setae, denser on lateral propodeal area. Pronotum laterally smooth, shining, with numerous delicate concentric striae; propleuron smooth, with few setae. Mesoscutum smooth shining, alutaceous only along anterior 1/5, with sparse white setae, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, deep, broad along entire length, with smooth bottom, posteriorly broader and slightly converging; anterior parallel line



indistinct, marked with smooth line, extending to 1/4 of mesoscutum length; parapsidal line indistinct or invisible; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid, slightly longer than broad, uniformly reticulate, posteriorly rounded, overhanging metanotum. Mesoscutellar foveae in the form of a narrow semilunar anterior impression of mesoscutellum, with smooth, glabrous bottom, not divided by median carina. Mesopleuron smooth, shining, with delicate indistinct transverse subparallel striae, visible in central part at mid height; speculum smooth, shining; mesopleural triangle smooth, with sparse white setae; dorsal and lateral axillar areas smooth, shining, with a few white setae; subaxillular bar smooth, glabrous, triangular, at posterior end higher than height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, delimiting smooth, shining area, upper part of sulcus strong, distinct. Metascutellum smooth, glabrous, shorter than height of smooth, glabrous ventral impressed area; metanotal trough smooth, glabrous, without setae; central propodeal area smooth, glabrous, with irregular rugae; lateral propodeal carinae bent slightly outwards at mid height; lateral propodeal area smooth, with white setae and piliferous points Nucha with longitudinal sulci laterally, smooth, glabrous dorsally. Tarsal claws toothed, with basal lobe.

Fore wing longer than body, hyaline, with cilia on margin, veins dark brown, distinct, radial cell open, 4.7× as long as broad; Rs not reaching wing margin, R1 very short; areolet present. Rs+M distinct, extending to 4/5 of distance between areolet and basalis, its projection reaching basalis at its mid height.

Metasoma as long as head+mesosoma, higher than long in lateral view; 2nd metasomal tergum extending to 1/3 length of metasoma in dorsal view, with setae anterolaterally; all terga smooth, glabrous, without micropunctures. Hypopygium without micropunctures, prominent part of ventral spine of hypopygium 7.5× as long as broad in ventral view, with few short setae ventrally.

Body length 0.9–1.9 mm (n = 3).

**Gall** (Fig. 161). Small, naked, hollow cylinders scattered on the underside of leaves. Each gall is regularly cylindrical, a bit swollen below the tip, a bit restricted basally, up to 5.0 mm in length and 2.5 mm in diameter. The exterior of the gall fairly smooth, entirely naked except for a blue or purplish scurf. The body of gall hollow, open at top, the open cavity penetrating to a third or a half of the gall, separated from the larval cell by a thin partition; larval cell floored with a thicker partition beneath which another cavity is to be found. Young galls straw and light rose pink, sometimes touched more purple red, the whole touched with an ashy-blue scurf; older galls becoming burnt red to purple brown or dark, dirty brown. Each gall

separated, often occurring in great numbers and dense masses, usually on under surfaces, rarely on upper surfaces of leaves.

**Biology.** Only the asexual generation is known, inducing galls on *Q. deserticola* (= *Q. texcocana*) (section *Quercus*, subsection *Leucomexicana*). Galls mature in autumn; adults emerge from February to mid-March.

**Distribution.** Mexico: Mexico City, Puebla (Kinsey 1937).

***Feron discalis* (Weld, 1926), comb. nov.**

**Figs 162–183**

*Diplolepis discalis* Weld, 1926: 24, female, gall.

*Andricus discalis* (Weld): Weld, 1951: 633.

**Type examined.** HOLOTYPE: Asexual female “Tijeras, N.M.”, “Cut out Nov. 1.21”, “*Quercus pungens*”, red label “Type No. 27190 USNM”, “*Diplolepis discalis* Weld” deposited in USNM, examined by GM. Specimen data and images available at <http://n2t.net/ark:/65665/3629a7172-440c-48df-a198-8b1c39flfa61>.

**Material examined.** Two asexual females labelled as “USA, Arizona, Chiricahua Mtns summit, AZ258, spAZI2, galltype 60, *Q. arizonica*, leg. J.A. Nicholls, 2007.10.26.”

**Diagnosis.** The only asexual *Feron* species with yellowish to reddish brown body, the head with frons bulging in frontal view and inner margins of eyes converging strongly ventrally, the mesoscutum uniformly alutaceous-reticulate, glabrous and with the mesoscutellum smooth and glabrous centrally, while posteriorly and laterally rugose.

**Re-description.** Asexual female (Figs 162–172, 174–183). Head, mesosoma, mandibles, mouthparts, legs and metasoma uniformly yellowish to light brown; antenna, central propodeal area and posterior visible tergites slightly darker than rest of body. Two colour extremes (yellow and reddish-brown) are illustrated.

Head alutaceous, with a few sparse setae on lower face; rounded, 1.2× as broad as high and slightly narrower than mesosoma in frontal view; 1.6× as broad as long in dorsal view. Broadest part of head in frontal view at mid-height of lower face. Gena alutaceous-reticulate, not broadened behind eye in frontal view, narrower than transverse diameter of eye; gena in lateral view equally narrow along entire length of eye. Malar space alutaceous, with some striae radiating from clypeus and reaching to half-length of malar space; eye 4.5× as high as length of malar space; malar sulcus absent. Inner margins of eyes strongly converging ventrally. POL 1.9× as long as OOL, OOL 2.4× as long as the diameter of lateral ocellus and

slightly longer than LOL, all ocelli ovate, of the same size. Antennal toruli located above mid-height of eyes. Transfacial distance 1.2× as long as height of eye; diameter of antennal torulus 2.0× as long as distance between them, distance between torulus and eye 1.4× as long as diameter of torulus; lower face smooth with a few white setae; slightly elevated median area and area between toruli smooth, glabrous, without setae. Clypeus impressed, rectangular, broader than high, alutaceous, with a few setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit large, rounded, deep, epistomal sulcus broad and deep, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex uniformly alutaceous, without striae and setae; area under central ocellus impressed, smooth, glabrous; occiput alutaceous, with dense setae; postocciput glabrous, with numerous delicate longitudinal interrupted parallel striae; postgena smooth, with few setae; posterior tentorial pit large, elongated, area below impressed; occipital carina black, clearly visible beside occipital foramen; occipital foramen slightly shorter than height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal sulci which diverge until occipital foramen, ending in posterior tentorial pit. Antenna nearly as long as body, scape, pedicel, F1–F5 light brown, subsequent flagellomeres dark brown to black, with 12 flagellomeres (suture between F11 and F12 indistinct), pedicel longer than broad, F1 longer than length of scape+pedicel, 1.2× as long as F2, F2 slightly longer than F3, F3=F4, subsequent flagellomeres shorter, broader and nearly equal in length, F12 slightly longer than F11; placodeal sensilla on F5–F12.

Mesosoma longer than high, with rare setae on pronotum laterally, mesopleural triangle, mesoscutellum and lateral area of propodeum. Pronotum smooth, with setae laterally, delicate transverse parallel striae along posterior edge; anterolateral edge of propodeum smooth, glabrous, without foveae; propleuron smooth, with sparse white setae. Mesoscutum longer than broad (greatest width measured across mesoscutum level with base of tegulae), uniformly alutaceous-reticulate. Notaulus complete, deep, posteriorly strongly converging and broader than anteriorly, with smooth, glabrous bottom; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line and parapsidal line indistinct, not traceable; median mesoscutal line in the form of a short broad smooth triangle; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid, longer than broad, broadest part in posterior 1/3; center part of mesoscutellum smooth, glabrous, rugose posteriorly and laterally, overhanging metanotum, with a few long setae. Mesoscutellar foveae in the form of a transverse, semilunar impression, broader than high,

with smooth, glabrous bottom, circumscutellar carina present. Mesopleuron smooth, with setae along ventral edge, with very delicate indistinct parallel striae in anterior half; mesopleural triangle smooth, with dense white setae and piliferous points; dorsal and lateral axillar areas smooth, with setae; axillula with delicate parallel longitudinal striae; subaxillary bar smooth, glabrous, triangular, posteriorly slightly higher than height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, lower part delimiting smooth area with few setae, upper part of sulcus indistinct. Metascutellum coriaceous, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with few setae; central propodeal area lyre-shaped, smooth, glabrous; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral propodeal area smooth, with long white setae and piliferous points. Nucha with longitudinal sulci dorsally and laterally and a net of irregular rugae. Tarsal claws with basal lobe.

Fore wing longer than body, with light brown veins, margin with dense long cilia; radial cell open, 4.5× as long as broad, R1 and Rs nearly reaching wing margin; areolet triangular, delimited by indistinct light brown veins; Rs+M indistinct, not traceable. Tarsal claws with basal lobe.

Metasoma longer than head+mesosoma, longer than high in lateral view; all metasomal tergites smooth, glabrous, 2nd metasomal tergum extending to 2/3 length of metasoma in dorsal view, with white setae anterolaterally, without micropunctures; all subsequent terga with rare, weak, very delicate micropunctures. Hypopygium with micropunctures, prominent part of ventral spine of hypopygium 7.8× as long as broad in ventral view.

Body length 1.7–1.8 mm (n = 2).

**Gall** (Fig. 173). A spangle gall, on the underside of leaf, 3.6–4.0 mm diameter, monolocular, yellow-green when young and growing, turn brown when mature, with raised rim and raised center, convex on upper surface, underside concave, the transversely placed larval chamber occupying the full height of the gall. A single or a few galls on one leaf (Weld 1926).

**Biology.** The asexual generation is only known, which induces galls on *Q. pungens* (section *Quercus*, subsection *Polymorphae*), *Q. arizonica* and *Q. turbinella* (both section *Quercus*, subsection *Leucomexicana*). Galls mature in late autumn; adults were cut out from galls in November; probably overwintering in galls and emerging in spring.

**Distribution.** USA: Arizona, New Mexico (Burks 1979).

*Feron discularis* (Weld, 1926), comb. nov.

## Figs 184–188

*Diplolepis discularis* Weld, 1926: 25, female, gall.

*Andricus discularis* (Weld): Weld, 1951: 633.

**Type examined.** HOLOTYPE: Asexual female “Sequoia Nat. Park, Cal.,” “Cut out Nov. 10”, “*Q. garryana*”, red label “Type No. 27191 USNM”, “*Diplolepis discularis* Weld” deposited in USNM, examined by GM. The type is present, however absent from the Type list. Specimen data and images available at <http://n2t.net/ark:/65665/3c82fa469-ecf2-491e-bb0d-b1778bff7d05>

**Diagnosis.** Asexual females belong to the group of *Feron* species in which the pronotum laterally with longitudinal carinae and the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, with piliferous points; as in *F. kingi* (asex) and *F. tubifaciens* (asex). Differs from those two species in the entirely black body; the frons bulging in frontal view, ocelli not elevated above the head; toruli located at the midheight of the head; the median mesoscutal line in the form of a short triangle.

**Re-description.** After Weld (1926) with modifications (Figs 184–186). Predominantly black, base of antenna and legs beyond coxae brownish; face and mesonotum with scattered setae. Head coriaceous, rounded bulging upward in frontal view and as broad as mesosoma in frontal view; gena not broadened behind eye, occiput not concave; Transfacial distance equal to or slightly longer than height of eye; malar space about 1/3 of eye height, without malar sulcus. Toruli located at mid height of head. Antenna longer than head+mesosoma with 12 flagellomeres, distal flagellomeres slightly broader; the antennomere lengths are 10: 6: 13: 10: 9: 8: 8: 7.5: 7: 7: 6.5: 6: 6: 8. Pronotum with delicate parallel striae laterally near tegula. Mesoscutum high-arched, longer than broad, finely coriaceous, with piliferous points, notaulus complete, deep, with smooth bottom; median mesoscutal line in the form of a short triangle. Mesopleuron smooth, glabrous, with small aciculate area in front. Tarsal claws with strong basal lobe. Fore wing hyaline, pubescent, ciliate on margins, veins brown; radial cell around 3.8× as long as broad; areolet present, Rs-M vein reaching 1/8 of the distance to basal. Disk of mesoscutellum delicately coriaceous antero-centrally, with strong rugae posteriorly and laterally; sides bounded by two straight diverging lines; mesoscutellar foveae rounded, separated medially, with smooth, glabrous bottom, not delimited by carinae posteriorly. Metascutellum rugose. Lateral propodeal carina bent strongly outwards, central propodeal area narrower anteriorly, broadened posteriorly, neck rugose. Metasoma longer than head+mesosoma, 2nd metasomal tergum with sparsely pubescent areas at base; prominent

part of the ventral spine of hypopygium 8.0× as long as broad in ventral view. Body length 1.6–1.95 mm.

**Gall** (Figs 187–188). Disk-shaped, about 6 mm in diameter by 1 mm thick, single or scattered in small numbers on underside of leaf in autumn. The upper surface is slightly concave, the edge sinuate, the margin reflexed nearly to the leaf surface. The transversely placed larval cell occupies the full height of the gall. Exit hole on top surface (Weld 1926).

**Biology.** The asexual generation only is known, inducing galls on *Q. garryana* (section *Quercus*, subsection *Dumosae*). Galls mature in September, adults were cut out in November.

**Distribution.** USA: CA (Weld 1926).

***Feron dumosae* (Weld, 1957), comb. nov.**

**Figs 189–202**

*Liodora dumosae* Weld, 1957: 111, female, male and gall.

**Types examined.** One paratype sexual female and gall “Stanford Univ. California. May 10”, “*Quercus dumosa*”, “1758”, red label “Paratype No. 63009 USNM”. Specimen data and images available at <http://n2t.net/ark:/65665/3c1624a96-f517-4880-83da-c8c458cfaf3a>

**Diagnosis.** Sexual females of this species are characterised by the brown to chestnut brown body, rarely darker; inner margins of eyes parallel or only slightly converging ventrally; the frons is flat, not or only slightly bulging in frontal view; the mesoscutum is smooth or partially alutaceous anteriorly and glabrous; the mesoscutellum with irregular rugae at least in lateral and posterior parts, sometimes dorsocentral part smooth, shining, without piliferous points; as in *F. amphorus* (asex), *F. clarkei* (sex) and *F. crystallinum* (sex). Differs from *F. amphorus* and *F. clarkei* in the transfacial distance which is as long as or slightly shorter than the height of eye, the eye more than 3.6× as high as length of the malar space; the pronotum laterally with short carinae only along posterior margin. Differs from *F. crystallinum* in the characters mentioned at couplet 19 in the key. Males are characterised by a brown or chestnut brown body, the notaulus reaching the pronotum, the mesoscutellum with irregular rugae at least in lateral and posterior parts without piliferous points; as in *F. clarkei*. However, in *F. dumosae* F1 1.6× as long as F2 (1.3× as long as F2 in *F. clarkei*) and the transfacial distance as long as or slightly shorter than the height of eye (longer than the height of the eye in *F. clarkei*).

**Re-description.** Sexual female (Figs 189–201). Head, mesosoma, metasoma dark brown to brown, antenna, mouthparts and legs yellow, with slightly darker coxae.

Head alutaceous, with sparse white setae on lower face, 1.2× as broad as high and slightly broader than mesosoma in frontal view, 2.0× as broad as long in dorsal view. Gena alutaceous, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, shining, with delicate striae radiating from clypeus and reaching eye, malar sulcus absent; eye 3.6× as high as length of malar space. Eyes slightly converging ventrally. POL 2.0× as long as OOL, OOL 1.6× as long as diameter of lateral ocellus and slightly longer than LOL, all ocelli ovate, of same size. Transfacial distance as long as height of eye or slightly shorter; diameter of antennal torulus as long as distance between them, distance between torulus and eye 1.3× as long as diameter of torulus; lower face alutaceous, glabrous, without white setae, without striae; slightly elevated median area alutaceous, glabrous, without setae. Clypeus rectangular, nearly 2.0× as broad as high, smooth, with long setae; ventrally rounded, not emarginate and without median incision; anterior tentorial pit large, rounded, indistinct, epistomal sulcus distinct, clypeo-pleurostomal line inconspicuous. Frons uniformly alutaceous, without striae and setae, interocellar area alutaceous. Vertex and occiput alutaceous, with sparse white setae; postocciput smooth, glabrous; postgena in the most part delicately coriaceous, smooth and glabrous along occipital foramen, postgenal bridge and hypostomata; posterior tentorial pit large, ovate, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly as broad as occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres, pedicel slightly longer than broad, flagellomeres slightly broadened towards apex; F1 2.0× as long as pedicel and 1.2× as long as F2; F2 1.2× as long as F3; F3=F4, F5=F6=F7, subsequent flagellomeres shorter, nearly equal in length; placodeal sensilla indistinct on all flagellomeres.

Mesosoma slightly longer than high, with sparse white setae, denser on lateral propodeal area. Pronotum smooth, shining, with sparse white setae, with some delicate striae anteroventrally; propleuron delicately coriaceous. Mesoscutum alutaceous in anterior half, smooth, shining posteriorly between notauli and alongside notauli, with sparse white setae, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, shallow, hardly traceable in anterior part, bottom smooth, posteriorly broader and slightly converging; anterior parallel line indistinct, marked with smooth line, extending to 1/3 of mesoscutum length; parapsidal line distinct, marked with smooth line; median mesoscutal line absent; parascutal carina broad, reaching notaulus.

Mesoscutellum trapezoid, slightly longer than broad, glabrous, shining, with net of irregular rugae, posteriorly rounded, overhanging metanotum. Mesoscutellar foveae separated by narrow elevated coriaceous central carina, ovate, with smooth, glabrous bottom. Mesopleuron smooth, shining, with delicate transverse subparallel striae in central part, absent anteriorly; speculum smooth, shining; mesopleural triangle smooth, with some delicate striae and sparse white setae; dorsal and lateral axillar areas delicately coriaceous, with a few white setae; subaxillular bar smooth, glabrous, with parallel sides, as high as height of metanotal trough, slightly higher at posterior end; metapleural sulcus reaching mesopleuron slightly above half of its height, delimiting coriaceous area, upper part of sulcus distinct. Metascutellum smooth, glabrous, slightly shorter than height of smooth, glabrous ventral impressed area; metanotal trough smooth, glabrous, without setae; central propodeal area delicately coriaceous, with a few irregular rugae; lateral propodeal carinae bent slightly outwards at mid-height; lateral propodeal area smooth, shining, with sparse white setae on piliferous points. Nucha very short with numerous sulci dorsally and laterally. Tarsal claws toothed, with basal lobe.

Fore wing longer than body, hyaline, with cilia on margin, veins light brown, hardly visible, radial cell open, 4.6× as long as broad; R1 and Rs reaching wing margin; areolet small, distinct. Rs+M narrow, visible along 1/2 of distance between areolet and basalis, its projection reaching basalis at its mid height.

Metasoma as long as head+mesosoma, longer than high in lateral view; 2nd metasomal tergum extending to 2/3 length of metasoma in dorsal view, without setae and micropunctures; all terga smooth, glabrous, without micropunctures. Hypopygium without micropunctures, prominent part of ventral spine of hypopygium short, slightly longer than broad in ventral view, without setae.

Body length 1.4–2.2 mm (n = 7) (Weld 1957).

**Male.** Similar to female, but antenna with 13 flagellomeres, F1 1.6× as long as F2, slightly curved and excavated. Body length 1.5–1.75 mm.

**Gall** (Fig. 202). Small, 2–3 mm, conical gall on leaf edge, slightly pubescent, fresh galls red-pinkish to pale brown, leaf blade twists slightly at the gall. The gall is difficult to distinguish from other similar sexual galls of *F. comatum*, *F. crystallinum* and *F. kingi*.

**Biology.** Rosenthal (1968) and Rosenthal & Koehler (1971) erroneously stated that *Liodora dumosae* was the sexual generation of *Andricus kingi*. Dailey & Menke (1980) subsequently corrected this mistake by demonstrating that Rosenthal & Koehler had mis-identified their sexual generation wasps as *L. dumosae* and instead had reared the then unknown sexual generation of *A. kingi*. Evans (1972) proposed that *L. dumosae* was the sexual generation of



*Andricus pattersonae* and transferred the later to *Liodora* under the new name combination *L. pattersonae*; this error was reiterated by Dailey & Menke (1980). However, this matching with *A. pattersonae* is in disagreement with genetic data presented herein (see under *F. pattersonae*), nor did Evans perform any rigorous biological experiments to match generations. In addition, Evans appears to have mis-identified his asexual generation galls (Fig 15 of Evans 1972) as they are too small and pale to be those of *A. pattersonae* and instead look like those of the new species *F. rucklei* described herein. Thus, until rigorous rearing experiments are conducted or genetic data are obtained, we consider *Feron dumosae* to be a valid distinct species known only from its sexual generation.

Galls occur on multiple oaks from section *Quercus*, subsection *Dumosae*: *Q. douglasii*, *Q. dumosa*, *Q. garryana* and *Q. lobata*. They mature in May and adults emerge soon after.

**Distribution.** USA: California.

***Feron gigas* (Kinsey, 1922), comb. nov.**

**Figs 203–215**

*Andricus gigas* Kinsey, 1922: 282, female, male, gall.

*Dryocosmus gigas* (Kinsey): Weld, 1952a: 334.

*Andricus crenatus* Weld, 1952b: 330, female (asex), gall. Synonymy in Dailey & Sprenger, (1973a).

**Types examined.** HOLOTYPE: sexual female of *Andricus gigas* “Merced Falls Cal., gall 3.28.20.”, “*Q. douglasii*, Kinsey coll.”, pink “*A. gigas* female, Holo-COTYPE” deposited in AMNH, NYC, examined by GM. *Andricus crenatus* HOLOTYPE: asexual female, “Los Gatos, Cal.”, “*Q. dumosa*”, “1735”, red label “Type No. 60117 USNM”, handwriting label “*Andricus crenatus* Weld”. Specimen data and images available at <http://n2t.net/ark:/65665/3ddf41be9-a5bb-4dc8-91b3-45e7d8fadfb6>

**Additional material.** Asexual females: 2 females “USA: CA, Del Puerto Canyon, *Q. douglasii*, leg. R. Challis, 2004.10.21”; 3 females “USA: CA, Clearlake, *Q. douglasii*, CA17, galltype 135, leg. J.A. Nicholls, 2007.11.03.”; 3 females “USA: CA, 30km SW of Williams, *Q. douglasii*, CA17, galltype 135, leg. J.A. Nicholls, 2007.11.02”. One male “USA: CA, Dye Creek Preserve, *Q. douglasii*, CA1037, gall type 239, leg. J.A. Nicholls, 2008.03.30”.

**Diagnosis.** Asexual females belong to the group of *Feron* species in which the body is never black; the head is rounded or trapezoid to triangular in frontal view, ocelli are not elevated above the frons; eyes are parallel or very slightly converging ventrally, the transfacial distance

is equal or longer than the height of eye; toruli located above the mid-height of eyes; the eye is less than 3.0× as high as the length of the malar space; lateral ocelli are smaller, OOL at least 2.5× as long as the diameter of ocellus, or if shorter then the head and mesosoma are not yellowish or light brown; the pronotum laterally with longitudinal carinae; the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points and the mesopleuron with a transverse reliculate-carinate band at mid-height; these characters are shared with *F. parmula* (asex), *F. tibiale* (asex), *F. syndicorum* (asex) and *F. stellulum* (asex). Differs from *F. tibiale* and *F. syndicorum* in the gena which is not broadened behind the eye in frontal view. It differs from *F. parmula* in having a malar space with a few delicate striae radiating from the clypeus, mesoscutellar foveae are defined and the prominent part of the ventral spine of the hypopygium 4.5× as long as broad in ventral view; see more characters at couplet 37 in the key. The most similar species is *F. stellulum* but in *F. gigas* the antenna has 12 flagellomeres (11 in *F. stellulum*), the eye 2.2× as high as the length of the malar space (longer in *F. stellulum*), veins are pale (brown in *F. stellulum*), the areolet absent (present in *F. stellulum*) and the central propodeal area without rugae (with rugae in *F. stellulum*). Sexual females of this species belong to the group of *Feron* species with a black body, the frons is flat, not or only slightly bulging in frontal view, inner margins of eyes never strongly converging ventrally, the mesoscutum uniformly alutaceous-reticulate, glabrous and the mesoscutellum is uniformly alutaceous with numerous setae on piliferous points; as in *F. comatum* (sex), *F. apiarium* (asex), *F. kingi* (sex) and *F. pattersonae* (sex). *Feron gigas* differs from these species in having notauli distinct only at their posterior end but discontinuous or absent at their finely coriaceous anterior end and the mesopleuron is smooth with transverse striae in its central part. Males differ from all other *Feron* in the notaulus which is narrow, distinct only posteriorly, fragmented or absent anteriorly where mesoscutum is delicately coriaceous.

**Re-description.** Asexual female (Figs 203–214). Body, antenna, legs, uniformly rusty brown, some specimens uniformly dark brown.

Head reticulate, with sparse setae on lower face, gena and posteriorly, 1.2× as broad as high and slightly narrower than mesosoma in frontal view; 2.0× as broad as long in dorsal view. Gena reticulate, not broadened behind eye in frontal view, in lateral view dorsal part of gena at least 2.0× narrower than transverse diameter of eye and much broader on ventral part. Malar space alutaceous, shining, with striae radiating from clypeus and reaching to 1/3 of malar space length; eye 2.2× as high as length of malar space; malar sulcus absent. Inner

margins of eyes parallel. POL 1.6× as long as OOL, OOL 2.1× as long as diameter of lateral ocellus and slightly longer than LOL, all ocelli ovate, of same size. Antennal toruli located above mid-height of eyes. Transfacial distance 1.3× as long as height of eye; diameter of antennal torulus 1.6× as long as distance between them, distance between torulus and eye 1.4× as long as diameter of torulus; lower face delicately coriaceous, with white setae; slightly elevated median area coriaceous, without setae. Clypeus impressed, rectangular, 1.5× as broad as high, delicately coriaceous, with transverse striae, with a few setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit large, rounded, deep, epistomal sulcus broad and deep, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex uniformly reticulate, without striae and setae; area under central ocellus impressed, smooth, glabrous; occiput, postocciput reticulate; postgena smooth, with few setae; posterior tentorial pit large, elongated, area below impressed; occipital carina black, clearly visible beside occipital foramen; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into strong postgenal sulci which diverge until half the height of postgenal bridge, beyond which sulci are parallel and run alongside foramen until 1/3 of its height. Antenna slightly longer than head+mesosoma, with 12 flagellomeres (suture between F12 and F11 indistinct but present); F1–F3 with sparse white setae, F4–F12 with dense setae; pedicel 1.7× as long as broad; F1 2.1× as long as pedicel and 1.2× as long as F2; F2=F3, F4 slightly shorter than F3, F5=F6 and shorter than previous; all subsequent flagellomeres shorter and equal in length; F12 slightly longer than F11; placodeal sensilla on F3–F12.

Mesosoma longer than high, with a few scattered setae. Pronotum smooth, with sparse setae along smooth anterolateral edge; with parallel transverse delicate interrupted striae laterally; propleuron alutaceous, with very sparse white setae. Mesoscutum longer than broad (greatest width measured across mesoscutum level with base of tegulae), uniformly alutaceous-reticulate. Notaulus complete, deep, posteriorly converging strongly and broader than anteriorly, with smooth and glabrous bottom; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line marked by smooth stripes, reaching to half-length of mesoscutum; parapsidal line indistinct, not marked; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum trapezoid, longer than broad, broadest part in posterior 1/3; center part of mesoscutellar disc rugoso-coriaceous, with stronger rugae posteriorly and laterally, overhanging metanotum, with long setae. Mesoscutellar foveae rounded, as broad as high,

with smooth, glabrous bottom, divided by a triangular coriaceous elevated carina. Mesopleuron with parallel delicate transverse striae, speculum smooth, glabrous; mesopleural triangle smooth, with dense white setae and piliferous points; dorsal and lateral axillar areas smooth, with setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, triangular, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron above half of its height, lower part delimiting smooth area with few setae, upper part of sulcus indistinct. Metascutellum coriaceous, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with a few setae; central propodeal area lyre-shaped, smooth, glabrous; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral propodeal area smooth, with long white setae and piliferous points. Nucha with net of irregular strong rugae dorsally and laterally. Tarsal claws with acute basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins light brown, radial cell open, 4.4× as long as broad; Rs and R1 nearly reaching wing margin; areolet absent, Rs+M invisible.

Metasoma longer than head+mesosoma, higher than long in lateral view; 2nd metasomal tergum extending to 2/3 length of metasoma in dorsal view, with patch of dense white setae anterolaterally, with band of micropunctures posteriorly; all subsequent terga and hypopygium with dense micropunctures; prominent part of ventral spine of hypopygium 4.7× as long as broad in ventral view, with few short white setae ventrally.

Body length 1.2–1.6 mm (n = 10).

The description of the sexual generation (female, male and gall) is given after Kinsey (1922), with some modifications.

Sexual female. Head black, mandibles rufous brown; antenna brown, basal three or four antennomeres yellowish brown; mesosoma and metasoma dark brown to black. Legs yellowish-brown, femora especially hind femora darker, coxae brown, tips of tarsi darker; finely and not densely hairy.

Head finely coriaceous, about as broad as mesosoma in frontal view, gena only slightly broadened behind eyes; frons and lower face minutely punctate, with sparse, fine setae on sides of head. Antenna with delicate setae, with 12 flagellomeres, F1 slightly longer than F2.

Pronotum smooth, shining with sparse setae on dorsal edge, with some delicate striae along posterior edge. Mesoscutum mainly smooth and shining, coriaceous anteriorly; notaulus fine but visible only posteriorly, less evident, discontinuous or absent anteriorly where area finely

coriaceous; median mesoscutal line, anterior parallel line and parapsidal line absent; mesoscutellum finely rugose, hairy, with small, elevated, smooth, shining area at apex; mesoscutellar foveae in the form of an anterior arcuate impression, shallow, smooth. Mesopleuron mostly smooth, shining with delicate striae only centrally. Fore wing hyaline, with fine, brown hairs, with cilia on margins; veins brown; areolet moderately small to closed; cubitus very fine, not reaching basalis; radial cell long and open, second abscissa of radius somewhat curved; first abscissa nearly straight, without projection. Tarsal claws simple.

Metasoma protruding dorsally, 2nd metasomal tergum occupying nearly half-length of metasoma, with a few setae anteroventrally; ventral spine of hypopygium yellow-piceous; smooth, shining, short, with a few setae ventrally.

Body length 1.5–2.0 mm (n = 3).

**Male.** Differs from the female as follows: antenna entirely brown, 13 flagellomeres; areolet smaller, metasoma short, with moderately long petiole. Body length around 1.5 mm.

**Galls.** Sexual galls are small, 1–2 mm in diameter, round, pale yellow, on catkin coming off catkin stem at same place as stamens, sometimes on edge of leaf. Asexual spangle galls (Fig. 215) about 4 mm in diameter, usually on the upper side of the leaf, saucer shaped, with a thin crenate margin when young, with a prominent hump in center. The mature gall has a lens-shaped larval cavity inside, on the floor of which is a thin, white, circular disk with radiating prominent lines.

**Biology.** Alternation of sexual and asexual generations was determined by Dailey & Sprenger (1973a). Alternate sexual and asexual generations are also confirmed herein using DNA data, with four individuals (three asexual females, one sexual male) sequenced for cytb and three individuals (two asexual females, one sexual male) sequenced for cytb. Cytb sequences were on average 0.82% divergent (range 0–1.66%; GenBank accessions KX683598, OQ446198–OQ446199) and ITS2 sequences were identical among the three individuals except for two additional bases within a polyA region in one sample (GenBank accessions OQ448240–OQ448242).

This species induces galls on *Q. douglasii* and *Q. dumosa* (section *Quercus*, subsection *Dumosae*). Young asexual galls are present in August, mature in autumn; asexual adults emerge in February. Sexual galls are mature in April; adults emerge by the end of April.

**Distribution.** USA: California.

***Feron izabellae* Melika, Nicholls & Stone, sp. nov.**

### Figs 216–227

**Type material.** HOLOTYPE: Asexual female “USA, CA, Friday Ridge Road, CA, *Q. garryana*, CA1600”, coll. 20.09.2014, leg. J. DeMartini. PARATYPES (4 asexual females) “USA, CA, Lake Berryessa Napa County, *Q. berberidifolia*, CA1752, coll. 27.10.2016, leg. J.DeMartini”, “USA, CA, Inspiration Point, Covelo, *Q. durata*, CA1792, coll. 11.10.2011, leg. J.DeMartini”; “USA, CA, *Q. durata*, CA1820, leg. J.DeMartini”; USA, CA, Middletown, Lake County, CA2386, *Q. durata*, coll. 29.10.2014, leg. J.DeMartini”. The holotype and one paratype female are deposited at the USNM, 2 female paratypes at the PHDNRL, 1 female paratype at the UB.

**Etymology.** Named in memory of the author G. Melika’s mother, Izabella, and in honour of G. Melika’s granddaughter who carries on the Izabella name.

**Diagnosis.** The asexual form of this species belongs to the *Feron* group in which the pronotum is laterally smooth to coriaceous, without carinae, and the mesoscutum is alutaceous to coriaceous, rugose-reticulate, or reticulate, sometimes with smooth areas and piliferous points, glabrous or pubescent; as in *F. atrimentum* (asex), *F. crystallinum* (asex), *F. pattersonae* (asex), and *F. sulfureum* (asex). It differs from those species in the following combination of characters: the frons is bulging in frontal view; ocelli are not elevated above the head, the transfacial distance is 1.4× as long as the height of eye, the eyes slightly convergent ventrally, and the metapleural sulcus reaching the mesopleuron on the upper 2/3 of its height. The most similar species is *F. albicomus* (asex) from which *F. izabellae* differs in having the head and mesosoma amber, the median mesoscutal line absent, mesoscutellar foveae divided by an elevated coriaceous triangle, and ventral spine of hypopygium 8.0× as long as broad in ventral view.

**Description.** Asexual female (Figs 216–226). Head, antenna, mouthparts, mesosoma, legs, metasoma uniformly light brown to yellowish; head posteriorly slightly darker.

Head alutaceous-reticulate, with denser setae on lower face, slightly higher than broad and as broad as mesosoma in frontal view; 1.9× as broad as long in dorsal view. Gena alutaceous-reticulate, slightly broadened behind eye in frontal view; gena in lateral view slightly narrower than transverse diameter of eye. Malar space delicately coriaceous, with striae radiating from clypeus and not reaching eye, malar sulcus absent; eye 2.7× as high as length of malar space. Inner margins of eyes slightly converging ventrally. POL 1.5× as long as OOL, OOL 2.5× as long as diameter of lateral ocellus and 1.3× as long as LOL, all ocelli ovate, of same size. Antennal toruli located above mid-height of eyes. Transfacial distance

1.6× as long as height of eye; frons nearly as high as height of lower face, diameter of antennal torulus 2.1× as long as distance between them, distance between torulus and eye equal to diameter of torulus; lower face alutaceous, with setae; slightly elevated median area and area between toruli delicately coriaceous, with a few setae. Clypeus impressed, flat, 2.0× as broad as high, smooth, with a few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, small; epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex and occiput uniformly alutaceous-reticulate, without striae and setae; postocciput and postgena alutaceous, with dense white setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen shorter than height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres, pedicel longer than broad; F1 1.3× as long as F2 and more than 1.9× as long as pedicel; F2 longer than F3, F4 slightly longer than F5, F6=F7=F8, subsequent flagellomeres nearly equal in length; F12=F11, placodeal sensilla on F6–F12.

Mesosoma slightly longer than high, without setae. Pronotum glabrous, with delicate short inconspicuous parallel striae along posterior edge, with piliferous points; propleuron smooth, with sparse short setae. Mesoscutum uniformly alutaceous-reticulate, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, distinctly impressed along entire length; posteriorly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line, parapsidal and median mesoscutal line absent; parascutal carina narrow, reaching notaulus. Mesoscutellum slightly longer than broad, with subparallel sides; central part of mesoscutellum disk coriaceous, along sides and posteriorly with strong rugae, overhanging metanotum, with sparse setae. Mesoscutellar foveae distinct, slightly impressed smooth, glabrous, with elevated central carina. Mesopleuron smooth, alutaceous only in most anterodorsal part; speculum smooth, glabrous; mesopleural triangle smooth, with white setae; dorsal and lateral axillar areas smooth, with white setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with subparallel sides, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron slightly above half of its height; upper part of sulcus indistinct; lower part of sulcus delimiting smooth area with dense long white setae. Metascutellum smooth, glabrous, as high as height of smooth,

glabrous ventral impressed area; metanotal trough smooth, glabrous, with white setae; central propodeal area lyre-shaped, smooth, glabrous, without rugae; lateral propodeal carinae distinct, bent outwards in posterior 1/3 of its height; lateral propodeal area smooth, with long dense white setae. Nucha with longitudinal sulci dorsally and laterally. Tarsal claws with strong basal lobe.

Fore wing longer than body, hyaline, with short cilia on margin, veins indistinct, yellowish to pale brown, radial cell open, 4.5× as long as broad; Rs and R1 nearly reaching wing margin; areolet small, triangular, indistinct. Rs+M indistinct, not reaching basalis, its projection reaching basalis in upper half.

Metasoma longer than head+mesosoma, slightly longer than high in lateral view; 2nd metasomal tergum extending to 1/3 length of metasoma in dorsal view, with numerous white setae anterolaterally, without micropunctures; all subsequent terga without micropunctures. Hypopygium without micropunctures, prominent part of ventral spine of hypopygium 5.3× as long as broad in ventral view, with a few long white setae ventrally.

Body length 1.5–1.8 mm (n = 5).

**Gall** (Fig. 227). A small (up to 5mm diameter) monolocular spangle gall on the underside of leaves. Initially a disc-shaped gall lying flat against the leaf surface, pink in middle and around the edge with cream circle in between. When galls mature the opposite sides of the disc fold up and touch. Informally called the pink bowtie gall wasp in Russo (2006, 2021).

**Biology.** Only the asexual generation is known which induces spangle leaf galls on *Q. berberidifolia*, *Q. douglasii*, *Q. dumosa* (= *Q. durata*), *Q. garryana* (all section *Quercus*, subsection *Dumosae*). Galls mature in September-October. Adults emerge soon afterwards.

**Distribution.** USA: CA (authors).

***Feron kingi* (Bassett, 1900), comb. nov.**

**Figs 228–255**

*Andricus kingi* Bassett, 1900: 316, female (asex), gall.

*Andricus pistillaris* Trotter, 1910: 117, female (asex), gall; synonymized in Weld, 1951: 634.

**Type examined.** *Andricus kingi* Bassett: Type No. 10495, asexual female, deposited at the Entomology Type Collection at the Academy of Natural Sciences of Philadelphia, not examined by the authors.

**Additional material.** Asexual females: 10 females “USA, CA, Stockton, *Q. lobata*, leg. K. Schick, 2004.02.29”; 6 females “USA, CA, Dye Creek Preserve, *Q. lobata*, leg. J. de Martini, 2001.09.22.”; 28 females “USA, CA, Clearlake, CA29, galltype 160, *Q. lobata*, leg. J.A.



Nicholls, 2007.11.03.”; 46 females “USA, CA, Delta College, Stockton, CA905, CA906, galltype 160, *Q. lobata*, leg. J.A. Nicholls, 2007.11.06.”; 9 females “USA, CA, Cosumnes River Preserve, CA927, 906, galltype 160, *Q. lobata*, leg. J.A. Nicholls, 2007.11.07.” **Sexual generation**: 6 males “USA, CA, Dye Creek Preserve, CA1050, galltype 237, *Q. douglasii*, leg. J.A. Nicholls, 2008.03.30”; 2 females and 1 male “USA, CA, Quail Ridge Reserve, CA1069, galltype 237, *Q. berberidifolia*, leg. J.A. Nicholls, 2008.04.04”; 1 female and 3 males “USA, CA, Delta college, Stockton, CA1047, galltype 237, *Q. lobata*, leg. J.A. Nicholls, 2008.03.28”. 3 females and 10 males: 6 males “USA, CA, Dye Creek Preserve, *Q. douglasii*, coll. J.A. Nicholls, 2008.03.30; CA1050”, 2 females and 1 male “USA, CA, Quail Ridge Reserve, *Q. berberidifolia*, coll. J.A. Nicholls, 2008.04.04; CA1069”; 1 female and 1 male “USA, CA, Delta College, Stockton, *Q. lobata*, 2008.03.28; CA1047”; 2 males “USA, CA, Cosumnes River Preserve, *Q. lobata*, coll. J.A. Nicholls, 2008.03.28; CA1060”. Specimens have been deposited at the USNM and PHDNRL.

**Diagnosis.** Asexual females belong to the *Feron* species group in which the pronotum laterally has longitudinal carinae and the mesoscutum is alutaceous to coriaceous, rugose-reticulate, reticulate, with piliferous points; as in *F. discularis* (asex) and *F. tubifaciens* (asex). Differs from *F. discularis* in the body colour, which is never black; the frons not bulging in frontal view, ocelli are not elevated above the head; toruli located in the upper half of the head; the median mesoscutal line is absent. The most similar species is *F. tubifaciens* but differs in colour, the gena is broadened behind the eye in frontal view, the clypeus is smooth, the fore wing longer than the body; for other characters see couplet 29 in the key. Sexual females belong to the group of *Feron* species with a black body, scape to F2 are dark brown (sometimes light brown but never yellowish), legs are reddish brown with at least the hind coxa darker, the frons is flat not or only slightly bulging in frontal view; toruli are located in the upper half of the head, inner margins of eyes never strongly converging ventrally, the mesoscutum is smooth or partially alutaceous anteriorly and glabrous, the notaulus is complete, the mesopleuron entirely smooth without transverse striae in the central part, the mesoscutellum uniformly alutaceous with numerous setae on piliferous points and the prominent part of the ventral spine of the hypopygium with setae; as in *F. apiarium* (asex) and *F. pattersonae* (sex). Differs from *F. apiarium* as the eyes converge ventrally, the eye at least 4.0× as high as length of the malar space, antennomeres with short setae, OOL 1.5× as long as diameter of the lateral ocellus, the notaulus sometimes weakly impressed anteriorly and the prominent part of the ventral spine of the hypopygium with few short setae ventrally. Most similar morphologically is *F. pattersonae*; see diagnostic characters at couplet 17 in the key.

Males are characterised by a black body, ocelli are moderately or not elevated above the frons, the notaulus reaches the pronotum and the mesoscutellum is uniformly alutaceous with numerous setae on piliferous points; these characters are as in *F. comatum* and *F. pattersonae*, but in *F. kingi* F1 longer than scape+pedicel, straight, not broadened and curved; all flagellomeres, scape and pedicel are uniformly coloured (F1 equal in length to scape+pedicel, slightly broadened and curved; all flagellomeres lighter than the scape and pedicel in *F. comatum*) and the head is ovate in frontal view, inner margins of eyes are parallel, space between central elevated area of the lower face to the lateral margin of the eye is sculptured, OOL shorter than the diameter of the lateral ocellus (triangular head, inner margins of eyes converging ventrally, central elevated area smooth and OOL as long as diameter of the lateral ocellus in *F. pattersonae*).

**Re-description.** Asexual female (Figs 228–238). Body, antenna, legs, uniformly rusty brown, some specimens uniformly dark brown.

Head with white setae, denser on lower face, occiput, postocciput and postgena, slightly broader than high and as broad as mesosoma in frontal view; 1.9× as broad as long in dorsal view. Gena alutaceous, broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space with striae radiating from clypeus and reaching eye; eye 2.9× as high as length of malar space; malar sulcus absent. Inner margins of eyes parallel. POL 2.2× as long as OOL, OOL 1.6× as long as diameter of lateral ocellus and slightly shorter than LOL, all ocelli ovate, lateral ocelli slightly larger than central ocellus. Transfacial distance slightly longer than height of eye; toruli located in the upper half of head and frons definitely shorter than lower face, diameter of antennal torulus 1.9× as long as distance between them, distance between torulus and eye nearly as long as diameter of torulus; lower face smooth with white setae; slightly elevated median area and area between toruli smooth. Clypeus ovate, slightly broader than high, smooth, with a few long setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit small, rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex, occiput uniformly reticulate, without striae and setae; area under central ocellus impressed, smooth, glabrous; postocciput and postgena reticulate, with a few setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into distinct postgenal sulci which strongly diverge toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than

head+mesosoma, with 12 flagellomeres; all flagellomeres with dense setae; pedicel 1.7× as long as broad; F1 2.0× as long as pedicel and 1.4× as long as F2; F2=F3; F4 to F6 equal in length, F7 to F11 equal in length, F12 slightly shorter than F11; placodeal sensilla on F4–F12.

Mesosoma slightly longer than high, with a few white setae. Propleura alutaceous with setae. Pronotum smooth, glabrous dorsally; laterally coriaceous, with dense setae; propleuron smooth, with dense white setae. Mesoscutum longer than broad (greatest width measured across mesoscutum level with base of tegulae), uniformly coriaceous; entirely and uniformly with scattered long white setae. Notaulus complete, shallow, posteriorly converging and broader than anteriorly, bottom smooth, glabrous; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line and parapsidal line indistinct or invisible; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum slightly longer than broad, with subparallel sides, broadest part in posterior 1/3; mesoscutellum rugose-coriaceous, overhanging metanotum, with dense long setae. Mesoscutellar foveae ovate, broader than high, with smooth, glabrous bottom, delimited all around by strong black carina. Mesopleuron entirely smooth, with setae only along ventral edge and some sparse setae along mid-height; mesopleural triangle smooth, with dense white setae; dorsal and lateral axillar areas smooth, glabrous, without setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with parallel sides, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus also distinct, sulcus separating smooth, glabrous area, with dense setae in lower part. Metascutellum rugose, higher than height of smooth, glabrous ventral impressed area; metanotal trough smooth, with dense setae; central propodeal area lyre-shaped, smooth, glabrous, with a few strong short irregular rugae; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral propodeal area smooth, with long white setae. Nucha with net of numerous irregular rugae. Tarsal claws with acute basal lobe.

Fore wing longer than body, hyaline, with short cilia on margin, veins brown, radial cell open, 4.4× as long as broad; Rs reaches wing margin, R1 nearly reaching wing margin; areolet absent. Rs+M indistinct, visible on 1/3 of distance between areolet and basalis, its projection reaching basalis at half of its height.

Metasoma longer than head+mesosoma, higher than long in lateral view; 2nd metasomal tergum extending to half-length of metasoma in dorsal view, with patch of dense white setae anterolaterally, with inconspicuous micropunctures extending to half-length of

tergum; all subsequent terga until tergum 5 and hypopygium without micropunctures; tergum 6 and 7 with micropunctures, prominent part of ventral spine of hypopygium 6.8× as long as broad in ventral view, with short white setae ventrally.

Body length 1.5–2.1 mm (n = 10).

The description of the sexual generation is given below for the first time.

Sexual female (Figs 241–244, 250–255). Head, mesosoma, metasoma dark brown, antenna slightly lighter; mouthparts, legs light brown with darker coxae.

Head alutaceous, with a few setae, denser on lower face, rounded, 1.2× as broad as high and slightly broader than mesosoma in frontal view; 2.2× as broad as long in dorsal view. Gena alutaceous, slightly broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, shining, glabrous, without sulcus and striae radiating from clypeus and reaching eye; eye 4.4× as high as length of malar space. Eyes slightly converging ventrally. POL 2.4× as long as OOL, OOL 1.5× as long as diameter of lateral ocellus and 0.8× as long as LOL, all ocelli slightly ovate, of same size. Transfacial distance as long as height of eye or slightly shorter; diameter of antennal torulus 1.4× as long as distance between them, distance between torulus and eye slightly shorter than diameter of torulus; lower face smooth, with dense white setae, without striae; slightly elevated median area delicately coriaceous, with few setae. Clypeus rectangular, nearly 2.0× as broad as high, smooth, with long setae; ventrally rounded, not emarginate and without median incision; anterior tentorial pit large, rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons uniformly alutaceous, without striae and setae; interocellar area alutaceous. Vertex, occiput and postocciput alutaceous; postgena alutaceous, without setae, with longitudinal delicate parallel striae along gular sulci; posterior tentorial pit large, elongated, area below impressed; occipital foramen slightly shorter than height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly broader than occipital foramen. Antenna longer than head+mesosoma, with 11 flagellomeres, pedicel longer than broad; F1 1.7× as long as pedicel and 1.2× as long as F2; F2 1.1× as long as F3; F3 slightly longer than F4, F5 1.1× as long as F6, subsequent flagellomeres nearly equal in length, F11 1.7× as long as F10; placodeal sensilla on F5–F11, absent on F1–F4.

Mesosoma 1.2× as long as high, with sparse white setae, except dense setae on lateral propodeal area. Pronotum smooth, with a few sparse setae, with some delicate striae laterally; propleuron alutaceous, glabrous. Mesoscutum smooth, with sparse white setae laterally and

along notaulus, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, deep, bottom smooth, posteriorly broader and strongly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line invisible; parapsidal line distinct, marked with broad slightly impressed line; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum ovate, slightly longer than broad; disk of mesoscutellum smooth, glabrous, dull rugose laterally and posteriorly, overhanging metanotum, with sparse long setae. Mesoscutellar foveae in the form of a narrow semi-lunar depression, not separated medially, with smooth, glabrous bottom. Mesopleuron entirely smooth, with setae in posteroventral part; mesopleural triangle smooth, glabrous, with some irregular striae and a few setae; dorsal and lateral axillar areas smooth, glabrous, with dense white setae; subaxillular bar smooth, glabrous, with parallel sides, as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus distinct, sulcus separating smooth, glabrous area, with a few setae in lower part. Metascutellum delicately coriaceous, 3.0× as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with some setae; central propodeal area lyre-shaped, smooth, glabrous, with net of irregular interrupted rugae; lateral propodeal carinae distinct, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae. Nucha with numerous sulci dorsally and laterally. Tarsal claws with very tiny basal lobe.

Fore wing longer than body, hyaline, with distinct dense cilia on margin, veins light brown, radial cell open, 4.6× as long as broad; R1 and Rs reaching wing margin; areolet small, triangular, closed, indistinct. Rs+M narrow, inconspicuous, its projection reaching basalis slightly below its mid height.

Metasoma as long as head+mesosoma, slightly longer than high in lateral view; 2nd metasomal tergum extending to half-length of metasoma in dorsal view, with a few short white setae and without micropunctures laterally; subsequent terga smooth, glabrous, without micropunctures. Hypopygium without micropunctures, prominent part of ventral spine of hypopygium 2.0× as long as broad in ventral view, with some short setae ventrally which do not extend beyond apex of spine.

Body length 2.0–2.2 mm (n = 5).

Male (Figs 245–249). Similar to female, body slightly darker; eye 4.8× as high as length of malar space; POL 3.6× as long as OOL, OOL 0.6× as long as LOL, diameter of lateral ocellus

1.4× as long as OOL, ocelli ovate, larger than in female; interocellar area elevated in frontal view; antenna longer than body, with 13 flagellomeres, F1 straight, not broadened and curved, F1 1.3× as long as F2, F2=F3, all subsequent flagellomeres nearly equal in length, F13=F12; placodeal sensilla on all flagellomeres.

Body length 1.7–1.9 mm (n = 5).

**Galls.** The sexual gall (Fig. 239) is small, 2–3 mm, conical gall on the leaf margin and/or catkin, slightly pubescent. Fresh galls are pinkish to pale brown, turn dark purple-black when mature, the leaf blade twists slightly at the gall. The gall is difficult to distinguish from similar sexual galls of *F. comatum*, *F. crystallinum* and *F. dumosae*. The asexual gall (Fig. 240) is red, monolocular, detachable, cone-shaped on both sides of the leaves, 5 mm high and 3–5 mm broad at the base. The cone rises from a flared, cup-shaped base, which is narrowly attached to the leaf. The apex of the gall is pointed, with a blunt tip. The gall is covered by fine pubescence; the larval chamber is large, occupying the most of the gall base. Occurs singly or in groups, up to dozens (Russo 2006, 2021).

**Biology.** *Liodora dumosae* was erroneously named as the sexual generation of *A. kingi* (Rosenthal 1968; Rosenthal & Koehler 1971, Burks 1979), but subsequent detailed examination of the type material showed that *L. dumosae* is a distinct species and Rosenthal's material represented the previously unknown and undescribed sexual generation of *A. kingi* (Dailey & Menke 1980; our examinations); herein we formally describe sexual *A. kingi* for the first time. Alternate sexual and asexual generations are also confirmed herein on the basis of similarity in cytb sequence data. Four individuals (two asexual females, one sexual female, one sexual male) had cytb sequences that were on average 0.23% divergent (range 0–0.47%; GenBank accessions OK041496, OQ446201–OQ446203).

Asexual galls have been collected from *Q. douglasii*, *Q. dumosa*, *Q. garryana*, and *Q. lobata* (section *Quercus*, subsection *Dumosae*) in late September and October; adults emerge early the following spring (Burks 1979). Mature sexual galls have been collected in late March and the beginning of April from *Q. berberidifolia*, *Q. douglasii*, and *Q. lobata* (section *Quercus*, subsection *Dumosae*); adults emerge soon after under laboratory conditions.

**Distribution.** USA: California.

***Feron parmula* (Bassett, 1900), comb. nov.**

**Figs 256–268**

*Andricus parmula* Bassett, 1900: 312, female, gall.

*Dryophanta discus* Bassett, 1900: 326, female, gall. Synonym in Weld (1951: 635)

**Type material.** *Andricus parmula* Bassett: Type No 10500, asexual female, deposited at the Entomology Type Collection at the Academy of Natural Sciences of Philadelphia, not examined by the authors.

**Additional material.** 25 asexual females, all from California: 2 females “USA, California, Hastings Reserve, *Q. lobata*, leg. Challis, 2004.10.23.”; 10 females “USA, California, Clearlake, *Q. lobata*, CA8, galltype 159; leg. J.A. Nicholls, 2007.11.03.”; 2 females “USA, California, Copperopolis, *Q. douglasii*, CA907, galltype 159; leg. J.A. Nicholls, 2007.11.06.”; 11 females “USA, California, Cosumnes River Preserve, *Q. lobata*, CA990, galltype 159; leg. J.A. Nicholls, 2007.11.07.”

**Diagnosis.** Asexual females belong to the group of *Feron* species in which the body is never black; the head is rounded or trapezoid to triangular in frontal view, ocelli are not elevated above the frons; inner margins of eyes are parallel or very slightly converging ventrally, the transfacial distance is equal to or longer than the height of eye; toruli are located above mid-height of eyes; the eye is less than 3.0× as high as length of the malar space; lateral ocelli smaller, OOL at least 2.5× as long as the diameter of ocellus, if shorter then the head and mesosoma are not yellowish or light brown; the pronotum laterally with longitudinal carinae; the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points and the mesopleuron with transverse reticulate-carinate band at mid-height; as in *F. gigas* (asex), *F. tibiale* (asex), *F. stellulum* (asex), and *F. syndicorum* (asex). Differs from *F. tibiale* and *F. syndicorum* in the gena which is not broadened behind the eye in frontal view, 2nd metasomal tergum with a band of micropunctures posteriorly and all subsequent terga with micropunctures. Differs from *F. gigas* and *F. stellulum* in that the malar space is without striae, mesoscutellar foveae absent or slightly impressed and the prominent part of the ventral spine of the hypopygium 7.0× as long as broad in ventral view; see more characters at couplet 37 in the key.

**Re-description.** Asexual female (Figs 256–267). Head, antenna, mesosoma, legs, metasoma uniformly light brown. Veins pale.

Head alutaceous-reticulate, with sparse setae on lower face, postgena, slightly higher than broad and as broad as mesosoma in frontal view; 2.0× as broad as long in dorsal view. Gena alutaceous-reticulate, not broadened behind eye in frontal view; gena in lateral view 2.0× narrower than transverse diameter of eye. Malar space delicately coriaceous, without striae, malar sulcus absent; eye 2.1× as high as length of malar space. Inner margins of eyes slightly converging ventrally. POL 2.3× as long as OOL, OOL 2.1× as long as diameter of

lateral ocellus and slightly shorter than LOL, all ocelli ovate, of same size. Antennal toruli located above mid-height of eyes. Transfacial distance 1.4× as long as height of eye; toruli located above mid height of head, frons shorter than height of lower face, diameter of antennal torulus 1.5× as long as distance between them, distance between torulus and eye 1.5× as long as diameter of torulus; lower face delicately coriaceous, without setae; slightly elevated median area and area between toruli delicately coriaceous, with a few setae. Clypeus impressed, flat, rectangular, broader than high, smooth, with few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, small; epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex and occiput uniformly alutaceous-reticulate, without striae and setae; postocciput and postgena glabrous, with very delicate, indistinct concentric lines around and laterad to occipital foramen and postgenal bridge; posterior tentorial pit large, elongated, area below impressed; occipital foramen shorter than height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna slightly shorter than body, with 12 flagellomeres, pedicel subglobose, slightly longer than broad; flagellomeres subsequently broadening towards apical end; F1 1.4× as long as F2 and 1.8× as long as pedicel; F2=F3=F4, F5=F6, F7 to F11 equal in length; F12 slightly longer than F11; placodeal sensilla on F4–F12.

Mesosoma nearly as long as high, without setae. Pronotum delicately coriaceous, with delicate striae, glabrous laterally; propleuron smooth, with sparse short setae. Mesoscutum uniformly reticulate, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, indistinct in anterior 1/4 of mesoscutum length, distinctly impressed along remainder of mesoscutum; posteriorly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line indistinct, impressed narrow stripes extending to 1/3 of mesoscutum length; parapsidal line marked with indistinct, narrow smooth, impressed area; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum elongated, longer than broad, broadest part in posterior 1/4 of its length; disk of mesoscutellum rugose, dull rugose laterally and posteriorly, overhanging metanotum, with sparse setae. Mesoscutellar foveae absent, slightly impressed anterior part delicately coriaceous like rest of disk, without central carina. Mesopleuron indistinctly delicately coriaceous, with stronger coriaceous sculpture in central transverse band extending across



mesopleuron at mid height; speculum and ventral half of mesopleuron smooth, glabrous, without transverse longitudinal striae; mesopleural triangle smooth, with a few white setae; dorsal and lateral axillar areas smooth, with a few white setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with subparallel sides, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height; upper part of sulcus indistinct; lower part of sulcus delimiting smooth area with dense long white setae. Metascutellum smooth, glabrous, shorter than height of smooth, glabrous ventral impressed area; metanotal trough smooth, glabrous, without setae; central propodeal area lyre-shaped, smooth, glabrous, without rugae; lateral propodeal carinae distinct, bent outwards in posterior 1/3 of its height; lateral propodeal area smooth, with long dense white setae. Nucha with numerous sulci laterally, smooth glabrous dorsally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with long dense cilia on margin, veins light brown, radial cell open, 4.2× as long as broad; Rs and R1 nearly reaching wing margin; areolet indistinct, hardly traceable or not. Rs+M indistinct, its projection reaching basalis below half of its height.

Metasoma longer than head+mesosoma, slightly longer than high in lateral view; 2nd metasomal tergum extending to 2/3 length of metasoma in dorsal view, with numerous white setae anterolaterally, with band of micropunctures posteriorly; all subsequent terga with micropunctures. Hypopygium without micropunctures, prominent part of ventral spine of hypopygium 7.0× as long as broad in ventral view, with few setae ventrally.

Body length 1.5–1.7 mm (n = 10).

**Gall** (Fig. 268). Minute, flat, sessile, saucer shaped, red spangle gall, on the underside of the leaves, 2.0 mm in diameter, with a slight elevation in the center, where the small larval cell is located (Russo 2006, 2021).

**Biology.** Only the asexual generation is known, which induces galls on *Q. douglasii*, *Q. dumosa*, *Q. garryana*, *Q. lobata* (section *Quercus*, subsection *Dumosae*), and *Q. engelmannii* (section *Quercus*, subsection *Leucomexicana*) (Burks 1979). Galls mature in April, adults emerge after soon (Russo 2006, 2021).

**Distribution.** USA: California (Burks 1979).

***Feron pattersonae* (Fullaway, 1911), comb. nov.**

**Figs 269–299**

*Andricus pattersonae* Fullaway, 1911: 352, female (asex), gall; Burks, 1978: 1087.

*Liodora pattersonae* (Fullaway): Evans 1972: 1813.

Sexual generation:

*Andricus pedicellatus* Kinsey, 1922: 284–285, male, female, gall; Melika & Abrahamson, 2002: 162, **syn. nov.**

*Dros pedicellatum* (Kinsey): Weld, 1951: 629.

**Types examined:** *Andricus pattersonae*: SYNTYPES: No. 5822 is deposited at the California Academy of Sciences Collection, was not examined by the authors. A cotype asexual female “L.S.Jr.U. Lot508 Sub52”, handwriting label “Stanford Univ., Calif.”, handwriting label “*Andricus pattersonae* Full.” “Beut. Coll. rec’d 1935”, red label “USNM cotype N52974”, a Weld handwriting label “*Andricus pattersonae* Full.” was examined by GM. *Andricus pedicellatus*: HOLOTYPE: Sexual female “Three Rivers Cal., Gall 3.23.20.”, “Q. Douglasii, Kinsey coll.”, red label “*Neuroterus pedicellatus*, Holo-COTYPE”, deposited in, NYC, examined by GM. Four sexual female paratypes, two males and many galls in the general collection of AMNH were also examined by GM.

**Additional material.** *Andricus pattersonae*, 12 asexual females: 3 females as “USA, California, 30km SW of Williams, ex *Quercus douglasii*, CA16, coll. 2007.11.02. leg. J. A. Nicholls” and 9 females as “USA, California, Dye Creek Preserve, ex *Quercus douglasii*, CA1177, coll. 2001.09.27 leg. J. A. Nicholls”. *Dros pedicellatum*: 3 sexual females labelled as “USA, California, Quail Ridge Reserve, ex *Quercus douglasii*, CA1038, coll. 2008.04.04. leg. J.A. Nicholls”.

**Diagnosis.** Asexual females belong to the group of *Feron* species in which the pronotum is without carinae, with dense setae and piliferous points; the mesoscutum is dark brown between notauli in anterior 1/3 of mesoscutum length; as in *F. crystallinum* (asex) and *F. sulfureum* (asex). *Feron pattersonae* differs from these species in the ovate head in frontal view; the pronotum is smooth, with dense setae and piliferous points; mesoscutellar foveae are fused; second metasomal tergum extending to 1/3 length of the metasoma in dorsal view. Sexual females belong to the group of *Feron* species with black body, scape to F2 are dark brown (sometimes light brown but never yellowish), legs are reddish brown with at least the hind coxa darker; the frons is flat, not or only slightly bulging in frontal view; toruli are located in the upper half of the head, inner margins of eyes are never strongly converging ventrally; the mesoscutum is smooth or partially alutaceous anteriorly and glabrous, the notaulus complete; the mesopleuron is entirely smooth without transverse striae in its central part; the mesoscutellum is uniformly alutaceous with numerous setae on piliferous points and the prominent part of the ventral spine of the hypopygium with setae; as in *F. apiarium* (asex)

and *F. kingi* (sex). Differs from *F. apiarium* in the eyes converging ventrally, the eye is at least 4.0x as high as length of the malar space, antennomeres with short setae, OOL 1.5x as long as diameter of the lateral ocellus, the notaulus sometimes weakly impressed anteriorly and the prominent part of the ventral spine of the hypopygium with few short setae ventrally. Most closely resembles *F. kingi* but differs in the number of flagellomeres (12 in *F. pattersonae*, 11 in *F. kingi*) and in other characters mentioned at couplet 17 in the key. Males are characterised by a black body, ocelli are only moderately or not elevated above the frons, the notaulus reaching the pronotum and the mesoscutellum is uniformly alutaceous with numerous setae on piliferous points; as in *F. comatum* and *F. kingi*. In *F. pattersonae* F1 longer than scape+pedicel, straight, not broadened and curved; flagellomeres, scape and pedicel are uniformly coloured (F1 is equal in length to scape+pedicel, slightly broadened and curved, flagellomeres lighter than scape and pedicel in *F. comatum*); the head is triangular in frontal view, inner margins of eyes converging ventrally, space between central elevated area of lower face to lateral margin of eye is smooth, OOL as long as diameter of the lateral ocellus (in *F. kingi* the head is ovate, inner margins of eyes are parallel, central elevated area of the lower face is sculptured, OOL shorter than the diameter of the lateral ocellus).

**Re-description.** Asexual female (Figs 269–280). Entire body, antenna, legs are uniformly reddish brown, with dark brown to black metascutellum and central propodeal area. In some specimens internotalar area in anterior half, posteroventral part of mesopleuron black; last flagellomeres darker than rest of antenna.

Head with a few long setae, denser on lower face, alutaceous below toruli, transverse, 1.2x as broad as high and slightly broader than mesosoma in frontal view; 1.8x as broad as long from dorsal view. Gena alutaceous, broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, glabrous, with numerous delicate parallel striae radiating from clypeus and reaching eye; malar sulcus absent; eye 2.3x as high as length of malar space. Eyes converging slightly ventrally. POL 2.1x as long as OOL, OOL 1.9x as long as diameter of lateral ocellus and slightly shorter than LOL, all ocelli slightly ovate, of same size. Transfacial distance 1.25x as long as height of eye; diameter of antennal torulus 1.7x as long as distance between them, distance between torulus and eye as long as diameter of torulus; lower face smooth, with dense white setae, without striae; slightly elevated median area alutaceous with a few setae. Clypeus impressed, trapezoid, smooth, with long setae; ventrally rounded, not emarginate and without median incision; anterior tentorial pit large, rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well

impressed. Frons uniformly reticulate, without striae and setae, interocellar area alutaceous. Vertex, occiput reticulate, without setae; postgena alutaceous with dense setae; postocciput alutaceous with delicate, longitudinal parallel striae and dense white setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen higher than height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which strongly diverge toward occipital foramen, postgenal bridge anteriorly broader than occipital foramen. Antenna longer than head+mesosoma, with 13 flagellomeres, pedicel 1.6x as long as broad; F1 2.6x as long as pedicel and 1.3x as long as F2; F2=F3, F4=F5, F5 1.3x as long as F6, all subsequent flagellomeres nearly equal in length; F13 slightly longer than F12; placodeal sensilla on F5–F11, absent on F1–F4.

Mesosoma slightly longer than high, with dense white setae, except bare central propodeal area. Pronotum smooth without striae laterally, with dense setae and piliferous points; propleuron alutaceous, glabrous. Mesoscutum with dense white setae, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae), alutaceous alongside notaulus, in between notauli rugose-reticulate in anterior 1/3 and smooth shining in posterior 2/3. Notaulus deep, with smooth bottom, incomplete, indistinct in anterior 1/5 of mesoscutum length; anterior parallel lines in the form of a narrow elevated smooth, glabrous stripes, extending to 1/3 of mesoscutum length; parapsidal line distinct, marked with broad slightly impressed line; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum ovate, longer than broad; overhanging metanotum, with dense long setae; disk of mesoscutellum delicately coriaceous, laterally dull rugose. Mesoscutellar foveae in the form of a semi-lunar depression, with smooth, glabrous bottom, without median carina separating them. Mesopleuron entirely smooth, with dense setae anteroventrally and ventrally; mesopleural triangle smooth, with dense setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangular, gradually higher towards the most posterior end, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus indistinct, lower part of sulcus separating smooth, glabrous area, with a few setae in lower part. Metascutellum rugose, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with some setae; central propodeal area lyre-shaped, smooth, glabrous, with net of irregular interrupted rugae in posterior 1/3; lateral propodeal carinae strong, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae. Nucha with strong sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with distinct dense cilia on margin, veins brown, distinct, radial cell open, 4.8× as long as broad; R1 and Rs nearly reaching wing margin; areolet small, triangular, closed, indistinct. Rs+M narrow, distinct, extending to 2/3 of length from areolet to basalis; its projection reaching basalis slightly below its mid height.

Metasoma as long as head+mesosoma, slightly longer than high in lateral view; 2nd metasomal tergum extending to 1/3 length of metasoma in dorsal view, with numerous white setae anteroventrally and without micropunctures; subsequent terga smooth, glabrous, with micropunctures. Hypopygium with micropunctures, prominent part of ventral spine of hypopygium 4.7× as long as broad in ventral view, with two rows of short setae ventrally which do not extend beyond apex of spine.

Body length 2.0–2.2 mm (n = 5).

Sexual female (Figs 284–287, 293–299). Head, antenna, mesosoma, metasoma dark brown to black, legs yellowish with darker mid and hind coxae. Fore wings hyaline, veins brown.

Head alutaceous, with a few setae, denser on lower face, rounded, very slightly higher than broad and broader than mesosoma in frontal view; 1.9× as broad as long from dorsal view. Gena alutaceous, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, glabrous, without striae; eye 5.0× as high as length of malar space. Eyes strongly converging ventrally. POL 2.4× as long as OOL, OOL 1.7× as long as diameter of lateral ocellus and slightly shorter than LOL, all ocelli slightly ovate, of same size. Transfacial distance shorter than height of eye; diameter of antennal torulus 1.7× as long as distance between them, distance between torulus and eye slightly shorter than diameter of torulus; lower face and slightly elevated median area alutaceous, with dense white setae, without striae. Clypeus rounded, smooth, with a few setae; ventrally rounded, emarginate, without median incision; anterior tentorial pit large, rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons uniformly delicately coriaceous to reticulate, without striae and setae, interocellar area alutaceous. Vertex, occiput and postocciput alutaceous; postgena smooth, with setae and piliferous points; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly broader than occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres, all flagellomeres with dense long setae, not broadened distally; pedicel slightly longer than broad; F1 3.0× as long as pedicel and 1.2× as long as F2; F2 1.3× as long as F3; F3=F4,

F5=F6, subsequent flagellomeres nearly equal in length; F12 1.2× as long as F11; placodeal sensilla on F3–F12.

Mesosoma as long as high, with sparse white setae along notauli, laterally on pronotum, mesoscutum and mesoscutellum; denser setae on dorsal and lateral axillar areas and lateral propodeal area. Pronotum alutaceous to smooth, with sparse setae, with very delicate parallel striae in lateroposterior part; propleuron alutaceous, glabrous. Mesoscutum alutaceous, glabrous in anterior half, smooth and glabrous in posterior half, with sparse white setae, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus narrow, complete, only slightly impressed anteriorly, bottom smooth, slightly converging posteriorly; anterior parallel line invisible; parapsidal line distinct, marked with broad slightly impressed line; median mesoscutal line absent or sometimes in the form of a short triangle; parascutal carina broad, reaching notaulus. Mesoscutellum slightly longer than broad; disk of mesoscutellum smooth, glabrous, sparsely pubescent laterally, with rugae laterally and posteriorly, overhanging metanotum, with sparse long setae. Mesoscutellar foveae in the form of a narrow semi-lunar depression, with smooth, glabrous bottom. Mesopleuron entirely smooth, glabrous, with a few setae in anteroventral part; mesopleural triangle smooth, with some irregular striae and a few setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangulate, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron in the lower half of its height, upper part of sulcus indistinct, lower part of sulcus delimiting smooth, glabrous area, with setae and which is as broad as high. Metascutellum coriaceous, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with dense white setae; central propodeal area lyre-shaped, smooth, glabrous, with irregular interrupted rugae basally; lateral propodeal carinae strong, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae. Nucha with few sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with distinct dense cilia on margin, veins brown, radial cell open, 5.2× as long as broad; R1 and Rs reaching wing margin; areolet triangular, closed, distinct. Rs+M narrow, distinct, reaching basalis at its mid height.

Metasoma as long as head+mesosoma, as long as high in lateral view; 2nd metasomal tergum extending to more than half-length of metasoma in dorsal view, with white setae and without micropunctures laterally; subsequent terga smooth, glabrous, without micropunctures. Hypopygium without micropunctures, prominent part of ventral spine of hypopygium 2.0× as

long as broad in ventral view, with some short setae ventrally which do not extend beyond apex of spine.

Body length 2.8–2.9 mm (n = 2).

**Male** (Figs 288–292). Similar to female, legs slightly darker; head triangular in frontal view; eye 4.5× as high as length of malar space; head posteriorly uniformly and entirely alutaceous; POL 2.7× as long as OOL, OOL as long as diameter of lateral ocellus and slightly shorter than LOL, ocelli ovate, larger than in female; interocellar area elevated in frontal view; antenna longer than body, pedicel as long as broad, with 13 flagellomeres, F1 straight, not swollen and curved, longer than scape+pedicel, F1 1.3× as long as F2, F2=F3=F4, all subsequent flagellomeres nearly equal in length, F13 slightly shorter than F12; placodeal sensilla on all flagellomeres. Body length 2.7 mm (n = 1).

**Gall.** Asexual gall (Figs 281–282) Relatively large, thin, flat spangle gall on underside of leaves, detachable, monolocular. about 9 mm in diameter, with irregular wavy margin. Green when young, becoming yellow or tan when mature. Sexual gall (Fig. 283) is a small, elongate capsule, 5–7 mm long, 1.0–1.5 mm wide, attached by a slender pedicel to the edge of the leaf, unilocular. The gall is sharp-tipped, broadest near the tip, continuing into a slender, thread-like stem, 5–12 mm long, evidently a continuation of a leaf vein. The gall is thin-walled, entirely hollow.

**Biology.** *Andricus pattersonae* and *Liodora dumosae* were erroneously paired by Evans (1972; restated by Dailey & Menke 1980). Evans (1972) appears to have mis-identified the asexual gall he found as *A. pattersonae*; his Figure 15 shows a gall much more similar to the new species *F. rucklei* described herein. Molecular data also refute Evans' pairing, instead establishing the correct matching of *A. pattersonae* with *A. pedicellatus*, with the associated synonymisation herein. Four individuals (two asexual females [= *A. pattersonae*], two sexual females [= *A. pedicellatus*]) were sequenced for cytb and ITS2. Cytb sequences were on average 1.14% divergent (range 0.23–1.90%; GenBank accessions OQ446204–OQ446206) and ITS2 sequences were on average 0.25% divergent (range 0–0.42%, including identical alleles in one asexual and one sexual individual; GenBank accessions OQ448243–OQ448246).

Asexual galls have been recorded from leaves on section *Quercus*, subsection *Dumosae* oaks: *Q. douglasii*, *Q. dumosa*, *Q. garryana*, and *Q. lobata* (Burks 1979), the gall matures by late autumn, adults emerge in late winter. Sexual galls occur on leaves of *Q. douglasii* (Burks 1979) and mature in April; adults emerge soon after.

**Distribution.** USA: California (Burks 1979).

***Feron roberti* Melika, Nicholls & Stone, sp. nov.**

**Figs 300–310**

**Type material.** HOLOTYPE: Asexual female “USA, AZ, Cypress picnic area, Santa Catalina Mtns, AZ226-232, spAZ14, galltype 80; ex *Q. rugosa*, 2007.10.28, leg. J.A. Nicholls”. PARATYPES (28 asexual female paratypes) labeled as the holotype. The female holotype and 10 female paratypes are deposited in the USNM, 18 female paratypes in the PHDNRL.

**Etymology.** Named after Robert Melika, son of G. Melika.

**Diagnosis.** Asexual females are members of the group of *Feron* species characterised by having a body which is never black; the head is rounded or trapezoid to triangular in frontal view, ocelli are not elevated above the frons; inner margins of eyes are parallel or very slightly converging ventrally, the transfacial distance is equal or longer than the height of eye; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as length of the malar space; lateral ocelli are smaller, OOL at least 2.5× as long as the diameter of the ocellus, if shorter, then the head and mesosoma are not yellowish or light brown; the pronotum laterally with longitudinal carinae; the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points and the mesopleuron is entirely smooth; as in *F. caepula* (asex), *F. rucklei* (asex), *F. serranoae* (asex), *F. stellare* (asex), *F. tecturnarum* (asex) and some *F. tibiale* (asex). Nevertheless, *F. roberti* differs from all these species in having a trapezoid head; the gena is not broadened behind the eye; the transfacial distance is equal to the height of the eye and the antenna has 11 flagellomeres (see more characters at couplet 39 in the key).

**Description.** Asexual female (Figs 300–309). Head, antennae, mesosoma, metasoma light brown to brown; mouthparts and legs lighter. Frons, interocellar area, postgena dark brown to black; mesosoma chestnut brown, without black patches on mesoscutum; metasoma dorsally dark brown to black.

Head trapezoid, broadest part above toruli, slightly higher than broad and slightly broader than mesosoma in frontal view, with sparse setae, denser on lower face; 2.2× broader than long in dorsal view. Gena alutaceous, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space with a few delicate striae radiating from clypeus and not reaching eye; eye 2.4× as high as length of malar space. Inner margins of eyes parallel. POL 2.1× as long as OOL, OOL slightly longer than diameter of



lateral ocellus and subequal to LOL, all ocelli ovate, of same size. Transfacial distance nearly equal to height of eye; toruli located above mid height of head, frons shorter than height of lower face, diameter of antennal torulus 1.6x as long as distance between them, distance between torulus and eye 1.1x as long as diameter of torulus; lower face smooth, with dense white setae; slightly elevated median area alutaceous, with few setae. Clypeus trapezoid, broader than high, almost smooth, with a few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons uniformly alutaceous-reticulate, without striae and setae, areas between toruli and between torulus and eye also reticulate; interocellar area coriaceous. Vertex and occiput alutaceous, with white long setae; postocciput and postgena glabrous, alutaceous-reticulate, with concentric lines around occipital foramen and postgenal bridge; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 11 flagellomeres, pedicel longer than broad; flagellomeres subsequently broadening towards apical end; F1=F2 and 2.0x as long as pedicel; F2 1.2x as long as F3; F3=F4, F5=F6, F7 to F10 equal in length; F11 slightly longer than F10; placodeal sensilla on F5–F11, absent on F1–F4.

Mesosoma longer than high, with a few white setae, setae denser along propleura and on lateral propodeal area. Pronotum smooth, with delicate parallel striae only in dorso-posterior quarter and with sparse setae laterally; propleuron smooth, glabrous, with delicate transverse parallel striae ventrally. Mesoscutum predominantly reticulate, smooth between notauli on anterior 1/3 and along parapsidal lines; white setae sparse in posterior half, much denser in anterior half of mesoscutum which is slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae); piliferous points absent. Notaulus deep, complete, posteriorly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line present, smooth; parapsidal line marked with broad smooth, impressed area; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum elongated, longer than broad, broadest part in posterior 1/4 of its length, circumscutellar carina present; disk of mesoscutellum reticulate, dull rugose laterally and posteriorly, overhanging metanotum, with sparse long setae. Mesoscutellar foveae in the form of a transverse semilunar impression, only slightly broader than high, with smooth, glabrous bottom, without central carina. Mesopleuron

smooth, glabrous, with transverse longitudinal parallel delicate striae only on the most ventral part; mesopleural triangle smooth, with dense, long white setae, hiding the surface sculpture; dorsal and lateral axillar areas smooth, with dense white setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with parallel sides, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron in lower 1/3 of its height; upper part of sulcus indistinct; lower part of sulcus delimiting smooth area with dense long white setae. Metascutellum smooth, glabrous, higher than height of smooth, glabrous ventral impressed area; metanotal trough smooth, with dense white setae; central propodeal area lyre-shaped, smooth, glabrous, without rugae; lateral propodeal carinae distinct, bent slightly outwards in posterior 1/3 of its height; lateral propodeal area smooth, with long dense white setae. Nucha with numerous sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with distinct dense cilia on margin, veins light brown, radial cell open, 4.8× as long as broad; Rs and R1 nearly reaching wing margin; areolet triangular, small, closed and distinct. Rs+M distinct, its projection reaching basalis at half of its height.

Metasoma as long as head+mesosoma, slightly longer than high in lateral view; 2nd metasomal tergum extending to 3/4 length of metasoma in dorsal view, with numerous white setae anterolaterally, smooth, without micropunctures; all subsequent terga and hypopygium smooth, without micropunctures. Prominent part of ventral spine of hypopygium 6.7× as long as broad in ventral view.

Body length 1.8–2.3 mm (n = 10).

**Gall** (Fig. 310). Pinkish leaf galls, turret-like with bristles all around, covered with more or less crystalline, fine, hair-like fibers, similar to *F. sulfureum*, *F. tibiale* and *F. tubifaciens*, however, in larger clusters (20+ galls) up to 20 mm wide and 25–30 mm long.

**Biology.** Only the asexual generation is known, which induces leaf galls on *Q. rugosa* (section *Quercus*, subsection *Leucomexicana*). Galls mature in the autumn dropping only with the leaf; adults emerge next year, in late March–April.

**Distribution.** USA, Arizona.

***Feron rucklei* Melika, Nicholls & Stone, sp. nov.**

**Figs 311–323**

**Type material:** HOLOTYPE. Asexual female “Canada, British Columbia, Ruckle Provincial Park, leg. J. Nicholls, 2007.11.12. Code BC352, spBC11; ex *Quercus garryana*”. PARATYPES (9 asexual females) with the same labels as the holotype, however, with

different collecting codes: BC349 – 1, BC350 – 2, BC352 – 1, BC354 – 1, BC355 – 1, BC356 – 3. The female holotype is deposited at the USNM, 9 female paratypes at the PHDNRL.

**Etymology.** The species is named after the site it was found, Ruckle Provincial Park.

**Diagnosis.** Asexual females belong to the group of *Feron* species in which the body is never black; the head is rounded in frontal view with a slightly elevated median area of lower face which is smooth and shining; the gena at least slightly broadened behind the eye; ocelli are not elevated above the frons; inner margins of eyes are parallel or very slightly converging ventrally; the transfacial distance is longer than height of the eye; the antenna with 12 flagellomeres, sometimes suture between F11 and F12 incomplete; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as length of the malar space; lateral ocelli are smaller, OOL at least 2.5× as long as the diameter of the ocellus, if shorter than the head and mesosoma are not yellowish or light brown; the pronotum laterally with longitudinal carinae; the mesoscutum is alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points; mesoscutellar foveae divided by a central carina; the mesopleuron is entirely smooth; as in *F. bakkeri* (asex), *F. caepula* (asex), *F. scutellum* (asex), and *F. stellare* (asex). Nevertheless, this species differs from *F. caepula* in the brown body colour sometimes with darker marks, and parallel eyes, while *F. caepula* is yellowish to light brown and has eyes converging strongly ventrally. Differs from *F. bakkeri* in having mesoscutellar foveae conspicuous and smooth, while they are inconspicuous and faintly rugose in *F. bakkeri*. Differs from *F. scutellum* in the coarsely rugose mesoscutellar disk, while in *F. scutellum* it is faintly reticulated and with a median elevated area. The most similar species is *F. stellare* but differs from it in having dark flagellomeres, the notaulus is complete and the third and subsequent metasomal terga with sparse micropunctures (more characters at couplet 47 in the key).

**Description.** Asexual female (Figs 311–321). Head and antennae dark brown, maxillary and labial palpi light brown; mesosoma and metasoma reddish brown; legs light brown.

Head with sparse white setae, denser on lower face and clypeus, 1.2× as broad as high and slightly broader than mesosoma in frontal view, 1.9× as broad as long from dorsal view. Gena alutaceous, very slightly broadened behind eye in frontal view, as broad as transverse diameter of eye in lateral view. Malar space alutaceous, glabrous, without striae; eye 2.4× as high as length of malar space. Inner margins of eyes slightly converging ventrally. POL 2.3× as long as OOL; OOL 1.8× as long as diameter of lateral ocellus and slightly shorter than LOL; all ocelli slightly ovate, of same size. Transfacial distance slightly longer than height of

eye; diameter of antennal torulus 1.6× as long as distance between them, distance between torulus and eye 1.3× as long as diameter of torulus; lower face smooth, with dense white setae, without striae; slightly elevated median area smooth, glabrous, without setae. Clypeus smooth, glabrous, quadrangular, only slightly broader than high; ventrally rounded, not emarginate, without median incision and with dense long setae; anterior tentorial pit large, rounded, epistomal sulcus and clypeo-pleurostomal line broad, well impressed. Frons and interocellar area delicately coriaceous to reticulate, without striae, with a few short setae. Vertex, occiput delicately coriaceous to reticulate, with sparse white setae; postgena and postocciput smooth, with dense long setae; posterior tentorial pit large, ovate, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which bend outwards; postgenal bridge anteriorly as broad as width of occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres, with dense long white setae; pedicel 1.65× as long as broad, flagellomeres broadening towards apex; F1 longer than scape+pedicel, F1 2.0× as long as pedicel and slightly longer than F2; F2 1.2× as long as F3; F3=F4, subsequent flagellomeres shorter, nearly equal in length, F12 slightly longer than F11; placodeal sensilla on F4–F12.

Mesosoma slightly longer than high, with sparse short white setae. Pronotum smooth, glabrous, with delicate parallel rugae posterolaterally, with dense setae along anterior rim; propleuron smooth, glabrous. Mesoscutum alutaceous, with a few white setae along notaulus and denser setae anteriorly, between notauli; slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, deep, with smooth, glabrous bottom; posteriorly strongly converging, distance between notauli shorter than distance between notaulus and lateral side of mesoscutum; anterior parallel and parapsidal lines distinct, marked with smooth lines; median mesoscutal line absent; parascutal carina narrow, smooth, reaching notaulus. Mesoscutellum longer than broad, trapezoid, uniformly rugose, broader in posterior 1/3, posteriorly slightly rounded, overhanging metanotum. Mesoscutellar foveae separated by triangular elevated coriaceous central carina, nearly rounded to slightly ovate, with smooth, glabrous bottom. Mesopleuron and speculum uniformly smooth, with a few setae ventrally; mesopleural triangle alutaceous, glabrous, with a few setae; dorsal and lateral axillar areas smooth, with a few white short setae; subaxillary bar smooth, glabrous, with subparallel sides, posteriorly shorter than height of metanotal trough; metapleural sulcus reaching mesopleuron at mid height, upper part of sulcus indistinct. Metascutellum coriaceous, as high as height of smooth, glabrous ventral impressed

area; metanotal trough smooth, with dense setae; central propodeal area smooth, glabrous, broad, lyre-shaped, without rugae; lateral propodeal carina bent strongly outwards at mid height; lateral propodeal area smooth, with long dense white setae. Nucha smooth, glabrous with numerous sulci dorsally and laterally. Tarsal claws toothed, with basal lobe.

Fore wing 1.5× as long as body, hyaline, margin with long dense cilia, veins pale yellow, radial cell open, 3.9× as long as broad; R1 and Rs nearly reaching wing margin; areolet triangular, indistinct, Rs+M inconspicuous, traceable along 1/3 of its length, its projection reaching basalis in lower half of its height.

Metasoma as long as head+mesosoma, higher than long in lateral view; 2nd metasomal tergum extending nearly to 2/3 of metasoma length in dorsal view, with numerous white setae anterolaterally, without micropunctures; subsequent terga with micropunctures, glabrous. Hypopygium with micropunctures, prominent part of ventral spine of hypopygium 5.6× as long as broad in ventral view, with short setae ventrally which do not extend beyond apex of spine.

Body length 2.0–2.3 mm (n = 8).

**Gall.** (Figs 322–323). Small spangle leaf gall, 5 mm across, somewhat star-shaped, flat against the leaf surface but with a central bump. Pale yellow with a darker centre when growing, becoming tan when mature. Typically multiple galls scattered across a single leaf. The same gall is depicted and described as an unknown species in Russo (2006, 2021; informally called the disk gall wasp) and Weld (1957, Fig. 174).

**Biology.** Only the asexual generation is known, which induces spangle leaf galls on *Q. garryana* (section *Quercus*, subsection *Dumosae*). Galls mature in November; adults emerge soon after under laboratory conditions.

This gall appears to be depicted in Evans (1972) in his Figure 15; those galls were also collected from *Q. garryana* in the same area (southern Vancouver Island). Evans experimentally matched these asexual galls with the sexual generation of *Liodora dumosae*, but mistakenly called them *A. pattersonae* (which has been matched to a different sexual form, *A. pedicellatus*, using DNA evidence elsewhere in this study). Hence we hypothesise that *F. rucklei* may be the alternate asexual form of *F. dumosae*, but further DNA evidence is required to test this suggestion.

**Distribution.** Canada, British Columbia, Ruckle Provincial Park. It is the first record of this genus for Canada.

***Feron scutellum* (Weld, 1930), comb. nov.**

**Figs 324–328**

*Andricus scutella* Weld, 1930: 29, female, gall.

**Type material.** HOLOTYPE. Asexual female “Camp Creek, Arizona”, “N.M. Capron Coll.”, “*Andricus scutella* Weld”, “cut out December”, red label “Type No. 42885 USNM”. PARATYPES (9 asexual females) labelled as the holotype, deposited in the collection of USNM. The female holotype and six paratypes are in the collection of the USNM, examined by VC-P. The type was examined based on photos taken by M. Buffington, USNM. Specimen data and images available at <http://n2t.net/ark:/65665/34db243c6-9449-4191-b59f-2cd26d2e18ab>

**Diagnosis.** Asexual females belong to the group of *Feron* species in which the body is reddish brown; the head is rounded in frontal view, ocelli are not elevated above the frons; inner margins of eyes slightly converging ventrally, the transfacial distance is longer than the height of eye; toruli are located above mid-height of eyes; the eye is less than 2.6× as high as length of the malar space; as in *F. bakkeri* (asex), *F. rucklei* (asex), and *F. stellare* (asex). Differs from *F. bakkeri* in having the mesoscutellar foveae distinct, but not defined posteriorly, with smooth bottom, and central part of mesoscutellar disk elevated and faintly reticulate, while the foveae are inconspicuous and faintly rugose and the mesoscutellar disk completely rugose in *F. bakkeri*. It differs from *F. stellare* and *F. rucklei* in having the disk of mesoscutellum faintly reticulated with the central part elevated, while it is coarsely rugose and not elevated in *F. stellare* and *F. rucklei*.

The gall resembles those of *Phylloteras cupella* (Weld, 1926), but lacks the in-rolled top margin and has a removable whitish bloom.

**Re-description.** Asexual female (Figs 324–327). Head, antenna, mesosoma, legs, metasoma uniformly reddish brown; base of metasoma and mesoscutellum lighter.

Head alutaceous-reticulate, with dense setae on lower face, slightly higher than broad and as broad as mesosoma in frontal view; 2.0× as broad as long in dorsal view. Gena alutaceous-reticulate, not broadened behind eye in frontal view; gena in lateral view 2.0× narrower than transverse diameter of eye. Malar space delicately coriaceous, without striae, malar sulcus absent; eye 2.1× as high as length of malar space. Inner margins of eyes converging ventrally. POL 1.9× as long as OOL, OOL 2.1× as long as diameter of lateral ocellus and slightly shorter than LOL, all ocelli ovate, of same size. Antennal toruli located at mid-height of eyes. Transfacial distance 1.4× as long as height of eye; frons shorter than

height of lower face, diameter of antennal torulus 3.0× as long as distance between them, distance between torulus and eye 1.5× as long as diameter of torulus; lower face smooth, with scattered setae; slightly elevated median area and area between toruli smooth with piliferous points, with a few setae. Clypeus impressed, flat, rectangular, broader than high, smooth, with a few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, small; epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex and occiput uniformly alutaceous-reticulate, without striae and setae. Antenna slightly shorter than body, with 11 flagellomeres, pedicel slightly longer than broad; F1 1.2× as long as F2 and above 2.0× as long as pedicel; F2 longer than F3, F4 slightly longer than F5, all subsequent flagellomeres nearly equal in length; placodeal sensilla on F3–F11.

Mesosoma nearly as long as high, without setae. Pronotum glabrous, with delicate short parallel striae along posterior edge, with piliferous points. Mesoscutum uniformly reticulate, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, distinctly impressed along entire length; posteriorly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line indistinct; parapsidal line marked with indistinct, narrow smooth, impressed area; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum slightly longer than broad, with subparallel sides; disk of mesoscutellum faintly rugose on lateral and posterior margins, central part of disk faintly reticulate, and elevated after central carina of mesoscutellar foveae, overhanging metanotum, with sparse setae. Mesoscutellar foveae not defined posteriorly, smooth, glabrous, with central carina. Mesopleuron smooth, alutaceous only on most anterior part; speculum smooth, glabrous, with transverse striae on most anterior part; mesopleural triangle smooth, with a few white setae; dorsal and lateral axillar areas smooth, with white setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with subparallel sides, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height; upper part of sulcus indistinct; lower part of sulcus delimiting smooth area with dense long white setae. Metascutellum dull alutaceous, glabrous, 1.5× longer than height of smooth, glabrous ventral impressed area; metanotal trough smooth, glabrous, without setae; central propodeal area lyre-shaped, smooth, glabrous, without rugae; lateral propodeal carinae distinct, bent outwards in posterior 1/3 of its height; lateral propodeal area smooth, with long dense white setae. Nucha with irregular sulci laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with cilia on margin, veins yellowish brown, radial cell open, 5.0× as long as broad; Rs and R1 nearly reaching wing margin; areolet distinct. Rs+M colourless, indistinctly reaching basalis, basalis slightly elongated on contact point.

Metasoma as long as head+mesosoma, as long as high in lateral view; 2nd metasomal tergum extending to 2/3 length of metasoma in dorsal view, with numerous white setae anterolaterally, with band of rare micropunctures posteriorly; all subsequent terga with rare micropunctures. Hypopygium without micropunctures, prominent part of ventral spine of hypopygium 5.8× as long as broad in ventral view, with numerous long white setae ventrally.

Body length 1.6–2.15 mm (n = 4).

**Gall** (Fig. 328). A cup-shaped leaf spangle gall, up to 4.5 mm in diameter and 3.5 mm high, purple-brown with a whitish bloom, attached to under side of leaf. The edge of the cup is thin, not in-rolled. The larval cell is 2 mm long by 0.7 mm in diameter and lies transversely at the very base of the cup. The exit hole is into the bottom of cup.

**Biology.** The asexual generation is only known, which induces galls on *Q. gambelii* (section *Quercus*, subsection *Dumosae*) and *Q. turbinella* (section *Quercus*, subsection *Leucomexicana*). Galls mature in late autumn, and adults were cut out from galls in December-January (Weld 1930).

**Distribution.** USA: AZ (Weld 1930).

***Feron serranae* Pujade-Villar & Cuesta-Porta, sp. nov.**

**Figs 329–341**

**Type material.** HOLOTYPE: Asexual female “Mexico (Code 171), Sierra de Guadalupe (MEX), ex *Quercus* sp., (10.i.2013) 15.i–15.ii.2013, leg. M. Serrano & A. Villegas (Miriam-323)” (UB). PARATYPES (9 asexual females): labelled as the holotype (3 females at PHDNRL, 6 females at UB).

**Etymology.** Species dedicated to Miriam Serrano Muñoz, the student who collected the galls.

**Diagnosis.** Asexual females are part of the *Feron* group characterised by never having a black body; head transversely ovate in frontal view; the gena at least slightly broadened behind the eye; antennae with 12 flagellomeres; lateral sides of pronotum longitudinally striated at least on posterior half, rest of pronotum alutaceous, matte; mesoscutum coarsely reticulated; mesopleuron finely striated to alutaceous on anterior margin; as in *F. tecturnarum* (asex), *F. tetyanae* (asex) and part of *F. tibiale* (asex). *Feron serranae* differs from these asexual forms



in its long mesoscutellum, 1.3× as long as broad and margined by a strong circumscutellar carina, while in the other species the mesoscutellum is only slightly longer than broad and the circumscutellar carina is absent.

**Description.** Asexual female (Figs 329–340). Head, and mesosoma reddish brown; metasoma reddish brown to dark brown, antennae slightly darker distally.

Head trapezoid in frontal view, broadest part level with halfway up eye, with sparse setae, denser on lower face; 2.1× as broad as long in dorsal view. Gena alutaceous, not or only very slightly broadened behind eye in frontal view in small specimens, narrower than transverse diameter of eye in lateral view. Malar space with a few delicate striae radiating from clypeus and reaching eye; eye 2.3× as high as length of malar space. Inner margins of eyes parallel. POL 1.3× as long as OOL, OOL 2.5× as long as diameter of lateral ocellus and 1.6× as long as LOL, all ocelli ovate, of same size. Transfacial distance 1.2× as long as height of eye; toruli located slightly above mid height of head, frons shorter than height of lower face, diameter of antennal torulus 1.5× as long as distance between them, distance between torulus and eye 1.3× as long as diameter of torulus; lower face smooth, with dense white setae; slightly elevated median area alutaceous, with few setae. Clypeus trapezoid, broader than high, alutaceous, with a few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons uniformly reticulate, without striae and with few setae, areas between toruli and between torulus and eye also alutaceous; interocellar area reticulate. Vertex, occiput, postgena alutaceous, with white long setae; postocciput alutaceous-reticulate, with concentric lines around occipital foramen and postgenal bridge; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 11 flagellomeres (some specimens with 12 flagellomeres with a distinct suture between F12 and F11), F6 until F11–F12 gradually broadening towards apical end, pedicel slightly longer than broad; F1 1.5× as long as pedicel and 1.2× as long as F2; F2=F3=F4, F5 to F10 nearly equal in length, F11 longer than F10; placodeal sensilla on F5–F11.

Mesosoma slightly longer than high, with sparse white setae, except for dense setae on lateral propodeal area. Pronotum striate, propleuron alutaceous, glabrous. Mesoscutum reticulate, smooth along parapsidal lines with sparse white setae, slightly broader than long

(greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, deep, bottom smooth, posteriorly broader and slightly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line distinct, in the form of a bare, smooth stripe, extending to half-length of mesoscutum; parapsidal line distinct, marked with broad impressed smooth glabrous stripes; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum ovate, slightly longer than broad, circumscutellar carina present; disk of mesoscutellum alutaceous with fine rugae, overhanging metanotum, with sparse setae. Mesoscutellar foveae shallow, fused, with smooth, glabrous bottom, occupying at least 1/3 of mesoscutellum length. Mesopleuron smooth, with setae in antero- and posteroventral part, and fine striae along anterior margin; mesopleural triangle smooth, with numerous short white setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangular, as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus distinct, lower part of sulcus separating smooth, glabrous area, with dense setae. Metascutellum alutaceous to smooth, glabrous, 3.0x as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with some setae; central propodeal area lyre-shaped, smooth, glabrous, with irregular interrupted rugae at the base in large specimens; lateral propodeal carinae strong, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae. Nucha with numerous sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with distinct dense cilia on margin, veins dark brown, radial cell open, 4.2x as long as broad; R1 and Rs not reaching wing margin; areolet small, triangular, closed and distinct. Rs+M distinct, its projection reaching basalis slightly above mid height.

Metasoma as long as head+mesosoma, higher than long than in lateral view; 2nd metasomal tergum extending to 2/3 of metasoma length in dorsal view, with short white setae anterolaterally, without micropunctures; subsequent terga and hypopygium smooth, glabrous, without micropunctures. Prominent part of ventral spine of hypopygium 6.5x as long as broad in ventral view, with some short setae ventrally which do not extend beyond apex of spine.

Body length 1.7–2.2 mm (n = 5).

**Gall** (Fig. 341). Brownish rounded unilocular galls on the underside of leaves, with an apical hole. Up to 6-8 mm in diameter.

**Biology.** Only the asexual generation is known, which induces galls on an unidentified white oak *Quercus* sp. (section *Quercus*, subsection *Leucomexicana*). The gall was found mature in January and the adults emerged soon after.

**Distribution.** Only known from Sierra de Guadalupe, Mexico State (Mexico).

***Feron splendens* (Weld, 1919), comb. nov.**

**Figs 342–353**

*Andricus splendens* Weld 1919: 254, female, gall.

**Types examined.** HOLOTYPE: Asexual female “Prescott, Ariz”, “15627a Hopk. U.S.”, red label “Type”, red label “Type No. 22328 USNM”, handwriting Weld’s label “*Andricus splendens* Weld”. deposited at the USNM, examined by GM. Specimen data and images available at <http://n2t.net/ark:/65665/327ad3c5f-f34f-45a5-8c8c-e073f017201a>. In the general collection in the AMNH a few dozen paratypes and thousands of non-type specimens of adults and galls are deposited. Paratypes and some non-paratype specimens were also examined by GM.

**Additional material.** Six asexual females and galls “Hillsboro, N.M., gall 12.26.19”, “*Q. grisea* Kinsey coll.”; 4 females and galls “Canatlan, 7N, Dgo 7400’ Mex., galls 11.9.31., females 4.30.32.”, “*Q. undata* Kinsey coll.”; two females “Sta. Izabel 6E, Chi. 6000’, Mex., galls 10.24.31, 547 females 4.21.32., *Q. undata* Kinsey coll.”.

**Diagnosis.** Asexual females belong to the group of *Feron* species without a black body; the head is quadrangular or ovate in frontal view, with ocelli elevated above the frons; inner margins of eyes are parallel or very slightly converging ventrally, the transfacial distance is equal to or longer than the height of the eye; toruli are located above mid-height of eyes; the eye less than 3.0× as high as the length of malar space; lateral ocelli are large, OOL subequal or at most 1.7× as long as the diameter of ocellus; the pronotum laterally with longitudinal carinae; the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points; as in *F. vitreum* (asex) and *F. verutum* (asex). Differs from *F. vitreum* in having the F1 subequal to or slightly longer than scape+pedicel and the transfacial distance longer than the height of eye. Differs from *F. verutum* in having a mesoscutum with some delicate transverse striae on its anterior part between notauli, anterior parallel lines indistinct and the mesoscutellar foveae separated by a broad carina. See other characters at couplet 33 in the key

**Re-description.** Asexual female (Figs 342–352). Head, antenna, mesosoma, legs rusty brown; metasoma slightly darker.

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Head transverse, 1.2× as broad as high in frontal view, with sparse setae, denser on lower face; 1.9× as broad as long in dorsal view; head as broad as mesosoma in frontal view. Gena reticulated, only very slightly broadened behind eye in frontal view, slightly narrower than transverse diameter of eye in lateral view. Malar space alutaceous, shining, with delicate striae radiating from clypeus and nearly reaching eye, malar sulcus absent; eye 2.1× as high as length of malar space. Inner margins of eyes parallel. POL 2.0× as long as OOL, OOL 1.5× as long as diameter of lateral ocellus and 1.2× as long as LOL, all ocelli ovate, central ocellus slightly bigger than lateral ocellus. Transfacial distance 1.2× as long as height of eye; torulus located slightly above mid height of eye, frons shorter than height of lower face, diameter of antennal torulus 1.6× as long as distance between them, distance between torulus and eye 1.1× as long as diameter of torulus; lower face delicately coriaceous, with sparse white setae; slightly elevated median area delicately coriaceous, with a few setae. Clypeus trapezoid, as broad as high, alutaceous, with a few long setae along ventral edge; ventrally rounded, emarginate and with delicate median incision; anterior tentorial pit rounded, large, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons delicately coriaceous to reticulate, without striae and with a few setae, small triangular area under central ocellus reticulated; areas between toruli and between torulus and eye reticulate; interocellar area delicately coriaceous to reticulate. Vertex, occiput, postgena delicately coriaceous to reticulate, with white long setae; postocciput smooth, glabrous; posterior tentorial pit large, elongate, area below impressed, glabrous; occipital foramen 2.0× as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulcus; postgenal sulcus indistinct, bent outwards reaching posterior tentorial pit, and postgenal bridge unusually broad. Head posteriorly with black narrow stripes. Antenna slightly longer than head+mesosoma, with 12 flagellomeres, distal half slightly darker; pedicel slightly longer than broad; F1 2.2× as long as pedicel and slightly longer than F2; F2 slightly longer than F3, F3=F4, F4 slightly longer than F5, F5=F6, F7 and subsequent flagellomeres until F10 nearly equal in length, F11 slightly shorter than F12; placodeal sensilla on F4–F12.

Mesosoma 1.2× as long as high, with sparse white setae. Pronotum smooth, with sparse setae, with delicate parallel concentric striae laterally; propleuron delicately coriaceous, without setae (propleuron absent in the figures). Mesoscutum alutaceous to reticulate alongside notauli, smooth, glabrous in posterior half between notauli and with some delicate transverse striae in anterior part between notauli; with sparse white setae; slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae).

Notaulus complete, distinctly impressed along entire length, with smooth bottom, slightly converging posteriorly; anterior parallel line indistinct, invisible; parapsidal line distinct, marked with narrow impressed smooth glabrous stripes; median mesoscutal line absent; parascutal carina narrow, extending to level of tegula. Mesoscutellum trapezoid, slightly longer than broad; disk of mesoscutellum uniformly dull rugose, slightly overhanging metanotum, with a few setae. Mesoscutellar foveae ovate, slightly broader than high, with smooth, glabrous bottom, divided by triangular coriaceous central elevated area. Mesopleuron and speculum entirely smooth, with setae in posteroventral quarter; mesopleural triangle smooth, with numerous short white setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, with parallel sides, slightly elevated, triangular in most posterior part and as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus distinct, lower part of sulcus separating smooth, glabrous area, with dense setae. Metascutellum smooth, glabrous, higher than height of smooth, glabrous ventral impressed area; metanotal trough smooth, with dense setae; central propodeal area lyre-shaped, smooth, glabrous, without rugae; lateral propodeal carinae distinct, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae and piliferous points. Nucha with net of irregular rugae dorsally and laterally. Tarsal claws toothed, with basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins distinct, brown, radial cell open, 4.0× as long as broad; R1 and Rs not reaching wing margin; areolet and Rs+M indistinct, its projection reaching basalis at its half height.

Metasoma slightly longer than head+mesosoma, higher than long in lateral view; 2nd metasomal tergum extending to 2/3 of metasoma length in dorsal view, with dense short white setae anterolaterally, without micropunctures; subsequent terga and hypopygium smooth, shining, without micropunctures; prominent part of ventral spine of hypopygium 5.8× as long as broad in ventral view, with a few short setae ventrally.

Body length 1.3–2.4 mm (n = 10).

**Gall** (Fig. 353). Single or scattered on the underside of leaf. Cylindrical with ends and middle slightly swollen, 2.0 mm in diameter and 3–5 mm high, with a crystalline appearance, covered with short stout blunt spines from which run faint decurrent ridges. Sessile, often lop-sided, spines more numerous on basal third. The gall is rosy red with a straw yellow band around the middle and some yellow at either end. The basal third is solid, with a thin-walled larval cell in the middle of the gall while the distal third or more is tubular with a slightly flared open end. The exit hole is in the hollow portion (Weld 1919).

**Biology.** Only the asexual generation is known, which induces leaf galls on *Q. grisea*, *Q. turbinella*, and *Q. x undata* (section *Quercus*, subsection *Leucomexicana*). Galls mature in late autumn; the larvae transform to adults in autumn but remain in the gall all winter and emerge the following spring in April-May.

**Distribution.** USA: AZ, NM (Burks 1979); Mexico: Chihuahua, Durango.

***Feron stellare* (Weld, 1926), comb. nov.**

**Figs 354–366**

*Andricus stellaris* Weld, 1926: 84, female, gall.

**Type examined.** HOLOTYPE: Asexual female “Sequoia Nat. Park, Cal.,” “*Q. garryana*”, “1783”, red label “Type No. 27215 USNM”, “*Andricus stellaris* Weld” deposited in USNM, examined by GM. Specimen data and images available at <http://n2t.net/ark:/65665/303039ff4-e0fe-4064-be9c-dbe097c266ba>.

**Additional material.** Asexual females. One female, designated as voucher specimen, compared with types at the USNM, by GM, labeled as “USA, California, Round Valley, CA1174, galltype 119; *Q. garryana*, leg. J.A. Nicholls, 2006.02.09”; one female “USA, California, Dye Creek Preserve, CA1169, galltype 135; *Q. douglasii*, leg. J.A. Nicholls”.

**Diagnosis.** Asexual females belong to the group of *Feron* species in which the body is not black; the head is rounded in frontal view with a smooth and shining slightly elevated median area of lower face; the gena at least slightly broadened behind the eye; ocelli are not elevated above the frons; inner margins of eyes are parallel or very slightly converging ventrally; the transfacial distance is longer than height of the eye; the antenna with 12 flagellomeres, sometimes suture between F11 and F12 incomplete; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as length of the malar space; lateral ocelli are smaller, OOL at least 2.5× as long as the diameter of the ocellus, if shorter than the head and mesosoma are not yellowish or light brown; the pronotum laterally with longitudinal carinae; the mesoscutum is alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points; mesoscutellar foveae divided by a central carina; the mesopleuron is entirely smooth; as in *F. bakkeri* (asex), *F. caepula* (asex), *F. rucklei* (asex), and *F. scutellum* (asex). Nevertheless, this species differs from *F. caepula* in the brown body colour, sometimes with darker marks and parallel eyes, while *F. caepula* is yellowish to light brown with eyes strongly convergent ventrally. Differs from *F. bakkeri* in having mesoscutellar foveae conspicuous and smooth, while inconspicuous and faintly rugose in *F. bakkeri*. Differs from *F. scutellum* in the coarsely rugose mesoscutellar disk, while it is faintly reticulated and with a

median elevated area in *F. scutellum*. The most similar species is *F. rucklei* but differs in the antennae having the first flagellomeres lighter than subsequent ones, the notaulus is incomplete, mesoscutellar foveae delimited posteriorly by a strong black carina, and metasoma without micropunctures.

**Re-description.** Asexual female (Figs 354–365). Head, antennae, mouthparts, mesosoma, metasoma dark brown, with darker mesoscutellum and propodeum; legs slightly lighter than body.

Head rounded with white setae on lower face, occiput, postocciput and postgena, slightly broader than high and as broad as mesosoma in frontal view; 1.7× as broad as long in dorsal view. Gena alutaceous, slightly broadened behind eye in frontal view, slightly narrower than transverse diameter of eye in lateral view. Malar space with a few striae radiating from clypeus and reaching eye; eye 2.7× as high as length of malar space; malar sulcus absent. Inner margins of eyes slightly converging ventrally. POL 1.7× as long as OOL, OOL 2.7× as long as diameter of lateral ocellus and slightly longer than LOL, all ocelli ovate, of the same size. Transfacial distance 1.2× longer than height of eye; toruli located in the upper half of head and frons distinctly shorter than lower face; diameter of antennal torulus 1.4× as long as distance between them, distance between torulus and eye slightly longer than diameter of torulus; lower face smooth with white setae and piliferous points; slightly elevated median area smooth, area between toruli reticulate. Clypeus rectangular, broader than high, delicately coriaceous, with a few long setae scattered all over; ventrally rounded, emarginate, without median incision; anterior tentorial pit small, rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons, interocellar area, vertex, occiput uniformly reticulate, without striae and setae; area under central ocellus impressed, smooth, glabrous; postocciput and postgena alutaceous, with few setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into distinct postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres (suture between F12 and F11 not always distinct but present); all flagellomeres with dense setae; pedicel 1.6× as long as broad; F1 2.3× as long as pedicel and 1.4× as long as F2; F2=F3=F4, F5=F6, subsequent flagellomeres gradually shorter, F12 slightly shorter than F11; placodeal sensilla white on F6–F12.

Mesosoma as long as high, with a few setae. Pronotum smooth, glabrous dorsally; laterally coriaceous, with denser setae on the anterior margin and delicate striae along posterior edge; propleuron smooth, with sparse white setae. Mesoscutum longer than broad (greatest width measured across mesoscutum level with base of tegulae), uniformly aluraceous-reticulate; with scattered white setae. Notaulus incomplete, not impressed in anterior 1/4, deep in posterior 3/4 of mesoscutum length, posteriorly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum. Anterior parallel line nearly absent, indicated only by some smooth areas; parapsidal line narrow, impressed, extending to half-length of mesoscutum; parascutal carina narrow, anteriorly reaching notaulus; median mesoscutal line in the form of a short smooth triangle. Mesoscutellum trapezoid, longer than broad, with subparallel sides, broadest part in posterior 1/3; circumscutellar carina broad, distinct laterally and posteriorly; mesoscutellum rugoso-coriaceous, overhanging metanotum, with long setae. Mesoscutellar foveae ovate, broader than high, with smooth, glabrous bottom, delimited all around by distinct black carina. Mesopleuron entirely smooth, with setae denser along ventral edge; mesopleural triangle smooth, with dense white setae; dorsal and lateral axillar areas smooth, glabrous, without setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, triangular, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron above half of its height, on lower part sulcus delimiting smooth, glabrous area with dense setae; upper part of sulcus indistinct. Metascutellum coriaceous, 2.0x as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with dense setae; central propodeal area lyre-shaped, smooth, glabrous; lateral propodeal carinae strong, broad and high, bent outwards in posterior 1/3; lateral propodeal area smooth, with long white setae. Nucha with net of numerous irregular rugae. Tarsal claws with acute basal lobe.

Fore wing longer than body, hyaline, with distinct dense cilia on margin, veins light brown, radial cell open, 4.5x as long as broad; Rs and R1 nearly reaching wing margin; areolet triangular, small, closed and indistinct. Rs+M indistinct, invisible.

Metasoma longer than head+mesosoma, slightly higher than long in lateral view; 2nd metasomal tergum extending to half-length of metasoma in dorsal view, with numerous white setae anterolaterally, without micropunctures; all subsequent terga and hypopygium without micropunctures, prominent part of ventral spine of hypopygium 6.3x as long as broad in ventral view.

Body length 1.7–2.1 mm (n = 3).



**Gall** (Fig. 366). A hemispherical gall, 3–4 mm in diameter and 2 mm high, covered with short, blunt crystalline protuberances with a circle of 12–15 longer, broad projections at the base, attached singly or scattered in small numbers on the underside of the leaf. The galls are yellowish-white, often tinged with red. The larval cell lies transversely in the very base of the gall and above it is a cavity above which the crystalline wall of the upper part of the gall is very thick (Weld 1926).

**Biology.** Only the asexual generation is known, which induces leaf galls on *Q. douglasii* and *Q. garryana* (section *Quercus*, subsection *Dumosae*) in autumn, the adults emerge the next spring in March (Weld 1926).

**Distribution.** USA: California (Burks 1979).

***Feron stellulum* (Burnett, 1974) comb. nov.**

**Figs 367–371**

*Andricus stellulus* Burnett, 1974: 299, female, gall.

**Type examined.** HOLOTYPE: Asexual female “Cajon Pass, San Bernardino Co., CA. 12.1974. Host: *Quercus dumosa*; emerged II-19-1974. J.A. Burnett Coll.”, “*Andricus stellulus* det. by J. Burnett”, red label “Holotype”, red label “Type No. 15448 USNM”, handwriting label “*Andricus stellulus* Burnett” deposited in USNM, not examined. Specimen data and images available at <http://n2t.net/ark:/65665/3f622315a-cbf9-4fb2-9eb6-c3694b2219c0>

**Diagnosis.** Asexual females belong to the group of *Feron* species characterised by a body which is not black; the head is rounded or trapezoid to triangular in frontal view, ocelli are not elevated above the frons; inner margins of eyes parallel or very slightly converging ventrally, the transfacial distance is equal to or longer than the height of eye; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as length of the malar space; lateral ocelli smaller, OOL at least 2.5× as long as the diameter of the ocellus, if shorter then the head and mesosoma are not yellowish or light brown; the pronotum laterally with longitudinal carinae; the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points and the mesopleuron in the mid-height with transverse reticulate-carinate band; as in *F. gigas* (asex), *F. parmula* (asex), *F. syndicorum* (asex) and some specimens of *F. tibiale* (asex). Differs from *F. tibiale* and *F. syndicorum* in having the gena which is not broadened behind the eye in frontal view. Differs from *F. parmula* in that the malar space has a few delicate striae radiating from the clypeus, mesoscutellar foveae defined and the prominent part of the ventral spine of the hypopygium 4.5× as long as broad in ventral view; see more

characters at couplet 37 in the key. The most morphologically similar species is *F. gigas* but *F. stellulum* has the antenna with 11 flagellomeres (12 in *F. gigas*), the eye 2.7× as high as the length of malar space (shorter in *F. gigas*), veins are brown (lighter in *F. gigas*), areolet present (absent in *F. gigas*) and the central propodeal area with rugae (without rugae in *F. gigas*).

**Re-description.** After Burnett (1974); the images (Figs 367–370) can also be consulted at: <http://n2t.net/ark:/65665/3f622315a-cbf9-4fb2-9eb6-c3694b2219c0>.

Head and mesosoma rufescent to yellow brown; antenna with black flagellomeres, legs yellowish brown; metasoma brown. Head coriaceous, transverse in dorsal view, as broad as mesosoma. Occiput flat, gena not broadened behind eyes; vertex slightly projected above as a truncate cone, base laterally extended to ocular sutures, several small humps in area of dorsal ocelli. Malar space 0.37× of eye height, with a few striae radiating from clypeus, malar sulcus absent. Interocellar area broader than high. Antenna filiform, with 11 flagellomeres, F1 longer than F2. Mesonotum coriaceous, with scattered setae; notaulus complete, broader posteriorly; median mesoscutal line absent, parapsidal lines marked with smooth stripes. Mesoscutellum with setae, disc reticulate, longer than broad. Mesoscutellar foveae smooth, partly striate, smooth and shining below. Tarsal claws with strong basal lobe. Propodeal carinae bent outwards, central propodeal area darker than rest of propodeum, glabrous, slightly rugose. Fore wing hyaline, pubescent, with dense cilia on margin, veins brown, radial cell open, 4.0× as long as broad, areolet distinct, Rs and R1 not reaching wing margin. Metasoma as high as long, as long as head+mesosoma; 2nd metasomal tergum with setae anterolaterally, micropunctate, subsequent terga with micropunctures, prominent part of ventral spine of hypopygium 4.5× as long as broad in ventral view. Body length 1.5–2.2 mm.

**Gall** (Fig. 371). Leaf gall. Monolocular and can be found on both sides of the leaves. Disk shaped (1.6–2.3 mm in diameter) with some points around the perimeter but erected on a long and slender pedicel, usually slightly broadening towards apex. The gall is almost twice as high as the diameter of the disk (2.3–5.6 mm in height). The surface is shiny and glabrous of a reddish colour, the pedicel is crimson, and the disk is rufous. Galls are found attached either to a secondary vein of the leaf blade or occasionally to the midrib, mature galls are typically associated with a brown necrosis around the point of attachment which extends laterally to the leaf-blade margin. Emergence holes made by the gall wasp are usually found in the lateral part of the gall disc (Burnett 1974).

**Biology.** Only the asexual generation is known, inducing galls on *Q. dumosa* (section *Quercus*, subsection *Dumosae*); adults start to emerge from February.

**Distribution.** USA: CA.

***Feron sulfureum* (Weld, 1926) comb. nov.**

**Figs 372–383**

*Diplolepis sulfurea* Weld, 1926: 33, female, gall.

*Andricus sulfureus* (Weld): Weld 1951: 636.

**Type examined.** HOLOTYPE: Asexual female “Huachuca Mnts. Ariz.”, “Bess. Canon”, “*Q. arizonica*”, “Cut out Dec. 3.19”, “910”, red label “Type No. 27193 USNM”, “*Diplolepis sulfureus* Weld” deposited in USNM, examined by GM. Specimen data and images available at <http://n2t.net/ark:/65665/33b71e4e4-8126-45ce-885e-8416e8853fd6>. According to Weld (1926) the paratype is deposited at the Leland Stanford Junior University, Stanford, California (not examined by the authors).

**Additional material.** 14 asexual females “USA, AZ, Chiricahua Mtns nr Portal, galltype 35, ex *Q. arizonica*, AZ51, coll. 2007.10.25, leg. J.A. Nicholls”; 26 females “USA, AZ, Chiricahua Mtns, western side, ex *Q. arizonica*, AZ50, coll. 2007.10.25, leg. J.A. Nicholls”; 14 females “USA, AZ, Chiricahua Mtns summit, AZ49, ex *Q. arizonica*, coll. 2007.10.25, leg. J.A. Nicholls”.

**Diagnosis.** Asexual females together with *F. pattersonae* (asex) and *F. crystallinum* (asex), belong to a group of *Feron* species in which the pronotum has dense setae and piliferous points, without carinae laterally; the mesoscutum is dark brown between notauli in anterior 1/3 of the mesoscutum length. Differs from *F. pattersonae* in the trapezoid head in frontal view (ovate in *F. pattersonae*) and mesoscutellar foveae are separated by a central carina (fused in *F. pattersonae*). The morphologically most similar species is *F. crystallinum* but in *F. sulfureum* the pronotum is smooth, without piliferous points and all flagellomeres are uniformly broad; for other characters see couplet 26 in the key.

**Re-description.** Asexual female (Figs 372–382). Head, antennae, mesosoma, metasoma dark brown; mouthparts light brown. Frons, interocellar area, central elevated area on lower face, gena behind eye, postgena, postoccipt black; propleura, mesoscutum between notauli in anterior 2/3 of mesoscutum length and stripes along parapsidal lines black; metasoma dorsally always darker, dark brown to black. Legs brown, with black coxae.

Head trapezoid, broadest part above toruli, slightly higher than broad and slightly broader than mesosoma in frontal view, with sparse setae, denser on lower face; 2.2× as broad

as long in dorsal view. Gena alutaceous, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space with a few delicate striae radiating from clypeus and not reaching eye; eye 3.8× as high as length of malar space. Inner margins of eyes parallel. POL 1.5× as long as OOL, OOL slightly longer than diameter of lateral ocellus and shorter than LOL, all ocelli ovate, of same size. Transfacial distance nearly equal to height of eye; toruli located above mid height of head, frons shorter than height of lower face, diameter of antennal torulus 1.5× as long as distance between them, distance between torulus and eye 1.1× as long as diameter of torulus; lower face alutaceous, with dense white setae; slightly elevated median area alutaceous-reticulate, with a few setae. Clypeus quadrangular, only slightly broader than high, delicately coriaceous, with a few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons uniformly alutaceous-reticulate, without striae and setae, areas between toruli and between torulus and eye also alutaceous; interocellar area delicately coriaceous. Vertex and occiput reticulate, with white long setae; postocciput and postgena alutaceous-reticulate, with concentric lines around occipital foramen and postgenal bridge; posterior tentorial pit large, ovate, area below impressed; occipital foramen higher than height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 11 flagellomeres (in some specimens, antenna with 12 flagellomeres, with a distinct suture between F12 and F11), pedicel longer than broad; F1 slightly longer than F2 and 2.0× as long as pedicel; F2=F3=F4, F5=F6, F7 to F10 equal in length; F11 longer than F10; placodeal sensilla on F4–F11.

Mesosoma longer than high, with few white setae, setae denser along propleuron and on lateral propodeal area. Pronotum smooth, without striae, with dense setae laterally, without piliferous points; propleuron smooth, with dense setae. Mesoscutum predominantly delicately coriaceous, smooth in between notauli in anterior 1/3 and along parapsidal lines; with white sparse setae and distinct piliferous points, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, slightly converging posteriorly; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line in the form of short, delicately impressed smooth stripes; parapsidal line marked with broad smooth, impressed area; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum elongated,

longer than broad, broadest part in posterior 1/4 of its length, circumscutellar carina present; disk of mesoscutellum reticulate, dull rugose laterally and posteriorly, overhanging metanotum, with sparse long setae. Mesoscutellar foveae transverse, broader than high, with smooth, glabrous bottom, with elevated coriaceous triangular central carina. Mesopleuron entirely smooth, glabrous, without striae, with a few long white setae along ventral edge; mesopleural triangle smooth, with dense, long white setae; dorsal and lateral axillar areas smooth, with dense white setae; axillula with delicate parallel longitudinal striae; subaxillular bar smooth, glabrous, with parallel sides, posteriorly as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height; upper and lower parts of sulcus distinct, delimiting smooth areas with dense long white setae. Metascutellum smooth, glabrous, higher than height of smooth, glabrous ventral impressed area; metanotal trough smooth, with dense white setae; central propodeal area lyre-shaped, smooth, glabrous, with a few irregular short rugae; lateral propodeal carinae distinct, slightly bent outwards in posterior 1/3 of its height; lateral propodeal area smooth, with long dense white setae and few visible piliferous points. Nucha with numerous sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with short cilia on margin, veins dark brown, radial cell open, 4.2× as long as broad; R1 nearly reaching wing margin, Rs reach wing margin; areolet triangular, small, closed and distinct. Rs+M distinct, its projection reaching basalis in lower 1/3 of its height.

Metasoma as long as head+mesosoma, slightly longer than high in lateral view; 2nd metasomal tergum extending to 3/4 length of metasoma in dorsal view, with numerous white setae anterolaterally, without micropunctures; all subsequent terga and hypopygium without micropunctures. Prominent part of ventral spine of hypopygium 5.5× as long as broad in ventral view, with few short white setae ventrally.

Body length 1.8–2.3 mm (n = 10).

**Gall** (Fig. 383). A hollow cone, sessile at base and open at apex, densely covered with long sulphur-yellow spines, on under surface of leaf, single or scattered, sometimes as many as nine on a leaf but usually only one to three. The cone is up to 7 mm high by 4 mm in diameter at base, with a crystalline surface, white or rosy when growing, the spines up to 4 mm long and often rosy at the tip. The larval cell lies transversely just below the middle of gall and below it is a small obconical cavity reaching to point of attachment. The lower part of the large distal cavity above larval cell is constricted by a narrow circular shelf.

**Biology.** Only the asexual generation is known, which induces galls on multiple oaks from section *Quercus*, subsection *Leucomexicana*: *Q. arizonica*, *Q. grisea* and *Q. oblongifolia*. Galls mature in the autumn dropping only with the leaf; adults emerge in late March-April.

**Distribution.** USA, Arizona only.

***Feron syndicorum* Pujade-Villar & Cuesta-Porta, sp. nov.**

**Figs 384–394**

**Type material.** HOLOTYPE, asexual female “Mexico (Code 077), La Cumbre (Monte Escobedo, ZAC), 22°19'8.9''N 103°38'53,42''W, ex *Q. potosina* Humb. & Bonpl Trell., (05, 11.2010) 15.12.2010, leg. C. Carrillo, O. Cabral, R. Treto & L. Landa” deposited in UB. PARATYPES (5 asexual females) labeled as the holotype. Two paratypes deposited in UB, and three paratypes in PHDNRL.

**Etymology:** Syndicus is the Latinization of the Greek σύνδικος (σύν = with and δίκη = justice), which means one who acts with justice. We use the plural because it is dedicated to the 5 ‘sindicis’ of October 1, 2017: Marc Marsal i Ferret (lawyer, he was a consultant to the Online University of Catalonia, UOC), Josep Pagès i Masó (Autonomous University of Bellaterra, UAB), Jordi Matas i Dalmases (Barcelona University, UB), Tània Verge i Mestre (Pompeu Fabra University, UPF) and Marta Alsina Conesa (lawyer, currently defender of the citizens of Girona). To them all for their commitment to democracy.

**Diagnosis.** Asexual females are part of the group of *Feron* species that are characterised by the body never being black; head trapezoid in frontal view; ocelli are not elevated above the frons; inner margins of eyes parallel or converging very slightly ventrally, the transfacial distance is longer than the height of eye; antenna with 12 flagellomeres, sometimes suture between F11 and F12 incomplete; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as the length of the malar space; the pronotum laterally with longitudinal carinae; the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, without distinct piliferous points; and the mesopleuron with a transversal striate band; as in *F. gigas* (asex), *F. parmula* (asex), *F. stellulum* and some specimens of *F. tibiale* (asex). Differs from *F. gigas*, *F. parmula*, and *F. stellulum* in having the gena broadened behind the eye. The most similar species is the asexual form of *F. tibiale* but in *F. syndicorum* the mesoscutum is finely alutaceous; the notaulus is complete but shallow and alutaceous at least on anterior 3/4 of its length; the mesoscutellar disk is strongly curved in lateral view, which makes the mesoscutum and mesoscutellum appear as two independent lobes in lateral view; and the subaxillary bar reaches 1/3 of the height of mesoscutellum. *Feron tibiale* (part) is coarsely

reticulated on the mesoscutum, has complete notaulus but which is inconspicuous on anterior 1/4 of its length; the mesoscutellum is flat in lateral view and forms a continuous curve with the mesoscutum in lateral view; and the subaxillular bar reaches half the height of metascutellum.

**Description.** Asexual female (Figs 384–393). Head, mesosoma, metasoma light brown to reddish brown; antennae slightly darker distally.

Head trapezoid in frontal view, broadest part on the level of half height of eye; with sparse setae, denser on lower face;  $2.0\times$  as broad as long in dorsal view. Gena alutaceous broadened behind eye in frontal view, subequal to transverse diameter of eye in lateral view. Malar space with a few delicate striae radiating from clypeus and reaching eye; eye  $2.6\times$  as high as length of malar space. Inner margins of eyes parallel. POL  $1.5\times$  as long as OOL, OOL  $2.0\times$  as long as diameter of lateral ocellus and  $1.3\times$  as long as LOL, all ocelli ovate, of same size. Transfacial distance  $1.1\times$  as long as height of eye; toruli located slightly above mid height of head, frons shorter than height of lower face, diameter of antennal torulus  $1.5\times$  as long as distance between them, distance between torulus and eye  $1.5\times$  as long as diameter of torulus; lower face smooth, with dense white setae; slightly elevated median area alutaceous, with a few setae. Clypeus trapezoid, broader than high, alutaceous, with a few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons uniformly alutaceous-reticulate, without striae and with a few setae, areas between toruli and between torulus and eye also alutaceous; interocellar area alutaceous-reticulate. Vertex, occiput, postgena alutaceous, with white long setae; postocciput alutaceous-reticulate, with concentric lines around occipital foramen and postgenal bridge; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 11 flagellomeres (some specimens with 12 flagellomeres with a distinct suture between F12 and F11), F6 until F11–F12 gradually broadening towards apical end, pedicel slightly longer than broad; F1  $1.5\times$  as long as pedicel and  $1.5\times$  as long as F2; F2=F3=F4, F5 to F10 nearly equal in length, F11 longer than F10; placodeal sensilla on F5–F11.

Mesosoma  $1.2\times$  as long as high, with sparse white setae, except dense setae on lateral propodeal area. Pronotum delicately striate, with sparse setae; propleuron alutaceous,

glabrous. Mesoscutum alutaceous to reticulate, with shallow piliferous points, smooth along parapsidal lines with sparse white setae, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, shallow, bottom smooth on posterior 1/4 of its length and alutaceous-reticulate on the anterior 3/4, posteriorly slightly broader and slightly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line distinct, in the form of a bare, smooth stripe, extending to half-length of mesoscutum; parapsidal line distinct, marked with broad impressed smooth glabrous stripes; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum ovate, slightly broader than long, circumscutellar carina absent; disk of mesoscutellum alutaceous, dull rugose laterally and posteriorly, overhanging metanotum, with dense setae. Mesoscutellar foveae oblique, inconspicuously divided by an alutaceous central elevated area; foveae with smooth, glabrous bottom, occupying at least 1/3 of mesoscutellum length. Mesopleuron delicately striate and glabrous, posterior margin smooth; with setae in ventral part; mesopleural triangle smooth, with numerous short white setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangular, as high as 1/3 of height of metascutellum; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus present, lower part of sulcus separating smooth, glabrous area, with dense setae. Metascutellum alutaceous to smooth, glabrous, 3.0× as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with some setae; central propodeal area lyre-shaped, glabrous, with irregular interrupted rugae at the base in large specimens; lateral propodeal carinae distinct, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae. Nucha with numerous sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with distinct dense cilia on margin, veins dark brown, radial cell open, 3.9× as long as broad; R1 and Rs not reaching wing margin; areolet small, triangular, almost indistinct. Rs+M distinct, not reaching basalis, its projection reaching basalis slightly above mid height.

Metasoma as long as head+mesosoma, higher than long than in lateral view; 2nd metasomal tergum extending to 2/3 of metasoma length in dorsal view, with short white setae anterolaterally, without micropunctures; subsequent terga and hypopygium smooth, glabrous, with micropunctures. Prominent part of ventral spine of hypopygium 4.8× as long as broad in ventral view, with some short setae ventrally which not extend beyond apex of spine.

Body length 2.1–2.2 mm (n = 2).



**Gall** (Fig. 394). Yellow crystalline leaf gall mass (aggregation of galls, 5-20 galls) on underside of leaf, to 20 mm long projecting from leaf by up to 15 mm. Larval chambers easily detachable from leaf and crystalline pubescence extremely brittle.

**Biology.** Only the asexual generation is known, which induces galls on *Q. potosina* (section *Quercus*, subsection *Leucomexicana*). The gall matures in late autumn and the adults emerge soon after.

**Distribution.** Mexico, La Cumbre (Monte Escobedo, State of Zacatecas).

*Feron tecturnarum* (Kinsey, 1920) comb. nov.

**Figs 395–408**

*Andricus tecturnarum* Kinsey, 1920: 312, female, gall. Weld, 1951: 636.

*Diplolepis tecturnarum* Kinsey: Weld, 1926: 34.

**Types examined.** The original description mentioned 8 asexual female cotypes without the designation of a holotype. Lectotype female was designated in Ferrer-Suay et al. (2017): “San Luis Potosi. Mex., Edw. Palmer Coll., loose in box”, “*Q. potosina*, Edw. Palmer coll.”, red “*Andricus tecturnarum*, Cotype”, deposited in AMNH, NYC, examined by GM.

**Additional material.** “Mexico (Code 014), Sierra Fria, (Aguascalientes, AGC), 20°11'51.1''N 102°35'29.5W, ex *Q. potosina*, (02-12-2010) 14.ii.2011: 6 asexual females (2 females PHDNRL, 4 females UB), leg. A. Equihua & E. Estrada”; “Mexico (Code 025), Carretera Nochistlán-Tlachichila, (Nochistlán de Mejía, ZAC), 21°27'29.1''N 102°50'4.2''W, ex *Q. potosina* Trell., (04-12-2010) 15.ii.2011: 13 asexual females (5 females PHDNRL, 8 females UB), leg. A. Equihua & E. Estrada”.

**Diagnosis.** Asexual females are part of the group of *Feron* species characterised by never having the body black; head transversely ovate in frontal view, with the median area of lower face elevated and alutaceous to delicately coriaceous; the gena at least slightly broadened behind the eye; ocelli are not elevated above the frons; OOL at least 2.5× as long as the diameter of the ocellus, inner margins of eyes parallel or very slightly converging ventrally, the transfacial distance is longer than the height of eye; antenna with 12 flagellomeres, sometimes suture between F11 and F12 incomplete; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as the length of the malar space; lateral ocelli smaller, the pronotum laterally with longitudinal carinae that reach at least half the length of the pronotum; the mesoscutum coarsely reticulated, without piliferous points and the mesopleuron is entirely smooth; as in *F. serranae* (asex), *F. tetyanae* (asex), and some *F. tibiale* (asex). *Feron tecturnarum* differs from *F. serranae* in having the mesoscutellum only

slightly longer than broad and without circumscutellar carina, while *F. serranoae* has the mesoscutellum 1.3x longer than broad and with a strong circumscutellar carina. The most similar species is the asexual form of *F. tetyanae* and both differ from *F. tibiale* in the chestnut or rusty brown body colour, frons not bulging, POL at least 1.4x longer than OOL, the genae not broadened behind the eyes, the mesoscutellar disk smooth or finely rugose and radial cell 3.7x longer than broad, while the *F. tibiale* within this group are yellowish or light brown, with the frons bulging, POL subequal to OOL, genae broadened behind the eyes, the mesoscutellar disk reticulate-coriaceous and radial cell 4.8x longer than broad. *Feron tecturnarum* differs from *F. tetyanae* in the body being uniformly rusty brown, the head of the same colour as the rest of the body, without dark marks, the frons is finely alutaceous, mesoscutellar foveae divided by a triangular elevated coriaceous central carina, while *F. tetyanae* is chestnut brown with the head darker than mesosoma in frontal view, the frons is coarsely coriaceous and the mesoscutellar foveae are divided by a fine carina.

**Re-description.** Asexual female (Figs 395–406). Head, mesosoma, metasoma rusty brown, antennae darker distally; legs lighter.

Head slightly transverse, ovate in frontal view, broadest part level with halfway up eye, with sparse setae, denser on lower face; 2.0–2.4× as broad as long in dorsal view. Gena alutaceous, broadened behind eye in frontal view, slightly broader than transverse diameter of eye in lateral view. Malar space with a few delicate striae radiating from clypeus and reaching eye; eye 2.2× as high as length of malar space. Inner margins of eyes parallel. POL 1.5× as long as OOL, OOL 2.6× as long as diameter of lateral ocellus and 1.6× as long as LOL, all ocelli ovate, of same size. Transfacial distance 1.3× as long as height of eye; toruli located slightly above mid height of head, frons shorter than height of lower face, diameter of antennal torulus 1.5× as long as distance between them, distance between torulus and eye 1.3× as long as diameter of torulus; lower face smooth, with dense white setae; slightly elevated median area alutaceous, with a few setae. Clypeus rectangular, broader than high, alutaceous, with a few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons uniformly alutaceous-reticulate, without striae and with a few setae, areas between toruli and between torulus and eye also alutaceous; intercellular area alutaceous-reticulate. Vertex, occiput, postgena alutaceous, with white long setae; postocciput alutaceous-reticulate, with concentric lines around occipital foramen and postgenal bridge; posterior tentorial pit large, elongated, area below impressed; occipital

foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which strongly diverge toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 11 flagellomeres (some specimens with 12 flagellomeres with a distinct suture between F12 and F11), pedicel slightly longer than broad; F1 2.0× as long as pedicel and 1.3× as long as F2; F2=F3=F4, F5 to F10 nearly equal in length, F11 longer than F10; placodeal sensilla on F5–F11.

Mesosoma 1.2× as long as high, with sparse white setae, except dense setae on lateral propodeal area. Pronotum alutaceous, with sparse setae, with some delicate striae in dorsoposterior quarter in lateral view; propleuron alutaceous, glabrous. Mesoscutum alutaceous to reticulate, smooth along parapsidal lines with sparse white setae, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus incomplete, deep, bottom smooth, posteriorly broader and slightly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line distinct, in the form of a bare, smooth stripe, extending to half-length of mesoscutum; parapsidal line distinct, marked with broad impressed smooth glabrous stripes; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum ovate, slightly longer than broad, circumscutellar carina present; disk of mesoscutellum dull rugose, and more coarsely rugose laterally and posteriorly, overhanging metanotum, with dense setae. Mesoscutellar foveae divided by a triangular elevated area, foveae with smooth, glabrous bottom, occupying at least 1/3 of mesoscutellum length. Mesopleuron smooth, with delicate striae on anterior margin, with setae in antero and posteroventral part; mesopleural triangle smooth, with numerous short white setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangular, as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus indistinct, lower part of sulcus separating smooth, glabrous area, with dense setae. Metascutellum alutaceous to smooth, glabrous, 3.0× as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with some setae; central propodeal area lyre-shaped, smooth, glabrous, with irregular interrupted rugae at the base in large specimens; lateral propodeal carinae strong, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae. Nucha with numerous sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with distinct dense cilia on margin, veins dark brown, radial cell open, 3.8× as long as broad; R1 and Rs not reaching wing margin; areolet small, triangular, closed, and distinct. Rs+M distinct, its projection reaching basalis slightly above mid height.

Metasoma as long as head+mesosoma, higher than long than in lateral view; 2nd metasomal tergum extending to 2/3 of metasoma length in dorsal view, with short white setae anterolaterally, without micropunctures; subsequent terga and hypopygium smooth, glabrous, with almost inconspicuous micropunctures. Prominent part of ventral spine of hypopygium 5.5× as long as broad in ventral view, with some short setae ventrally which do not extend beyond apex of spine.

Body length 2.2–2.4 mm (n = 15).

**Gall** (Figs 407–408). Reddish-yellow furry leaf gall mass; a gregarious cluster of individual cells, 10–25 galls, placed on the underside of leaf, to 20 mm long projecting from leaf by up to 15 mm.

**Biology.** The asexual generation is only known, which induces galls on *Q. potosina* (section *Quercus*, subsection *Leucomexicana*). Previous host records for the name *Andricus tecturnarum* from white oaks found in the south-west of the USA (e.g. Weld 1960, Burks 1979) are almost definitely attributable to the newly described species *F. tetyanae*, which is newly recognised in this study as being distinct from *F. tecturnarum* (based on both morphology and DNA sequences). The gall matures in late autumn, adults start emerging the next February.

**Distribution.** Mexico: San Luis Potosi (Kinsey 1920, authors).

***Feron tetyanae* Melika sp. nov.**

**Figs 409–428**

**Type material.** HOLOTYPE asexual female “USA, AZ, 25miles S of Flagstaff on I17, galltype 40b, ex *Q. turbinella*, AZ422; coll. 2007.10.31., leg. J.A. Nicholls”. PARATYPES (86 asexual females): 19 females “USA, AZ, 25miles S of Flagstaff on I17, galltype 40b, ex *Q. turbinella*, AZ422; coll. 2007.10.31., leg. J.A. Nicholls”; 3 females “USA, AZ, Chiricahua Mtns nr Portal, ex *Q. turbinella*, AZ500, AZ501, AZ509; coll. 2007.10.31., leg. J.A. Nicholls”; 65 females “USA, AZ, Chiricahua Mtns summit, ex *Q. turbinella*, AZ552, AZ581, AZ527; coll. 2007.10.26., leg. J.A. Nicholls”. The holotype and five paratypes deposited at the USNM, 71 paratypes deposited in the PHDNRL and 10 paratypes in UB (Barcelona).

**Etymology.** Species is dedicated to Tetyana Melika, wife of the second author, for her unconditional understanding and many years support for his studies of world Cynipidae.

**Diagnosis.** Asexual females are in the group of *Feron* species characterised by never having the body black; head transversely ovate in frontal view; the gena at least slightly broadened behind the eye; ocelli are not elevated above the frons; inner margins of eyes parallel or very slightly converging ventrally, the transfacial distance is longer than the height of eye; antenna with 12 flagellomeres, sometimes suture between F11 and F12 incomplete; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as the length of the malar space; lateral ocelli smaller, OOL at least 2.5× as long as the diameter of the ocellus, if shorter than the head and mesosoma are not yellowish or light brown; the pronotum laterally with longitudinal carinae; the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points and the mesopleuron is entirely smooth; as in *F. caepula* (asex), *F. rucklei* (asex), *F. scutellum* (asex), *F. stellare* (asex) and some *F. tibiale* (asex). Differs from *F. caepula*, *F. rucklei*, *F. scutellum* and *F. stellare* in having the slightly elevated median area of the lower face alutaceous to delicately coriaceous, matte, and the mesoscutellar foveae are fused or divided by an incomplete triangular coriaceous elevated area. *Feron tetyanae* belongs to the morphological species group comprising *F. serranae* (asex), *F. tecturnarum* (asex) and some *F. tibiale* (asex). The most similar species is the asexual form of *F. tecturnarum* and both differ from *F. tibiale* in the chestnut or rusty brown body colour, frons not bulging, POL at least 1.4× as long as OOL, the genae not broadened behind the eyes, the mesoscutellar disk smooth or finely rugose and radial cell 3.7× as long as broad, while the *F. tibiale* within this group are yellowish or light brown, with the frons bulging, POL subequal to OOL, genae broadened behind the eyes, the mesoscutellar disk reticulate-coriaceous and radial cell 4.8× as long as broad. *Feron tetyanae* differs from *F. tecturnarum* in the chestnut brown body with the head darker than mesosoma in frontal view, the frons is coarsely coriaceous and the mesoscutellar foveae are divided by a fine carina while in *F. tecturnarum* the body is uniformly rusty brown, the head of the same colour as the rest of the body, without dark marks, the frons is finely alutaceous, mesoscutellar foveae divided by a triangular elevated coriaceous central carina.

**Description.** Asexual female (Figs 409–427). Head, mesosoma, metasoma chestnut brown, head always darker than mesosoma; antennae slightly lighter; mouthparts, legs lighter, with darker coxae. In some specimens antennae darker towards apical end; mesosoma in between notauli in anterior half dark brown to black and black stripes present along parapsidal lines.

Head slightly transverse, ovate in frontal view, broadest part level with halfway up eye, with sparse setae, denser on lower face; 2.2× as broad as long in dorsal view. Gena alutaceous, not or only very slightly broadened behind eye in frontal view in small specimens, narrower than transverse diameter of eye in lateral view. Malar space with a few delicate striae radiating from clypeus and reaching eye; eye 2.3× as high as length of malar space. Inner margins of eyes parallel. POL 1.7× as long as OOL, OOL 2.5× as long as diameter of lateral ocellus and 1.2× as long as LOL, all ocelli ovate, of same size. Transfacial distance 1.3× as long as height of eye; toruli located slightly above mid height of head, frons shorter than height of lower face, diameter of antennal torulus 1.2× as long as distance between them, distance between torulus and eye 1.4× as long as diameter of torulus; lower face smooth, with dense white setae; slightly elevated median area alutaceous, with a few setae. Clypeus rectangular, broader than high, alutaceous, with a few long setae along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons uniformly alutaceous-reticulate, without striae and with a few setae, areas between toruli and between torulus and eye also alutaceous; interocellar area alutaceous-reticulate. Vertex, occiput, postgena alutaceous, with white long setae; postocciput alutaceous-reticulate, with concentric lines around occipital foramen and postgenal bridge; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly slightly broader than occipital foramen. Antenna longer than head+mesosoma, with 11 flagellomeres (some specimens with 12 flagellomeres with a distinct suture between F12 and F11), F6 until F11–F12 gradually broadening towards apical end, pedicel slightly longer than broad; F1 1.4× as long as pedicel and 1.3× as long as F2; F2=F3=F4, F5 to F10 nearly equal in length, F11 longer than F10; placodeal sensilla on F5–F11.

Mesosoma 1.2× as long as high, with sparse white setae, except dense setae on lateral propodeal area. Pronotum smooth, with sparse setae, with some delicate striae in dorsoposterior quarter in lateral view; propleuron alutaceous, glabrous. Mesoscutum alutaceous to reticulate, smooth along parapsidal lines with sparse white setae, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, deep, bottom smooth, posteriorly broader and slightly converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum;

anterior parallel line distinct, in the form of a bare, smooth stripe, extending to half-length of mesoscutum; parapsidal line distinct, marked with broad impressed smooth glabrous stripes; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum ovate, slightly longer than broad, circumscutellar carina present; disk of mesoscutellum smooth, glabrous, dull rugose laterally and posteriorly, overhanging metanotum, with dense setae. Mesoscutellar foveae fused in the form of a semilunar depression, with smooth, glabrous bottom, occupying at least 1/3 of mesoscutellum length. Mesopleuron entirely smooth, with setae in antero and posteroventral part; mesopleural triangle smooth, with numerous short white setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangular, as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus indistinct, lower part of sulcus separating smooth, glabrous area, with dense setae. Metascutellum alutaceous to smooth, glabrous, 3.0x as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with some setae; central propodeal area lyre-shaped, smooth, glabrous, with irregular interrupted rugae at the base in large specimens; lateral propodeal carinae strong, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae. Nucha with numerous sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with distinct dense cilia on margin, veins dark brown, radial cell open, 3.7x as long as broad; R1 and Rs not reaching wing margin; areolet small, triangular, closed and distinct. Rs+M distinct, its projection reaching basalis slightly above mid height.

Metasoma as long as head+mesosoma, higher than long than in lateral view; 2nd metasomal tergum extending to 2/3 of metasoma length in dorsal view, with short white setae anterolaterally, without micropunctures; subsequent terga and hypopygium smooth, glabrous, without micropunctures. Prominent part of ventral spine of hypopygium 5.0x as long as broad in ventral view, with some short setae ventrally which do not extend beyond apex of spine.

Body length 1.4–2.2 mm (n = 15).

**Gall** (Fig. 428). Reddish-yellow furry leaf gall mass, a gregarious cluster of individual cells. Hairs covering the gall cluster are quite brittle and crystalline. On underside of leaf, to 20 mm long, projecting from leaf by up to 15 mm.

**Biology.** Only the asexual generation is only known, which induces galls on *Q. arizonica*, *Q. oblongifolia*, *Q. turbinella* and *Q. toumeyi* (section *Quercus*, subsection *Leucomexicana*) and on *Q. gambelii* (section *Quercus*, subsection *Dumosae*) (Burks 1979). The gall matures in late autumn and adults start emerging the next spring. This species is newly recognized as being

distinct from *F. tecturnarum* (based on both morphology and DNA sequences); all specimens we have examined from previous collectors taken in the USA south-west and identified as *F. tecturnarum* show the diagnostic characters of *F. tetyanae*, so we consider that all records of *F. tecturnarum* from the USA should actually be attributed to the new taxon *F. tetyanae*.

**Distribution.** USA: New Mexico, Arizona.

***Feron tibiale* Kinsey, 1937 comb. rev.**

**Figs 429–463**

*Feron tibiale* Kinsey, 1937: 70, female, gall.

*Feron tostum* Kinsey, 1937: 71, female, gall; **syn. nov.**

*Feron uterinum* Kinsey, 1937: 72, female, gall; **syn. nov.** Figs 453–463.

*Andricus tibialis* (Kinsey) Weld, 1952a: 310.

*Andricus tostus* (Kinsey) Weld, 1952a: 310.

*Andricus uterinus* (Kinsey) Weld, 1952a: 310.

**Types examined.** Holotypes and paratypes of *F. tibiale*, *F. uterinum*, and *F. tostum* deposited at the AMNH, NYC were examined. ***Feron tibiale***, HOLOTYPE asexual female “Mex (City) 25E D.F. 7000’, Mex. Gall 1-2-32, 138 fms. 3-2-32”, “*Q. texcocana*, Kinsey coll.”, red “*Xystoteras tibialum*”; PARATYPES (10 asexual females) “Mex (City) 25E, D.F. 7000’ Mex. Gall 1.2.32, 48 females 3.15.32.”, “*Q. texcocana* Kinsey Coll.”, red Kinsey’s handwriting label “*Xyst. tibialum* Paratype”. Holo- ~~Paratype~~. ***Feron tostum***, HOLOTYPE asexual female “Namiquipa 30W Chi. 5200’, Mex. Gall 10-18-31, very many fms. 3-10-32”, “*Q. chihuahuensis*, Kinsey coll.”, red “*Xyst. tostum*, Holo- ~~Paratype~~”. ***Feron uterinum***, HOLOTYPE asexual female “Queretaro 28N Qro 7300’, Mex. Gall 1-17-32, 6 fms. 3-26-32”, “*Q. chihuahuensis*, Kinsey coll.”, red “*Xyst. uterium*, Holo- ~~Paratype~~”; PARATYPES (9 asexual females on 5 pins and one gall) “Queretaro 28N, Qro 7300’ Mex. Galls 1.17.32, 119 females 3.10.32”, “*Q. chihuahuensis* Kinsey coll.”, red handwriting label “*Xyst. uterinum* Paratype”. The general collection of the AMNH in NYC holds a large number of deposited paratypes.

**Additional material.** 56 asexual females: “MEX-101, Mexico, Ciudad de Mexico, Santa Fe, ex *Q. rugosa*, (16.i.2018) 17-31.i.2018: 10 females, leg. O.Cabral, R.Treto, L.G.Landa & C.Carrillo”; “MEX-195, Mexico, Mexico, San Felipe del Progreso, Tunal Salto, ex *Q. glaucoides*, (15.ii.2014) 21.ii.2014: 4 females, leg. R. D. García-Martiñón”; “MEX-205, Mexico, Mexico, San Felipe del Progreso, Tunal Salto, ex *Q. glaucoides*, (26.xii.2013) 14-16.ii.2014: 23 females (plus one specimen for DNA extraction), leg. R. D. García-Martiñón”;



“MEX-208, Mexico, Mexico, San Felipe del Progreso, Tunal Salto, ex *Q. glabrescens*, (26.xii.2013) 21-23.i.2014: 11 females (plus one specimen for DNA extraction), leg. R. D. García-Martiñón”; “MEX-500, Mexico, Mexico, Tepoztlán, Arcos del Sitio (19°45'36.9" N, 99°20'40.4" W), ex *Q. obtusata*, (09.ix.2007) 08.x.2007: 9 females, leg. Chagoyán-García.”.

**Diagnosis.** Asexual females belong to the group of *Feron* species characterised by never having a black body; head rounded or trapezoid to triangular in frontal view, ocelli are not elevated above the frons; inner margins of eyes parallel or very slightly converging ventrally, the transfacial distance is equal to or longer than the height of eye; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as length of the malar space; lateral ocelli are smaller, OOL at least 2.5× as long as the diameter of the ocellus, if shorter then the head and mesosoma are not yellowish or light brown; the pronotum laterally with longitudinal carinae; the mesoscutum is alutaceous to coriaceous, rugose-reticulate or reticulate, without piliferous points.

Specimens of *F. tibiale* can be divided into two different morphological groups with respect to sculpturing of their mesopleuron, either smooth or with a transverse reticulated-carinated band. The morphotype with a transverse band at mid-height of mesopleuron is similar to *F. gigas* (asex), *F. parmula* (asex), *F. stellulum* (asex) and *F. syndicorum* (asex). *Feron tibiale* differs from *F. gigas*, *F. parmula* and *F. stellulum* in having the gena broadened behind the eye in frontal view (while the gena is not broadened behind the eye in frontal view in *F. gigas*, *F. parmula* and *F. stellulum*). The most similar species is the asexual form of *F. syndicorum* but that species differs from the asexual form of *F. tibiale* (part) in that the mesoscutum is finely alutaceous; the notaulus is complete but shallow and alutaceous at least on anterior 3/4 of its length; the mesoscutellar disk is strongly curved in lateral view, which makes the mesoscutum and mesoscutellum form two independent lobes in lateral view; and the subaxillular bar reaches 1/3 of the height of mesoscutellum. *Feron tibiale* (part) is coarsely reticulated on the mesoscutum, has a complete notaulus which is inconspicuous on anterior 1/4 of its length; the mesoscutellum is flat in lateral view and forms a single curve with the mesoscutum in lateral view; and the subaxillular bar reaches half the height of metascutellum.

The specimens with smooth mesopleura belong to the group of *Feron* species characterised by having antennae with 12 flagellomeres; head transversely ovate in frontal view, lateral sides of the pronotum longitudinally striated at least on the posterior half, remainder of the pronotum alutaceous, matte; as in *F. serranae* (asex), *F. tecturnarum* (asex) and *F. tetyanae* (asex). This morphotype of *F. tibiale* differs from *F. serranae* in having the

mesoscutellum slightly longer than broad and circumscutellar carina absent, while the mesoscutellum is 1.3× as long as broad and with a strong circumscutellar carina in *F. serranae*. *Feron tibiale* differs from *F. tecturnarum* and *F. tetyanae* in the yellowish to light brown body colour, the frons bulging in frontal view, POL subequal to OOL, the mesoscutum is uniformly reticulate-coriaceous, the center of the mesoscutellar disk coriaceous; radial cell around 4.8× as long as broad, while the other two species are reddish brown to dark brown, the frons is not bulging, POL at least 1.4× as long as OOL, the mesoscutum alutaceous to reticulate, the center of the mesoscutellar disk is smooth or finely rugose, and the radial cell measures around 3.7× as long as broad.

**Re-description.** Asexual female (Figs 429–439, 441–452, 453–463). Body, including mouthparts, legs uniformly light brown; antennae light brown, darker from F7 or F8.

Head transverse, 1.2× as broad as high in frontal view, with sparse setae, denser on lower face; 2.1× as broad as long in dorsal view; head narrower than mesosoma in frontal view. Gena alutaceous, broadened behind eye in frontal view, as broad as transverse diameter of eye in lateral view. Malar space alutaceous, with a few delicate striae radiating from clypeus and not reaching eye; eye 2.0× as high as length of malar space. Inner margins of eyes parallel. POL 1.9× as long as OOL, OOL 1.9× as long as diameter of lateral ocellus and 2.0× as long as LOL, all ocelli black, ovate, of same size. Transfacial distance 1.3× as long as height of eye; torulus located slightly above mid height of eye, frons shorter than height of lower face, diameter of antennal torulus 1.2× as long as distance between them, distance between torulus and eye 1.2× as long as diameter of torulus; lower face delicately coriaceous, with dense white setae; slightly elevated median area delicately coriaceous, with a few setae. Clypeus slightly broader than high, alutaceous, with sparse long setae, especially along ventral edge; ventrally rounded, not emarginate and without median incision; anterior tentorial pit rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons delicately coriaceous to reticulate, without striae and with a few setae, small triangular area under central ocellus smooth, glabrous; areas between toruli and between torulus and eye delicately coriaceous; interocellar area delicately coriaceous to reticulate. Vertex, occiput, postgena delicately coriaceous to reticulate, with white long setae; postocciput delicately coriaceous to reticulate, with delicate indistinct concentric lines around occipital foramen and postgenal bridge; posterior tentorial pit large, elongate, area below impressed, glabrous; occipital foramen slightly shorter than height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulcus; postgenal sulcus bent

strongly outwards, reaching posterior tentorial pit and postgenal bridge unusually broad. Antenna slightly longer than head+mesosoma, with 12 flagellomeres, pedicel slightly longer than broad; F1 2.1× as long as pedicel and 1.2× as long as F2; F2 slightly longer than F3, F4=F5, F6 slightly longer than F7, F8=F9=F10=F11, F12 slightly longer than F11; placodeal sensilla indistinct, visible on F5–F12.

Mesosoma slightly longer than high, with sparse white setae, denser on lateral propodeal area. Pronotum smooth, with sparse setae, with delicate parallel concentric striae laterally; propleuron smooth, with sparse setae. Mesoscutum uniformly reticulato-coriaceous, with sparse white setae between notauli anteriorly and along notauli, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, distinctly impressed on all length, with smooth, glabrous bottom; anterior parallel line indistinct, in the form of a bare, smooth stripe, extending to 1/3 length of mesoscutum; parapsidal line distinct, marked with broad impressed smooth glabrous stripes; median mesoscutal line absent; parascutal carina narrow, reaching notaulus. Mesoscutellum trapezoid, slightly longer than broad; center of disk of mesoscutellum coriaceous, dull rugose laterally and posteriorly, overhanging metanotum, with a few setae. Mesoscutellar foveae semiquadrangular, broader than high, with smooth, glabrous bottom, usually divided by an incomplete triangular coriaceous elevated area (in some specimens hardly traceable), rarely complete. Mesopleuron mainly smooth, glabrous, sometimes with delicate parallel longitudinal striae in anterodorsal part, with setae along ventral edge; mesopleural triangle smooth, with short white setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangular, as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus distinct, lower part of sulcus separating a smooth glabrous densely pubescent area. Metascutellum smooth, slightly higher than height of smooth, glabrous ventral impressed area; metanotal trough smooth, with dense setae; central propodeal area lyre-shaped, smooth, glabrous, with irregular interrupted rugae at the base; lateral propodeal carinae strong, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae on piliferous points. Nucha with net of irregular rugae, with few distinct parallel longitudinal sulci laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins light brown, radial cell open, 4.8× as long as broad; R1 and Rs not reaching wing margin; areolet small, triangular, closed, delimited with indistinct veins, Rs+M visible on 3/4 of distance between areolet and basalis, its projection reaching basalis at its half height.

Metasoma slightly longer than head+mesosoma, higher than long in lateral view; 2nd metasomal tergum extending to more than half of metasoma length in dorsal view, with short white setae anterolaterally, without micropunctures; subsequent terga and hypopygium smooth, glabrous, with indistinct micropunctures; prominent part of ventral spine of hypopygium 5.7× as long as broad in ventral view, with a few short setae ventrally.

Body length 0.9–2.6 mm (n = 12).

**Gall** (Fig. 440). Individual galls swollen, cylindrical, flaring at the broadened tip, covered with more or less crystalline processes, with a few broad filaments (chiefly at the base of each gall), with almost all of the fibers fine, hair-like. Galls clustered, forming a more or less solid and tangled mass up to 27 mm in diameter and 13 mm high. Purple rose and light brown when young, becoming light straw brown to russet, rosy brown, or dark brown with age (Kinsey 1937).

**Biology.** Only the asexual generation is known, which induces galls on section *Quercus*, subsection *Leucomexicana* oaks: *Q. arizonica*, *Q. chihuahuensis*, *Q. deserticola* (= *Q. texcocana*) according to Kinsey (1937); adults emerge mainly during January–February (Kinsey 1937). *Quercus glabrescens*, *Q. glaucoides*, *Q. obtusata*, and *Q. rugosa* are new host records for this study.

Two species described by Kinsey (1937), *F. tostum* and *F. uterinum*, are morphologically consistent with the series of specimens that Kinsey called *F. tibiale*. They simply represent geographical variants of that species and hence we synonymise the names in this study.

The conspecific status of the two morphological variants within this species (one with a smooth mesopleuron, the other having a mesopleuron with a transverse reticulated-carinated band) was confirmed using DNA sequence data. One individual from each of the two morphotypes was sequenced for cytb and ITS2; both individuals had identical sequences for both genes (GenBank accessions OQ446186, OQ446241, OQ448247–OQ448248).

**Distribution.** Mexico: Mexico City, Chihuahua, Durango, Querétaro (Kinsey 1937); also from the State of Mexico in this study.

***Feron tubifaciens* (Weld, 1926) comb. nov.**

**Figs 464–475**

*Xanthoteras tubifaciens* Weld, 1926: 53, female, gall.

*Trichoteras tubifaciens* (Weld): Weld 1951: 625.

*Andricus tubifaciens* (Weld): Melika & Abrahamson 2002: 162.

**Types examined.** HOLOTYPE: Asexual female “Sequoia Nat. Park, Cal.”, “Cut out Nov. 10”, “*Q. garryana*”, “1785”, red label “Type No. 27201 USNM”, “*Xanthoheras tubifaciens* Weld” deposited in USNM, examined by GM. Specimen data and images available at <http://n2t.net/ark:/65665/3ffef724-e7dc-45df-af95-997079719085>. Weld (1926) designated 39 paratypes which are deposited in different institutions all over the USA (not examined by the authors).

**Additional material.** 48 asexual females “USA, CA, Berry summit, Arcata, CA4; galltype 150, ex *Q. garryana*, coll. 2007.11.04., leg. J.A. Nicholls”.

**Diagnosis.** This is the only *Feron* species with a uniformly imbricate frons and the clypeus with short interrupted delicate transverse striae. Asexual females belong to the *Feron* species group characterised by having the pronotum laterally with longitudinal carinae and the mesoscutum alutaceous to coriaceous, rugose-reticulate or reticulate, with piliferous points; as also occurs in *F. discularis* (asex) and *F. kingi* (asex). Differs from *F. discularis* in the body colour, which is never black; the frons is not bulging in frontal view, ocelli are not elevated above the head; toruli are located in the upper half of the head; the median mesoscutal line absent. The most similar species is *F. kingi* but differs from it in colour, the gena is not broadened behind the eye in frontal view and the fore wing is only slightly longer than length of the body; for other characters see couplet 29 in the key.

**Re-description.** Asexual female (Figs 464–474). Head, antennae, metasoma dark brown to black, mesosoma reddish brown with some darker tints; mouthparts and legs reddish brown.

Head transverse, alutaceous, with dense white setae all over, except frons and vertex with sparse setae; rounded, 1.2× as broad as high and slightly broader than mesosoma in frontal view; 1.9× as broad as long from dorsal view. Gena alutaceous, not broadened behind eye in frontal view, narrower than transverse diameter of eye in lateral view. Malar space alutaceous, glabrous, with a few striae radiating from clypeus, malar sulcus absent; eye 1.9× as high as length of malar space. Inner margins of eyes parallel. POL 1.3× as long as OOL, OOL 3.0× as long as diameter of lateral ocellus and 1.3× as long as LOL, all ocelli slightly ovate, of same size. Transfacial distance 1.6× as long as height of eye; diameter of antennal torulus as long as distance between them, distance between torulus and eye 1.4× as long as diameter of torulus; lower face smooth to delicately alutaceous, with dense white setae, without striae; elevated median area alutaceous, with narrow elevated keel running from clypeus towards base of toruli. Clypeus rectangular, nearly 2.0× as broad as high, impressed, with short interrupted numerous transverse striae; ventrally rounded, not emarginate, with

long setae and without median incision; anterior tentorial pit large, rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons uniformly imbricate, without striae and setae, interocellar area alutaceous. Vertex, occiput alutaceous; postocciput with numerous short delicate transverse interrupted striae; postgena alutaceous, with dense setae; posterior tentorial pit large, elongated, area below impressed; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulci which diverge strongly toward occipital foramen, postgenal bridge anteriorly broader than occipital foramen. Antenna longer than head+mesosoma, with 12 flagellomeres, pedicel slightly longer than broad; F1 2.0× as long as pedicel and 1.1× as long as F2; F2 1.2× as long as F3; F3=F4, F5 1.1× as long as F6, subsequent flagellomeres nearly equal in length, F12=F11; placodeal sensilla on F5–F12.

Mesosoma nearly as long as high, with sparse white setae, except dense setae on lateral propodeal area. Pronotum smooth, with sparse setae, with numerous parallel delicate striae laterally; propleuron smooth, glabrous. Mesoscutum alutaceous, with some smooth areas, with sparse white setae and distinct piliferous points, slightly longer than broad (greatest width measured across mesoscutum level with base of tegulae). Notaulus complete, deep, bottom smooth, posteriorly broader and converging; at posterior end the distance between notauli shorter than distance between notaulus and side of mesoscutum; anterior parallel line invisible; parapsidal line distinct, marked with broad slightly impressed line; median mesoscutal line absent; parascutal carina broad, reaching notaulus. Mesoscutellum ovate, slightly longer than broad; disk of mesoscutellum alutaceous, glabrous, dull rugose laterally and posteriorly, overhanging metanotum, with dense long setae. Mesoscutellar foveae ovate, with smooth, glabrous bottom, divided by a narrow rugose elevated median area. Mesopleuron entirely smooth, with setae in posteroventral and anteroventral parts; most posterodorsal part with striae; mesopleural triangle smooth, with some longitudinal striae and a few setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangulate, posteriorly higher than height of metanotal trough; metapleural sulcus reaching mesopleuron in upper 1/3 of its height, upper part of sulcus indistinct, sulcus separating smooth, glabrous area, with some setae in lower part. Metascutellum delicately coriaceous, as high as height of smooth, glabrous ventral impressed area; metanotal trough smooth, with some setae; central propodeal area lyre-shaped, smooth, glabrous, with very short rugae in the most posterior part; lateral propodeal carinae distinct, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae. Nucha with delicate sulci dorsally and laterally. Tarsal claws with basal lobe.

Fore wing slightly longer than length of body but shorter and narrower than typically-sized wings in *Feron*. Fore wing hyaline, with distinct dense cilia on margin, veins light brown, radial cell open, 4.0× as long as broad; R1 and Rs reaching wing margin and slightly projected; areolet small, indistinct. Rs+M narrow, inconspicuous, visible on 2/3 length between areolet and basalis; its projection reaching basalis at half height.

Metasoma as long as head+mesosoma, higher than long in lateral view; 2nd metasomal tergum extending to half-length of metasoma in dorsal view, with patch of dense white setae anterolaterally, without micropunctures; subsequent terga and hypopygium smooth, glabrous, without micropunctures. Prominent part of ventral spine of hypopygium 5.0× as long as broad in ventral view, with white setae ventrally.

Body length 1.5–2.35 mm (n = 100) (Weld 1926).

**Gall** (Fig. 475). Convex mass of tubular galls standing side by side in a compact cluster on the underside of the leaf. The mass measures up to 25 mm long by 15 mm wide. The individual galls are easily detached, white or cream-coloured, up to 9 mm long, tapering gradually from the base to a diameter of about 3 mm at the distal open end, the distal portion covered with tapering spines which are often rosy at the tip. The single larval cell lies midway along the length of the gall and measures about 2 mm long by 1.2 mm in diameter (Weld 1926).

**Biology.** Only the asexual generation is known, inducing galls on *Q. garryana* (section *Quercus*, subsection *Dumosae*) (Weld 1926, Burks 1979). Galls mature in October–November.

**Distribution.** USA: California.

***Feron verutum* Kinsey, 1937 comb. rev.**

**Figs 476–488**

*Feron verutum* Kinsey, 1937: 75, female, gall.

*Andricus verutus* (Kinsey) Weld, 1952a: 310.

**Types examined.** HOLOTYPE: Asexual female “Rio Verde 14 mi S.L.P. 6500”, Mex. Gall 12.4.31, 63 fms. 5-12-32”, “*Q. macrophylla*, Kinsey coll.”, red “*Xyst. verutum*, Holo-Paratype”. PARATYPES (4 asexual females) with the same labels as the holotype. Holotypes and paratypes deposited at the AMNH were examined by GM. In the general collections of the AMNH a large number of paratypes are also deposited.

**Additional material.** 2 asexual females “MEX-421, Mexico, Ciudad de Mexico, Santa Fe, ex *Q. rugosa*, (16.i.2018) 17-31.i.2018, 2 females, leg. D. Cibrián-Tovar & U. Barrera-Ruiz”.

**Diagnosis.** Asexual females belong to the group of *Feron* species in which the body is never black; the head is quadrangular or ovate in frontal view, with ocelli elevated above the frons; inner margins of eyes parallel or very slightly converging ventrally; the transfacial distance is equal to or longer than height of eye; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as the length of malar space; lateral ocelli are large, OOL subequal or at most 1.7× as long as the diameter of ocellus; the pronotum laterally with longitudinal carinae; the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points; as in *F. splendens* (asex) and *F. vitreum* (asex). Differs from *F. vitreum* in the F1 being subequal or slightly longer than scape+pedicel; the transfacial distance is longer than the height of eye. Differs from *F. splendens* in that the mesoscutum without striae in anterior part between notauli, anterior parallel lines as a bare smooth stripe, mesoscutellar foveae are separated by a thin carina, posteriorly not delimited by a carina.

**Re-description.** Asexual female (Figs 476–487). Body, including mouthparts, antennae, legs uniformly light brown.

Head quadrangular, 1.2× as broad as high in frontal view, with sparse setae; 2.1× as broad as long in dorsal view; head narrower than mesosoma in frontal view. Gena alutaceous, not broadened behind eye and with parallel sides in frontal view, narrower than transverse diameter of eye in lateral view in ventral part. Malar space alutaceous, with a few delicate striae radiating from clypeus and not reaching eye; eye 2.6–3.0× as high as length of malar space. Inner margins of eyes parallel. POL 1.5–2.7× as long as OOL, OOL slightly shorter than diameter of lateral ocellus and slightly longer than LOL, all ocelli ovate, of same size. Transfacial distance slightly longer than height of eye; torulus located above mid height of eye, frons shorter than height of lower face, diameter of antennal torulus 1.4x as long as distance between them, distance between torulus and eye equal to diameter of torulus; lower face delicately coriaceous, with white setae; slightly elevated median area, delicately coriaceous, with a few setae. Clypeus rectangular, more than 2.0× as broad as high, alutaceous, glabrous, without setae along ventral edge; ventrally straight, not emarginate and without median incision; anterior tentorial pit rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons coriaceous, without striae and with a few setae, small triangular area under central ocellus coriaceous; areas between toruli and between torulus and eye delicately coriaceous; interocellar area coriaceous. Vertex, occiput, postgena, postocciput smooth, with sparse white long setae; postgena with parallel concentric black stripes; posterior tentorial pit large, elongate, area below impressed, glabrous; occipital



foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulcus; postgenal sulcus bent strongly outwards, reaching posterior tentorial pit; postgenal bridge broad, as high as occipital foramen. Antenna slightly longer than head+mesosoma, with 12 flagellomeres, pedicel longer than broad; F1 2.2× as long as pedicel, slightly longer than scape+pedicel and slightly longer than F2; F2=F3, F4 shorter than F3 and slightly longer than F5, F6 longer than F7, F8=F9, F9 slightly longer than F10, F10=F11=F12; placodeal sensilla indistinct, visible on F4–F12.

Mesosoma slightly longer than high, with sparse white setae, denser along anterolateral edge of pronotum and on lateral propodeal area. Pronotum smooth, with sparse setae, with delicate parallel concentric striae laterally; propleuron smooth, with sparse long white setae. Mesoscutum delicately coriaceous, smooth, glabrous in between notauli in posterior half, longer than broad (greatest width measured across mesoscutum level with base of tegulae), with sparse white setae in anterior 1/3 of mesoscutum length. Notaulus complete, distinctly impressed on entire length, with smooth, glabrous bottom; at posterior end the distance between notauli only just larger than width of notaulus on its posterior margin; anterior parallel line in the form of a bare, smooth stripe, extending to 1/3 length of mesoscutum; parapsidal line marked with broad smooth glabrous stripes; median mesoscutal line absent; parascutal carina narrow, reaching notaulus. Mesoscutellum trapezoid, longer than broad; disk of mesoscutellum uniformly dull rugose, overhanging metanotum, with a few scattered setae. Mesoscutellar foveae semiquadrangular, slightly broader than high, with smooth, glabrous bottom, divided by distinct narrow central carina. Mesopleuron entirely smooth, glabrous, with setae in anteroventral part; mesopleural triangle smooth, with dense short white setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangular, as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus distinct, lower part of sulcus separating delicately coriaceous area, with a few setae. Metascutellum smooth, glabrous with delicate longitudinal parallel striae, taller than height of smooth, glabrous ventral impressed area; metanotal trough smooth, with sparse white setae; central propodeal area lyre-shaped, smooth, glabrous; lateral propodeal carinae strong, bent outwards in posterior 1/3; lateral propodeal area smooth, with long dense white setae on piliferous points. Nucha without sulci dorsally, with sulci only laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins brown, radial cell open, 4.8× as long as broad; R1 and Rs not reaching wing margin; areolet

indistinct, Rs+M distinct along 1/2 of distance between areolet and basalis, its projection reaching basalis at half of its height.

Metasoma longer than head+mesosoma, slightly higher than long in lateral view; 2nd metasomal tergum extending to 2/3 of metasoma length in dorsal view, with numerous white setae anterolaterally, without micropunctures; subsequent terga and hypopygium smooth, glabrous, without micropunctures; prominent part of ventral spine of hypopygium 5.7× as long as broad in ventral view, with few short setae ventrally.

Body length 1.6–2.8 mm (n = 3).

**Gall** (Fig. 488). Individual galls long and slender, uniformly cylindrical or flaring at the top, more or less covered with distinctly crystalline processes all of which are broad and blunt, filamentous, not fine nor hairlike. The whole cluster forming a spiny mass in which the individual galls are still prominent, the clusters up to 30 mm in diameter and 12 mm high. Bright purple rose and straw colour when fresh, darkening with age (Kinsey 1937).

**Biology.** Only the asexual generation is known, which induces galls on section *Quercus*, subsection *Leucomexicana* oaks: *Q. magnoliifolia*, and *Q. rugosa* (Kinsey 1937). Fresh mature galls in January, adults emerge in April (Kinsey 1937). The type material is labelled as collected from *Q. macrophylla*, but Kinsey did not define the authorship of the host species. Two possible hosts coexist within the distribution of *F. verutum*: *Q. magnoliifolia* (= *macrophylla* Née), or *Q. resinosa* (= *macrophylla* sensu Trel.).

**Distribution.** Mexico: San Luis Potosi, Guanajuato (Kinsey 1937); also from Ciudad de Mexico state in this study.

#### ***Feron vitreum* Kinsey, 1937 comb. rev.**

##### **Figs 489–513**

*Feron vitreum* Kinsey, 1937: 76, female, gall.

*Feron validum* Kinsey, 1937: 73, **syn. nov.** Figs 502–513.

*Andricus vitreus* (Kinsey) Weld, 1952a: 311.

*Andricus validus* (Kinsey) Weld, 1952a: 310.

**Types examined.** For *Feron vitreum*: HOLOTYPE: Asexual female “Mex(City) D.F. 9200’, Mex. Gall 1.12.32, 100 fms. 3.10.32”, “*Q. rhodophlebia*, Kinsey coll.”, red “*Xyst. vitreum*, Holo- ~~Para~~type”. PARATYPES (4 asexual females) with the same labels as the holotype. For *Feron validum*: HOLOTYPE: Asexual female “Cuernavaca Mor 8700’, Mex. Gall 1-7-32, 41 fms. 4-10-32”, “*Q. texcocana*, Kinsey coll.”, red “*Xyst. validum*, Holo- ~~Para~~type”. Holotypes and 4 paratype asexual females with the same labels as the holotype, deposited in the AMNH

were examined by GM. In the general collection of AMNH a large number of paratypes are also deposited.

**Additional material.** 28 asexual females: “MEX-326, Mexico, Morelos, Coajomulco, ex *Q. rugosa*, (04.x.2016) 15-30.iv.2017: 27 females, leg. E. Castillo”; “MEX-421, Mexico, Ciudad de Mexico, Santa Fe, ex *Q. rugosa*, (16.i.2018) 17-31.i.2018: 1 female, leg. D. Cibrián-Tovar & U. Barrera-Ruíz”.

**Diagnosis.** Asexual females belong to the group of *Feron* species without a black body; the head is quadrangular or ovate in frontal view, with ocelli elevated above the frons; inner margins of eyes parallel or very slightly converging ventrally; the transfacial distance is equal to or longer than the height of the eye; toruli are located above the mid-height of eyes; the eye is less than 3.0× as high as the length of malar space; lateral ocelli are large, OOL subequal or maximum 1.7× as long as the diameter of ocellus; the pronotum laterally with longitudinal carinae; the mesoscutum alutaceous to coriaceous, rugose-reticulate, reticulate, without piliferous points; as in *F. splendens* (asex) and *F. verutum* (asex). *Feron vitreum* differs from these two species in having the F1 distinctly longer than scape+pedicel and the transfacial distance being equal to or slightly shorter than the height of the eye.

**Re-description.** Asexual female (Figs 489–500, 502–513). Body, including mouthparts, antenna, legs uniformly light brown; antenna from F5 dark brown.

Head quadrangular, 1.1× as broad as high in frontal view, with sparse setae; 2.1× as broad as long in dorsal view; head narrower than mesosoma in frontal view. Gena alutaceous, not broadened behind eye and with parallel sides in frontal view, narrower than transverse diameter of eye at ventral end in lateral view. Malar space alutaceous, with a few delicate striae radiating from clypeus but not reaching eye; eye 2.4× as high as length of malar space. Inner margins of eyes parallel. POL 2.5× as long as OOL, OOL slightly shorter than diameter of lateral ocellus and LOL slightly longer than OOL, all ocelli ovate, of same size. Transfacial distance slightly shorter than height of eye; torulus located above mid height of eye, frons shorter than height of lower face, diameter of antennal torulus 1.2× as long as distance between them, distance between torulus and eye slightly shorter than diameter of torulus; lower face delicately coriaceous with white setae; slightly elevated median area delicately coriaceous with a few setae. Clypeus rectangular, broader than high, alutaceous, glabrous, with setae along ventral edge; ventrally straight, not emarginate and without median incision; anterior tentorial pit rounded, distinct, epistomal sulcus distinct, clypeo-pleurostomal line well impressed. Frons coriaceous, without striae and with a few setae, small triangular area under

central ocellus coriaceous; areas between toruli and between torulus and eye delicately coriaceous; interocellar area coriaceous. Vertex, occiput, postgena, smooth, with sparse white long setae; postocciput smooth, with concentric lines around occipital foramen and postgenal bridge; posterior tentorial pit large, elongate, area below impressed, glabrous; occipital foramen as high as height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulcus; postgenal sulcus bent strongly outwards, reaching posterior tentorial pit; postgenal bridge unusually broad. Antenna slightly longer than head+mesosoma, with 12 flagellomeres, pedicel longer than broad; F1 2.4× as long as pedicel, much longer than scape+pedicel and 1.2× as long as F2; F2 nearly equal to F3, F3=F4=F5, F6 slightly longer than F7, F8 slightly longer than F9, F9=F10, F10=F11, F12 shorter than F11; placodeal sensilla indistinct, visible on F4–F12.

Mesosoma slightly longer than high, with sparse white setae, with denser setae on lateral propodeal area. Pronotum smooth, with sparse setae, with delicate parallel concentric striae laterally; propleuron smooth, with sparse long white setae. Mesoscutum delicately coriaceous, smooth, glabrous in between posterior half of notauli, longer than broad (greatest width measured across mesoscutum level with base of tegulae), with sparse white setae in anterior 1/3 of mesoscutum length. Notaulus complete, distinctly impressed along entire length, with smooth, glabrous bottom, converging strongly posteriorly with a short distance between notauli posteriorly; anterior parallel line in the form of a bare, smooth stripe, extending to 1/3 length of mesoscutum; parapsidal line distinct, marked with broad smooth glabrous stripes; median mesoscutal line absent; parascutal carina narrow, reaching notaulus. Mesoscutellum trapezoid, longer than broad; disk of mesoscutellum uniformly dull rugose, overhanging metanotum, with a few scattered setae. Mesoscutellar foveae ovate, slightly longer than high, with smooth, glabrous bottom, divided by broad elevated smooth triangular area. Mesopleuron entirely smooth, glabrous, with setae in anteroventral part; mesopleural triangle smooth, with numerous short white setae; dorsal and lateral axillar areas smooth, with dense white setae; subaxillular bar smooth, glabrous, triangular, as high as height of metanotal trough; metapleural sulcus reaching mesopleuron at half of its height, upper part of sulcus indistinct, invisible, lower part of sulcus separating smooth area, with dense setae. Metascutellum smooth, glabrous with delicate longitudinal parallel striae, higher than height of smooth, glabrous ventral impressed area; metanotal trough smooth with dense setae; central propodeal area lyre-shaped, smooth, glabrous, with a few short parallel striae in posterolateral part; lateral propodeal carinae strong, bent outwards in posterior 1/3; lateral propodeal area

smooth, with long dense white setae. Nucha without sulci dorsally, with sulci only laterally. Tarsal claws with basal lobe.

Fore wing longer than body, hyaline, with short dense cilia on margin, veins brown, radial cell open, 4.8× as long as broad; R1 and Rs not reaching wing margin; areolet indistinct, Rs+M distinct along half of distance between areolet and basalis, its projection reaching basalis at half of its height.

Metasoma longer than head+mesosoma, longer than high in lateral view; 2nd metasomal tergum extending to 4/5 of metasoma length in dorsal view, with numerous white setae anterolaterally, without micropunctures; subsequent terga and hypopygium smooth, glabrous, without micropunctures; prominent part of ventral spine of hypopygium 4.1× as long as broad in ventral view, with a few short setae ventrally.

Body length 1.2–2.8 mm (n = 10).

**Gall** (Fig. 501). Individual galls long and slender, uniformly cylindrical or flaring at the top, fairly well covered with distinctly crystalline processes all of which are broad and blunt, filamentous, none of which are fine or hair-like. Galls clustered, forming a spiny mass in which the individual galls are quite prominent, the clusters up to 55 mm in diameter and 17 mm high. Bright purple rose and straw colour when fresh, darkening with age (Kinsey 1937).

**Biology.** Only the asexual generation is known, which induces galls in October-January, on section *Quercus*, subsection *Leucomexicana* oaks: *Q. deserticola* Trel. (= *Q. texcocana* Trel.), and *Q. rugosa* (= *Q. rhodophlebia*), adults emerge in April.

Kinsey (1937) described another species, *F. validum*, which we consider is morphologically consistent with Kinsey's series of specimens of *F. vitreum* and simply represents a geographical variant of that species; hence we synonymise the name in this study.

**Distribution.** Mexico: Luis Potosi, Guanajuato (Kinsey 1937).

## Discussion

We demonstrate here that *Feron* is a valid genus, phylogenetically allied to the Nearctic and Neotropical genera *Dros*, *Prokius* and *Phylloteras*. Morphologically it can be distinguished from these genera by having two smooth or almost smooth areas between the lower face and clypeus, the frons is sculptured, and the malar sulcus is absent. *Dros* is the sister genus to *Feron*, and a close morphological relationship between the adults of *Dros* and some *Feron* species (*F. amphorus*, *F. crystallinum*, *F. discale*) is apparent as these *Feron* species have the primarily smooth body that is typical for all *Dros* species; however, in *Feron* species at least the frons is sculptured and never smooth as in *Dros*.

*Feron* was synonymized with *Andricus* by Weld (1951). The closely related genus *Dros* was also erroneously synonymized into *Andricus* (Melika & Abrahamson 2002) but has recently been re-established (Pujade-Villar *et al.* 2017). The lineage containing the type species of *Andricus* (henceforth termed *Andricus sensu stricto*) is nested in a separate well-supported clade that is distinct from *Feron* and *Dros* (Fig. 514), thus supporting the re-establishment of *Feron* as a valid genus. In addition, the recently re-established or described Nearctic genera *Druon*, *Striatoandricus*, *Trichoteras* and *Disholandricus* have also been characterised as distinct from *Andricus* with corroborating molecular and morphological evidence (see Fig 514; Zimmermann 2018, Cuesta-Porta *et al.* 2020, Melika *et al.* 2021, Cuesta-Porta *et al.* 2022). Yet despite these revisions, *Andricus* remains polyphyletic with multiple Nearctic lineages divergent from *Andricus s.s.* (Fig 514, also Blaimer *et al.* 2020, Cuesta-Porta *et al.* 2022), highlighting the requirement for further taxonomic revision of Nearctic Cynipini.

The genus *Feron* is present throughout the Nearctic; the majority of known species are present in the USA (primarily the Pacific coast and inland southwest), with the single species *F. rucklei* having a distribution that extends as far north as southern Canada, and seven species known only from Mexico (see Table 2). Alternate asexual and sexual generations have been matched for five species (*F. atrimentum*, *F. crystallinum*, *F. gigas*, *F. kingi* and *F. pattersonae*); alternate generations remain to be determined for three species currently known only from their sexual generation (*F. clarkei*, *F. comatum* and *F. dumosae*) and for the majority of species within the genus that are known only from their asexual generation. However, as mentioned in their respective species accounts, while *F. dumosae* is only known from its sexual generation we suspect it may represent the alternate generation of *F. rucklei*.

The phylogenetic analysis (Fig. 514) indicates that there are three major species groups within *Feron*: a *Feron* 'sensu stricto' clade containing species upon which Kinsey based his original description of this genus, a second lineage that we name the *Feron* 'spangle galler' clade, plus a monotypic lineage containing *F. parmula*. While all species induce their asexual galls (where known) on leaves, the gross asexual gall morphology differs between the two speciose lineages but is relatively conserved within lineages. The *Feron sensu stricto* clade, represented by 10 species in the molecular analysis, is primarily a Mexican and southwest USA radiation (Table 2). The asexual galls of seven of these species are tightly clustered aggregations of tubular/cylindrical larval cells covered in dense, somewhat crystalline pubescence; the other three species all typically induce multiple tubular galls per leaf but more widely scattered across the leaf rather than as a single midrib cluster, with the

surface structure of those galls varying from crystalline hairs (*F. sulfureum*) or micro-hairs (*F. amphorus*), to blunt spines (*F. splendens*). Six more species probably belong in this clade (see Table 2): *F. syndicorum* and *F. verutum* induce pubescent gregarious midrib clusters; *F. apiarium* and *F. serranae* have a gall structure very similar to *F. amphorus*; and *F. scutellum* and *F. cylindratum* have galls similar to *F. splendens* in their basic cylindrical structure but with a smooth surface rather than having blunt spines.

The spangle galler clade, represented by nine species in the molecular analysis, appears to be a Pacific coast radiation with a single lineage extending to the US southwest (represented by *F. discale* and *F. caepula*; Table 2). Asexual galls within this clade have more variable morphology among species but are typically small smooth spangles, often with multiple galls per leaf. The asexual galls tend to have either a flat disc-like morphology (as in *F. discale*, *F. gigas*, *F. izabellae*, *F. pattersonae* and *F. rucklei*) or are roundish to conical and sometimes with crystalline hairs (*F. atrimentum*, *F. caepula*, *F. kingi*, *F. stellare*). A disc-like morphology is also shared by the asexual galls of *F. californicum*, *F. discularis* and *F. stellulum* (although the latter is raised from the leaf surface on a stalk), while the rounder morphology is shared by *F. bakkeri* and *F. albicomus*). Finally, *Feron parmula* falls into its own lineage, distinct from either *Feron* sensu stricto or the spangle galler clade, despite its asexual gall having a disc-like morphology similar to some species in the spangle galler clade.

All known sexual galls induced by *Feron* species are small, thin-walled, often pointed galls integral to leaves, catkins or buds, although there are some with more divergent characters such as having the larval cell suspended on radiating fibers (*F. atrimentum*) or on an extended pedicel (*F. pattersonae*). However, the basic morphology of these sexual galls is relatively conserved and rather similar to that known for sexual generations galls from the related genera *Prokius* (Medianero *et al.* 2021) and *Phylloteris* (Nicholls *et al.* 2022). In addition, there is no obvious relationship between the appearance of the sexual gall and the *Feron* species groups defined by the molecular analysis; for example, *F. crystallinum* in the *Feron* sensu stricto clade induces a sexual gall very similar in morphology to those of *F. gigas* or *F. kingi*, both in the spangle galler clade. Therefore, the two species *F. clarkei* and *F. comatum*, known only from their sexual generations, are unplaced concerning the major species groups (Table 2) pending molecular analysis, although as noted above we expect *F. dumosae* to be a member of the spangle galler clade.

*Feron* species are exclusively associated for both their asexual and sexual generations with host oaks from *Quercus* section *Quercus*. Most species are restricted to a single subsection within section *Quercus*, typically reflecting their spatial distribution (Table 2).

Most species in the Pacific coast radiation of the spangle galler clade induce galls on oaks within subsection *Dumosae*, the only white oak group present through most of that region (see Manos & Hipp 2021); the exceptions gall species in the southwestern oak subsections *Leucomexicana* and *Polymorphae*. Likewise, most species in the Mexican and southwestern USA *Feron* sensu stricto clade induce galls on oaks from within the subsection *Leucomexicana* radiation, although a few species also gall sympatric oaks from other section *Quercus* subsections. Finally, the biology of *Feron* species distributed in the eastern USA most likely reflects host shifts onto two of the section *Quercus* subsections present in that region (*Albae*, *Stellatae*; Table 2). Interestingly, the apparent rarity of *Feron* taxa in the eastern Nearctic could imply that the single asexual generation known from that region, *F. apiarium*, could represent the alternate generation of either of the two eastern species known only from their sexual generation (*F. comatum* or *F. clarkei*) – further work is required to test both this suggestion and other hypotheses of host shifts and biogeographic patterns in this genus.

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**FIGURES 447–450.** *Feron tibiale*, **comb. rev.**, asexual female, carinated mesopleuron variant. 447, mesosoma, lateral view, 448, mesoscutum, dorsal view, 449, mesoscutellum, dorsal view, 450, metascutellum and propodeum, posterodorsal view.

**FIGURES 451–452.** *Feron tibiale*, **comb. rev.**, asexual female, carinated mesopleuron variant. 451, fore wing, 452, metasoma, lateral view.

**FIGURES 453–457.** *Feron uterinum*, syn. of *Feron tibiale*, **comb. rev.**, asexual female. 453–456, head: 453, frontal view, 454, dorsal view, 455, posterior view, 456, lateral view. 457, mesosoma and propleura, frontal view.

**FIGURES 458–461.** *Feron uterinum*, syn. of *Feron tibiale*, **comb. rev.**, asexual female. 458, mesosoma, lateral view, 459, mesoscutum, dorsal view, 460, mesoscutellum, dorsal view, 461, metascutellum and propodeum, posterodorsal view.

**FIGURES 462–463.** *Feron uterinum*, syn. of *Feron tibiale*, **comb. rev.**, asexual female. 462, fore wing, 463, metasoma, lateral view.

**FIGURES 464–468.** *Feron tubifaciens*, **comb. nov.**, asexual female. 464–467, head: 464, frontal view, 465, dorsal view, 466, posterior view, 467, lateral view; 468, antenna.

**FIGURES 469–472.** *Feron tubifaciens*, **comb. nov.**, asexual female. 469, mesosoma and propleura, frontal view, 470, mesosoma, lateral view, 471, mesoscutum and mesoscutellum, dorsal view, 472, metascutellum and propodeum, posterodorsal view.

**FIGURES 473–475.** *Feron tubifaciens*, **comb. nov.**, asexual generation. 473–474, asexual female: 473, fore wing (not scaled), 474, metasoma, lateral view. 475, galls.

**FIGURES 476–481.** *Feron verutum*, **comb. rev.**, asexual female. 476–479, head: 476, frontal view, 477, dorsal view, 478, posterior view, 479, lateral view; 480, antenna. 481, mesosoma and propleura, frontal view.

**FIGURES 482–485.** *Feron verutum*, **comb. rev.**, asexual female. 482, mesosoma, lateral view, 483, mesoscutum, dorsal view, 484, mesoscutellum, dorsal view, 485, metascutellum and propodeum, posterodorsal view.

**FIGURES 486–488.** *Feron verutum*, **comb. rev.**, asexual generation. 486–487, asexual female: 486, fore wing, 487, metasoma, lateral view. 488, galls.

**FIGURES 489–494.** *Feron vitreum*, **comb. rev.**, asexual female. 489–492, head: 489, frontal view, 490, dorsal view, 491, posterior view, 492, lateral view; 493, antenna. 494, mesosoma and propleura, frontal view.

**FIGURES 495–498.** *Feron vitreum*, **comb. rev.**, asexual female. 495, mesosoma, lateral view, 496, mesoscutum, dorsal view, 497, mesoscutellum, dorsal view, 498, metascutellum and propodeum, posterodorsal view.

**FIGURES 499–501.** *Feron vitreum*, **comb. rev.**, asexual generation. 499–500, asexual female: 499, fore wing, part, 500, metasoma, lateral view. 501, galls.

**FIGURES 502–507.** *Feron validum*, *syn. of Feron vitreum*, **comb. rev.**, asexual female. 502–505, head: 502, frontal view, 503, dorsal view, 504, posterior view, 505, lateral view; 506, antenna. 507, propleura, frontal view.

**FIGURES 508–511.** *Feron validum*, *syn. of Feron vitreum*, **comb. rev.**, asexual female. 508, mesosoma, lateral view, 509, mesoscutum, dorsal view, 510, mesoscutellum, dorsal view, 511, metascutellum and propodeum, posterodorsal view.

**FIGURES 512–513.** *Feron validum*, *syn. of Feron vitreum*, **comb. rev.**, asexual female. 512, fore wing, 513, metasoma, lateral view.

**FIGURE 514.** Majority-rule consensus tree showing the phylogenetic relationships of the genus *Feron* **comb. rev.** based on a Bayesian analysis of a concatenation of four loci (cytochrome *b*, the D2 region of the 28S rRNA gene, long-wavelength opsin and wingless). Limits of the re-established *Feron* are indicated by the grey shaded box, along with an indication of sub-clades within this genus. The type species of the genus *Andricus* is shown by the black star, with the lineage we consider to be true *Andricus* highlighted. Numbers above nodes indicate posterior probability support.

## Tables

**Table 1.** Percentage pairwise genetic distances among 20 species of *Feron*, based upon 433 base pairs of the cytochrome *b* gene using a HKY distance correction. Species are sorted by the within-genus lineage to which they belong. The number of individuals sequenced per species is indicated next to the species name, with an asterisk “\*” to highlight instances where that sampling involved rearing individuals from multiple host plant species. Values on the diagonal (in bold) indicate variation within a species; off-diagonal values indicate between-species distances.

**Table 2.** Summary of biological data for *Feron* species indicating the subclade to which the species belongs, the host plant organ galled by each generation (where known), the host plant subsectional classification within *Quercus* section *Quercus* (following Manos & Hipp 2021) and the biogeographic region within the Nearctic in which the species occurs. Subclade is as indicated in Fig. 514, although is predicted based on asexual gall and adult morphology for those species that were not included in the phylogenetic analysis. The species included in the molecular analysis are indicated by “\*” after their species name.

### **Supplementary information**

**Supplementary Table 1.** Information for specimens sequenced in this study, including collection details, generation (sexual or asexual), sex and host oak species. GenBank accession numbers (for new data from this study and previously published sequences) are provided for each specimen/gene combination.

**Supplementary File 1.** Final alignment and parameters used for the multilocus Bayesian analysis (see ‘Material and Methods’ and Fig. 514). The data set is formatted for a Nexus file and the parameters according to the requisites for the software MrBayes.

**Supplementary Figure 1.** Neighbour-joining tree showing the phylogenetic relationships of the species of *Feron* based on the cytochrome b locus. The host plant and the locality of origin are indicated in every terminal.