

Taxonomy and systematics

A new gall wasp species (Hymenoptera: Cynipidae), *Andricus protector* Pujade-Villar and Cuesta-Porta sp. nova (Hymenoptera: Cynipidae: Cynipini), from Mexico

***Una especie nueva de avispa agalladora (Hymenoptera:
Cynipidae), Andricus protector Pujade-Villar and Cuesta-Porta
sp. nova (Hymenoptera: Cynipidae: Cynipini) de México***

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Abstract

A new species of oak gall wasp, *Andricus protector* Pujade-Villar and Cuesta-Porta sp. nova, known only from its asexual generation that induces deciduous galls on buds of *Quercus crassifolia* Humb. and Bonpl. (*Lobatae* section), is described from Mexico. Diagnosis, distribution and biological data of the new species are given. The validity of *Andricus* species from Mexico is commented. Four species are proposed here to have dubious affiliation: *Andricus burnetti* (Dailey and Sprenger, 1983), *A. marmoreus* Kinsey, 1920, *A. setifer* (Karsch, 1880) and *A. strues* (Kinsey, 1938).

Keywords: Hymenoptera; Cynipidae; *Andricus*; New species; Mexico; *Quercus crassifolia*

Resumen

Se describe una especie nueva de avispa agalladora, *Andricus protector* Pujade-Villar y Cuesta-Porta sp. nova de México, conocida solo por su generación asexual, que induce agallas deciduas en yemas de *Quercus crassifolia*

Humb. y Bonpl. (sección *Lobatae*). Se proporcionan la diagnosis, los datos de distribución y biológicos de la nueva especie. Se comenta la validez de las especies de *Andricus* de México. Cuatro especies tienen afiliación dudosa: *Andricus burnetti* (Dailey y Sprenger, 1983), *A. marmoreus* Kinsey, 1920, *A. setifer* (Karsch, 1880) y *A. strues* (Kinsey, 1938).

Palabras clave: Hymenoptera; Cynipidae; *Andricus*; Especie nueva; México; *Quercus crassifolia*

Introduction

Oak gall wasps (Hymenoptera: Cynipidae: Cynipini) represent the most diverse group within the Cynipidae family, comprising over 1,000 described species in 59 genera (Buffington et al., 2020; Melika, Pujade-Villar et al., 2021; Ronquist et al., 2015; Stone et al., 2002). These wasps induce galls on Fagaceae, primarily on oaks (*Quercus* L.). In America, north of Mexico, nearly 500 cynipid species have been recorded (Burks, 1979) in association with 90 species of *Quercus* (Nixon, 2008). In contrast, Europe has approximately 150 described species of cynipids (Melika 2006), despite having only about 30 *Quercus* species (Uotila, 2011). More specifically, only in the Iberian Peninsula, about 70 cynipid species associated with 10 *Quercus* species have been documented (Nieves-Aldrey, 2001). Under the same rule-of-thumb, the Mexican oak gall wasp fauna is likely extraordinarily rich, with many species yet to be described, as Mexico is home to 135-161 *Quercus* species, 86 of which are endemic (Nixon, 1993a, b; Zavala, 1998; Valencia, 2004).

The recorded number of Mexican cynipid species has varied considerably over time. Pujade-Villar et al. (2009) listed 157 cynipid species, with 42 species attributed to the genus *Andricus* Hartig, 1840. In a subsequent review, Pujade-Villar and Ferrer-Suay (2015) increased the number of Mexican cynipid species to 183, and 43 species of *Andricus*. More recently, Martínez-Romero et al. (2022) listed 205 species, 30 of which were assigned to *Andricus*. The genus *Andricus* is the most diverse, with more than 400 species described worldwide (Melika, Nicholls et al., 2021; Stone et al., 2002), and one of the most taxonomically complex among oak gall wasps.

Since the review by Pujade-Villar et al. (2009), several species previously classified under *Andricus* have been reassigned to other genera, including *Disholandricus* Melika, Pujade-Villar and Nicholls, 2021, *Dros* Kinsey, 1937, *Druon* Kinsey, 1937, *Erythres* Kinsey, 1937, *Femuros* Kinsey, 1937, *Feron* Kinsey, 1937, *Protobalandricus* Melika, Nicholls and Stone, 2018, *Striatoandricus* Pujade-Villar, 2020, and *Trichoterus* Ashmead, 1897. In Mexico, a total of 31 species of *Andricus* are listed (Martínez-Romero et al., 2022), later also *A. cylindratum* (Kinsey, 1937), *A. tecturnarum* Kinsey, 1920, *A. tibialis* Kinsey,

1937 (= *A. tostum* Kinsey, 1937) (= *A. uterinus* Kinsey, 1937), *A. vitreus* Kinsey, 1937 (= *A. validus* Kinsey, 1937) and *A. verutus* Kinsey, 1937 were transferred to *Feron* by Cuesta-Porta et al. (2023). Furthermore, since Martínez-Romero et al. (2022), 2 additional *Andricus* species have been described from Mexico, *A. coombesi* Pujade-Villar and Pérez-Torres, 2024 and *A. mazahua* García-Martinón and Pujade-Villar, 2024 (Pujade-Villar et al., 2024, García-Martinón et al., 2024), bringing the current number of *Andricus* species in Mexico to 25. Among these, 18 species induce galls on branches, 4 attack buds (rarely leaves or petioles), 1 is found exclusively on leaves, and 1 in acorns. The host of *A. aztecus* remains unknown, although it is suspected to induce tuberous galls (Martínez-Romero et al., 2022). The new species described here attacks the buds of *Q. crassifolia* (*Lobatae* section), producing a distinctive spherical gall with the larval chamber surrounded by longitudinal air chambers divided by thin partitions of spongy tissue.

Materials and methods

Asexual adult gall wasps (♂) of the new species described herein were extracted dead from galls on *Quercus crassifolia* in Oaxaca (Mexico) years after being collected. They were preserved in 100% ethanol in the laboratory by the second author.

The description of the new species follows the current terminology of morphological structures specific for Cynipidae (Liljeblad & Ronquist, 1998; Melika, 2006) and more general sources such as the Hymenoptera Anatomy Ontology Portal (Yoder et al., 2010). Abbreviations for the fore wing venation follow Ronquist and Nordlander (1989); cuticular surface terminology follows that of Harris (1979). Measurements and abbreviations used here include: F1-F11, 1st and subsequent flagellomeres; POL (postocellar distance), the distance between the inner margins of the posterior ocelli; OOL (ocellar-ocular distance), the distance from the outer edge of a posterior ocellus to the inner margin of the compound eye; LOL, 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.

The scanning electron microscope (SEM) pictures were taken by the first author at the University of Barcelona (UB) using a field-emission gun environmental scanning electron microscope (FEI Quanta 200 ESEM), with low-resolution imaging without gold-coating the specimens. The photographs of the galls and habitus were taken by the second author with a Canon PowerShot SX510 HS digital camera and a digital camera mounted on Carl Zeiss microscopy III followed by processing with GIMP 2.8 (GNU Image Manipulation Program), respectively.

The type material of the new species is deposited in the University of Barcelona (UB), Catalonia (J. Pujade-Villar coll.).

Andricus protector Pujade-Villar and Cuesta-Porta sp. nova

(Figs. 1-3)

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Diagnosis. The new species differs from all Mexican *Andricus* species by the following combination of characters: mesoscutum transversally rugose; median mesoscutal line present, with smooth bottom; margin of the fore wing shortly ciliated; second metasomal tergum smooth anteriorly, anterolaterally with dense white setae, and a band of punctures in the posterior third; subsequent terga and hypopygium punctuate, without setae. *Andricus protector* is closely related to *Andricus formosalis* Weld, 1944 (Fig. 3B), but differs from it by the following characters: antenna and legs brown to black (yellowish in *A. formosalis*); inner margins of eyes parallel (converging ventrally in *A. formosalis*); head quadrate and slightly broader than the mesosoma (triangular, narrower than the mesosoma in *A. formosalis*); F1 1.2 × as long as F2 (only slightly longer in *A. formosalis*); placodeal sensilla inconspicuous (present in *A. formosalis*); pronotum completely rugose (with parallel ridges in the posterior margin in *A. formosalis*); median mesoscutal line long and wide (short and becoming almost inconspicuous in *A. formosalis*); mesoscutellar foveae quadrate, separated by a carina, not delimited posteriorly (triangular, widely separated and well-delimited posteriorly in *A. formosalis*); 2nd metasomal tergum occupying most of the metasoma (very short in *A. formosalis*). Also, the galls of both species are different: with a velvety reddish surface when young and spherical when mature in *A. protector* sp. nova, and with a velvety whitish surface when young and ovoid when mature in *A. formosalis*.

The new species can be morphologically similar to other *Andricus* inducing tuberos galls in branches. Despite the great divergence in gall morphology

between *A. protector* and the tuberos galls, *Andricus guanajuatensis*, *A. montezumus*, *A. peredurus* and *A. protector* have the mesoscutum transversally carinate, whilst the rest of Mexican species that induce tuberos galls have the mesoscutum strongly wrinkled. *Andricus protector* has a wide band of punctuation in the second metasomal tergum and a medial mesoscutal line (both characters absent in *A. guanajuatensis*, *A. montezumus*, and *A. peredurus*).

Description. Asexual female. Body black (Fig. 3A); mandibles brown, maxillary and labial palpi light brown; antenna brown, scape black; tegula dark brown to black; legs black, tibiae I and II and all tarsomeres brown; metasoma chestnut brown to black; fore wing veins light.

Head (Fig. 1A-D) 1.3 × as broad as high and very slightly broader than mesosoma in frontal view, 2.1 × as broad as long in dorsal view. Gena coriaceous, broadened behind eye, around 1.4 × as broad as transverse diameter of eye; malar space with striae radiating from clypeus and reaching eye; eye 3.1 × as high as length of malar space. Inner margins of eyes parallel. POL 2.0× as long as OOL, OOL 1.3 × as long as diameter of lateral ocellus, 1.3 × as long as LOL, ocelli rounded, all 3 equal in size. Transfacial distance as long as height of eye and 1.35 × as long as height of lower face (distance between antennal rim and ventral margin of clypeus); diameter of antennal torulus 3.3 × as long as distance between them, distance between torulus and eye as long as diameter of torulus. Lower face coriaceous, setose, with some irregular weak striae, with elevated median area coriaceous, with irregular weak striae, without setae. Clypeus quadrate, flat, carinated, ventrally slightly curved, not emarginate and slightly incised medially; with anterior tentorial pit, epistomal sulcus and clypeo-pleurostomal line distinct. Frons, interocellar area and vertex strongly coriaceous, with some weak rugae between ocelli and eye; occiput carinate, with few short setae; postgena punctate, pubescent; postocciput and postocciput around occipital foramen weakly carinate, glabrous; posterior tentorial pit oval; hypostomal carina emarginate, present at the basis of postgenal sulci, gular sulci present; occipital foramen longer than height of postgenal bridge.

Antenna (Fig. 1E, F) as long as head + mesosoma, with 13 flagellomeres, sometimes with a partial suture towards the middle of F12, rarely F13 fused; pedicel 1.6 × as long as broad, F1 0.8 × as long as length of scape + pedicel and 1.25 × as long as F2, F3 0.8 × as long as F2, F3 as long as F4, F5 as long as F6, F7 slightly shorter than F6 and equal as F8, F9 slightly shorter than F8 and equal as F10, F11 slightly shorter than F10, F12 + 13 shorter than F10 + F11, F12 as long as F11 and slightly longer than F13;

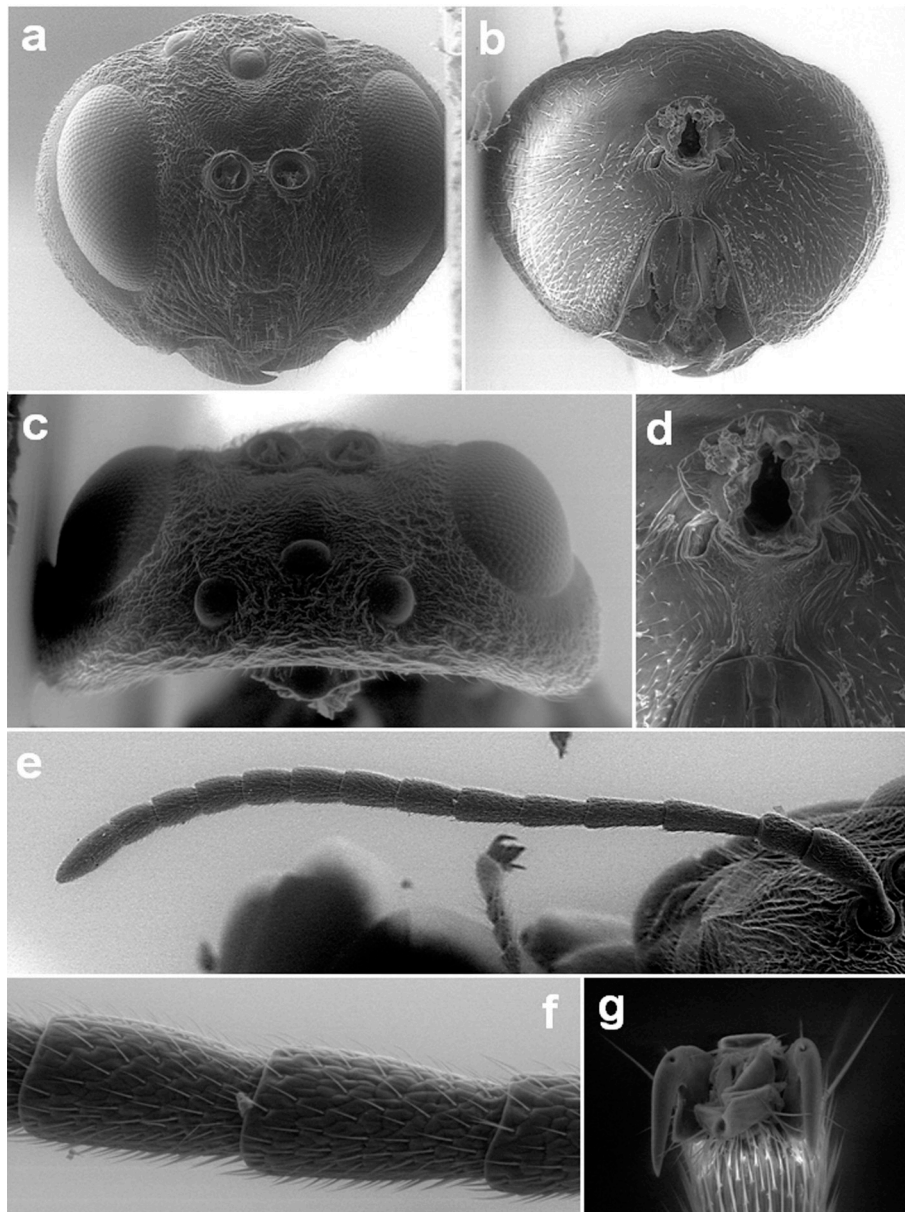


Figure 1. *Andricus protector* sp. nova. a) Head in frontal view; b) head in posterior view; c) head in dorsal view; d) detail of gula; e) antenna; f) F4 and F5; g) tarsal claws.

placodeal sensilla inconspicuous on F5 - F12, absent on F1 - F4. Antennal formula: 14:11 x 7: 20: 16: 13: 13: 12: 12. 11: 11: 10: 10: 9: 9: 8.

Mesosoma (Fig. 2A-C) slightly longer than high in lateral view. Pronotum rugose with coriaceous interspaces, glabrous, emarginate along lateral and dorsal edges. Propleuron alutaceous with weak irregular rugae and sparse setae. Mesoscutum rugose, with coriaceous interspaces, glabrous, broader than long (width measured across base

of tegulae). Notaulus complete; median mesoscutal line present, extends 1/3 of mesoscutum length, with smooth bottom; anterior parallel line impressed, extends to half of mesoscutum length, coriaceous, glabrous; parapsidal line incised and surrounded by coriaceous surface, extends 2/3 of mesoscutum; parascutal carina narrow, coriaceous, reaching notaulus. Transscutal articulation deep, distinct. Mesoscutellum quadrate, shorter than mesoscutum, uniformly rugose, slightly overhanging

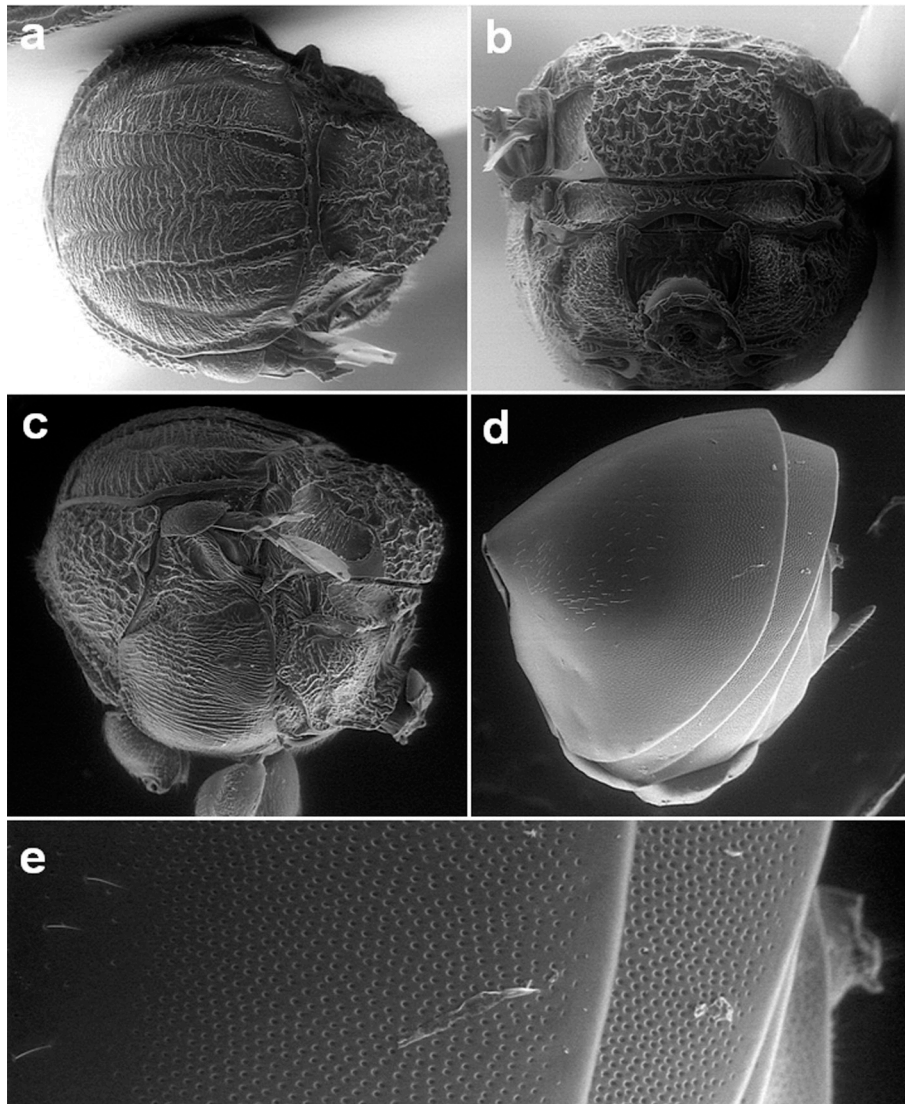


Figure 2. *Andricus protector* sp. nova. a) Mesosoma in dorsal view; b) mesosoma in posterior view; c) mesosoma in lateral view; d) metasoma; e) detail 2nd and 3rd metasomal segments.

metanotum; mesoscutellar foveae big, quadrate, with smooth to alutaceous bottom, open basally with some rugae, distinctly divided by a central carina with coriaceous sculpture. Mesopleuron including speculum rugose-carinate, with coriaceous interspaces, sparsely pubescent; mesopleural triangle coriaceous-rugose, with sparse white setae. Metapleural sulcus reaching mesopleuron above half its height, upper part of sulcus inconspicuous; dorsal axillar area rugose, glabrous; lateral axillar area and axillar carina weakly carinated, glabrous; subaxillular bar with parallel sides smooth, glabrous; metanotal trough smooth, setose. Metascutellum sub-

rectangle coriaceous, glabrous, ventral impressed area smooth. Lateral propodeal carinae distinct, broad, parallel but basally curved towards the nucha; central propodeal area coriaceous, glabrous, without central longitudinal carina, with some rugae; lateral propodeal area coriaceous rugose, glabrous; nucha with delicate rugae.

Fore wing (Fig. 4A) slightly longer than body, hyaline, with the margin shortly ciliate; radial cell open, $3.0 \times$ as long as broad, R1 and Rs not reaching the wing margin; areolet present, large; Rs + M visible in $2/3$ of its length, its projection reaching basal vein slightly below half of its height.

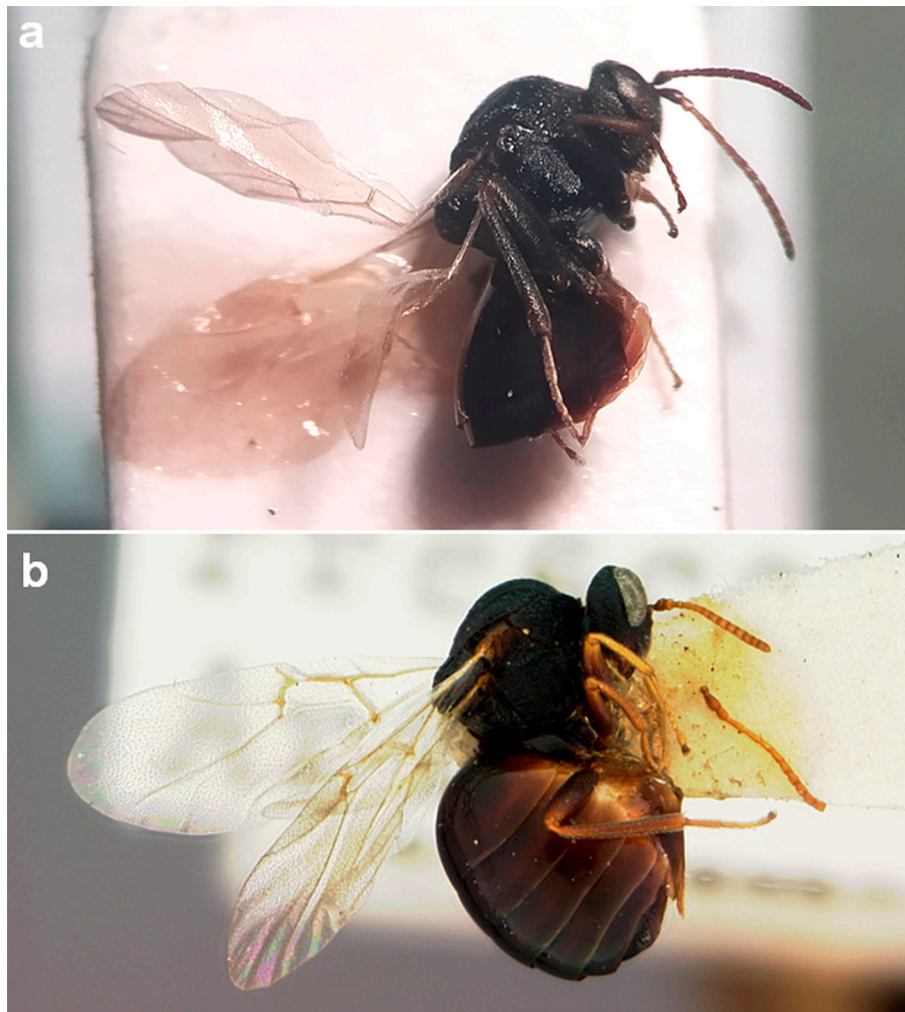


Figure 3. Lateral habitus of a) *Andricus protector* sp. nova., b) *A. formosalis* [Picture obtained from Type Search of Smithsonian Entomological Collections, <http://n2t.net/ark:/65665/m36fc57b94-797e-4d41-b88c-58776f4ed1d3>]

Legs with a reticulate sculpture. Tarsal claws with a basal lobe (Fig. 1G).

Metasoma (Fig. 2D, E) shorter than head + mesosoma, longer than high in lateral view, 2nd metasomal tergum smooth anteriorly with dense white setae anterolaterally and a band of punctures in the posterior third; subsequent terga and hypopygium punctuate, without setae; prominent part of the ventral spine of the hypopygium $5.0 \times$ as long as broad in ventral view, with short and sparse white setae, without apical tuft. Body length 3.7-3.8 mm ($n = 3$).

Gall (Fig. 4B, C). Unilocular, spherical gall located on the axillary buds of *Q. crassifolia*, in clusters of 2-4, with average size of 11.6 mm ($SD \pm 0.46$ mm, $N = 20$). Light yellowish red with short pubescent surface when young, turning brown and glabrous when mature. Inside a single

larval cell located in the center, surrounded by multiple radiating empty chambers. All chambers are surrounded by spongy tissue. The consistency of the gall is not very hard.

Taxonomic summary

Type material. Holotype: asexual female “MEX, La Resinera, Santa Catarina Ixtepeji (Ixtepec, Oaxaca), *Q. crassifolia*, (30.vii.2021) extr. 18.v.24”, R. Clark leg. (black label); “holotype *Andricus protector* Pujade-Villar and Cuesta-Porta n. sp., desig. JP-V 2023” (red label). Paratypes: 3 asexual females with same data as the holotype. Holotype and 3 paratypes are deposited in the collection of JP-V (University of Barcelona, UB), one of them dissected for SEM imaging.

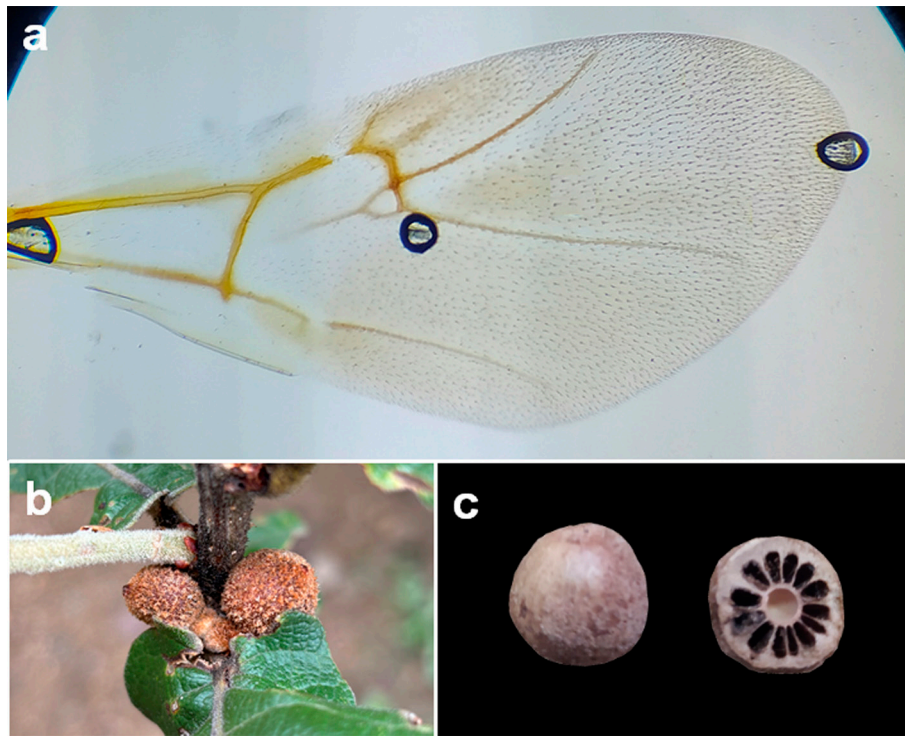


Figure 4. *Andricus protector* sp. nova. a) Forewing; b) young galls; c) mature gall and cut gall.

Etymology. Named for the species' gall model in which the larval chamber is protected (surrounded) by multiple empty chambers.

Host plant. Known only from *Q. crassifolia* (Lobatae section). This oak species is distributed in Mexico (Chiapas, Chihuahua, Guerrero, Guanajuato, Hidalgo, Jalisco, Estado de México, Michoacán, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tlaxcala, Veracruz, and Zacatecas) and Guatemala. Distribution. Mexico (Oaxaca).

Biology. Only the asexual generation is known. The galls appear in mid-June and fall to the ground between August and September, rarely in October. Once in the ground, the galls absorb a lot of soil moisture during the rainy season, which explains why they were very soft when they were collected. This might have affected the development of the adults and prevented them from emerging. The extracted adults were dead, but perfectly preserved.

Discussion

Of the total of 25 *Andricus* species known from Mexico (Table 1), *Andricus burnetti* (Dailey & Sprenger, 1983) was described in the genus *Trichoteras* and transferred to *Andricus* by Melika and Abrahamson (2002), it is

associated with oaks of the *Protobalanus* section which matches with most *Trichoteras* species, however the gall differs from the rest of *Trichoteras* and is more similar to *Feron. Andricus marmoreus* Kinsey, 1920 has a gall similar to those of *Disholcaspis*, but the adult has simple tarsal claws and an unusual mesoscutal sculpture for a Mexican species of *Disholcaspis*. The gall of *A. setifer* (Karsch, 1880) may correspond to some of the genus *Striatoandricus*. Lastly, *A. strues* (Kinsey, 1938) was originally described in the genus *Conobius* Kinsey, 1938, which was later synonymized under *Andricus* by Melika and Abrahamson (2002), but unlike what is mentioned in the original description of *Conobius*, *A. strues* has the margin of its fore wings ciliated. Concerning *Callirhytis quercusbatatoides*, Pujade-Villar et al. (2014) mentioned that this species probably belongs to *Andricus*; later, in Pujade-Villar and Ferrer-Suay (2015), it is considered as an *Andricus* species but the formal change is not indicated; and finally, in Martínez-Romero et al. (2022) it is definitively named as *Andricus quercusbatatoides* (Ashmead, 1881).

Among the rest of *Andricus* species reported from Mexico, the gall morphology and host association is still remarkably diverse (Table 1): one species attacks acorns, 4 induce galls on leaves and/or buds, 3 attack branches

without causing globular tuberous galls and 13 induce tuberous galls. The gall of *A. aztecus* (Cameron, 1888) is unknown, although it may induce tuberous galls.

The alternating life cycle is only known in one of the species (*A. quercuslaurinus*); the rest remain known by their asexual form except in *A. protuberans* and *A. sphaericus*, of which only the sexual generation is known. The Mexican *Andricus* induce galls in the sections *Quercus*, *Lobatae*, *Virentes*, and *Protobalanus* (Martínez-

Romero et al., 2022; Table 1). The species described here corresponds to an asexual form inducing galls in *Lobatae* section.

Andricus species with linear elements in the mesoscutum (wrinkles or carinae) are restricted to tuberous gall specie (except *A. mazahua*). This trait is also present in the species here described, but *A. protector* does not induce tuberous galls. Among the Mexican *Andricus* species that produce galls on buds, *A. burnetti* is associated with

Table 1

Andricus species reported in Mexico after this study, indicating the known generation of their lifecycle (Known generation), the plant organ they attack (Plant organ), and the host oak association (Host section). Species marked with an asterisk are considered of unclear affiliation in the Discussion section.

Species	Authors	Known generation	Plant organ	Host section
<i>Andricus aztecus</i>	(Cameron, 1888)	Asexual	Unknown	Unknown
<i>Andricus bonanseai</i>	Mayr, 1905	Asexual	Branch (tuberous)	Lobatae, Quercus
<i>Andricus breviramuli</i>	Pujade-Villar, 2014	Asexual	Branch (non-tuberous)	Quercus
<i>Andricus burnetti</i> *	(Dailey and Sprenger, 1983)	Asexual	Buds/leaf	Protobalanus
<i>Andricus carrilloi</i>	Pujade-Villar, 2013	Asexual	Branch (tuberous)	Quercus
<i>Andricus coombesi</i>	Pujade-Villar and Pérez-Torres, 2024	Asexual	Acorn	Lobatae
<i>Andricus dugesi</i>	Beutenmüller, 1917	Asexual	Branch (tuberous)	Lobatae, Quercus
<i>Andricus durangensis</i>	Beutenmüller, 1911	Asexual	Branch (tuberous)	Lobatae
<i>Andricus furnaceus</i>	Kinsey, 1920	Asexual	Branch (tuberous)	Quercus
<i>Andricus fusiformis</i>	Pujade-Villar, 2014	Asexual	Branch (non-tuberous)	Lobatae, Quercus
<i>Andricus guanajuatensis</i>	Pujade-Villar, 2013	Asexual	Branch (tuberous)	Lobatae, Quercus
<i>Andricus marmoreus</i> *	Kinsey, 1920	Asexual	Branch (non-tuberous)	Quercus
<i>Andricus mazahua</i>	García-Martinón and Pujade-Villar, 2024	Asexual	Branch (tuberous)	Lobatae
<i>Andricus montezumus</i>	Beutenmüller, 1913	Asexual	Branch (tuberous)	Quercus
<i>Andricus peredurus</i>	Kinsey, 1920	Asexual	Branch (tuberous)	Quercus
<i>Andricus protector</i>	Pujade-Villar & Cuesta-Porta, sp. nova.	Asexual	Buds/leaf	Lobatae
<i>Andricus protuberans</i>	Pujade-Villar and Ferrer-Suay, 2015	Sexual	Buds/leaf	Lobatae
<i>Andricus quercusbatatoides</i>	(Ashmead, 1881)	Asexual	Branch (tuberous)	Virentes
<i>Andricus quercuslaurinus</i>	Melika and Pujade-Villar, 2009	Sex. and asex.	Branch (non-tuberous)	Lobatae
<i>Andricus rochai</i>	Pujade-Villar, 2018	Asexual	Buds/leaf	Quercus
<i>Andricus santafe</i>	Pujade-Villar, 2013	Asexual	Branch (tuberous)	Quercus
<i>Andricus setifer</i> *	(Karsch, 1880)	Asexual	Branch (non-tuberous)	Unknown
<i>Andricus sphaericus</i>	Pujade-Villar, 2016	Sexual	Buds/leaf	Quercus
<i>Andricus strues</i> *	(Kinsey, 1938)	Asexual	Buds/leaf	Quercus
<i>Andricus tumefaciens</i>	Pujade-Villar and Paretas-Martínez, 2012	Asexual	Branch (tuberous)	Lobatae, Quercus
<i>Andricus tumeralis</i>	Pujade-Villar, 2009	Asexual	Branch (tuberous)	Quercus

Q. palmeri (*Protobalanus* section), while *A. protuberans*, *A. rochai*, and *A. strues* are associated with species in the *Quercus* section. Although *A. protuberans* has also been reported on oaks from the *Lobatae* section, Cuesta-Porta, Cibrián-Tovar et al. (2022) suggested that these records require further confirmation. *Andricus protector* has a very peculiar gall containing a set of empty chambers radially surrounding the central larval chamber. The gall of the newly described species is very similar to the gall of *A. formosalis* known from Arizona also associated with the *Lobatae* section, but the adults are morphologically different (see Diagnosis and Fig. 3).

Air chambers in galls are hypothesized to act as a defensive mechanism against parasitoids by hindering oviposition or confusing parasitoids simulating larval chambers and (Pujade-Villar et al., 2025; Stone & Cook 1998; Stone et al., 2002). Several independent cynipid lineages have converged into gall morphologies with hollow internal spaces in the parenchyma, such as the galls of *Atrusca*, *Kinseyella*, and some *Amphibolips* in the Nearctic and *Trichagalma* in Eastern Palearctic, usually exhibit radiating filaments that connect the larval chamber with the outer shell of the gall; or less common cases of free rolling larval chambers like some *Disholcaspis* or *Belizinella* (Cuesta-Porta et al., 2020, 2024, 2025; Ide & Koyama, 2023; Pujade-Villar et al., 2010). In the case of *A. protector* and *A. formosalis*, galls have hollow longitudinal chambers divided by longitudinal parenchymatous partitions. Despite the gall similarity, the adults of *A. protector* and *A. formosalis* exhibit significant differences (see Diagnosis). Further research is needed to determine the phylogenetic relationships between *A. protector* and the rest of *Andricus* species. The generic limits of the American *Andricus* species are still under revision and more data is needed to confirm that the similarities between *A. protector* and *A. formosalis* are phylogenetically informative or the result of morphological convergence.

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References

- Buffington, M. L., Forshage, M., Liljeblad, J., Tang, C. T., & van Noort, S. (2020). World Cynipoidea (Hymenoptera): A key to higher-level groups. *Insect Systematics and Diversity*, 4, 1–69. <https://doi.org/10.1093/isd/ixaa003>
- Burks, B. D. (1979). Superfamily Cynipoidea. In K.V. Krombein, P. D. Hurd Jr., D. R. Smith, & B. D. Burks (Eds.), *Catalog of Hymenoptera in America North of Mexico. Vol. 1.* (pp. 1045–1107). Symphyta and Apocrita. Washington D.C.: Smithsonian Institution Press.
- Cuesta-Porta, V., Equihua-Martínez, A., Estrada-Venegas, E. G., Cibrián-Tovar, D., Barrera-Ruiz, U. M., Ordaz-Silva, S. et al. (2020). Revision of the *Amphibolips* species of the “*nassa*” complex from Mexico and Central America (Hymenoptera: Cynipidae). *Zootaxa*, 4877, 1–50. <https://doi.org/10.11646/zootaxa.4877.1.1>
- Cuesta-Porta, V., Cibrián-Tovar, D., Barrera-Ruiz, U. M., Melika, G., & Pujade-Villar, J. (2022). *Andricus protuberans* Pujade-Villar and Ferrer-Suay is a sexual form (Hym., Cynipidae, Cynipini). *Folia Entomológica Mexicana (nueva serie)*, 8, e0081004. <https://doi.org/10.53749/fem.0081004>
- Cuesta-Porta, V., Melika, G., Nicholls, J. A., Stone, G. N., & Pujade-Villar, J. (2023). Re-establishment of the Nearctic oak cynipid gall wasp genus *Feron* Kinsey, 1937 (Hymenoptera: Cynipidae: Cynipini), including the description of six new species. *Zootaxa*, 5366, 001–174. <https://doi.org/10.11646/zootaxa.5366.1.1>
- Cuesta-Porta, V., Cooke-McEwen, C., Melika, G., Romero-Rangel, S., Equihua-Martínez, A., Estrada-Venegas, E. G. et al. (2024). Review of the Mexican species of *Disholcaspis* Dalla Torre & Kieffer with the description of eleven new species. *Zootaxa*, 5498, 1–100. <https://doi.org/10.11646/zootaxa.5498.1.1>
- Cuesta-Porta, V., Melika, G., Ferrer-Suay, M., Vera-Ortiz, A., & Pujade-Villar, J. (2025). Review of the Nearctic and Neotropical genus *Atrusca* Kinsey, 1930 (Hymenoptera: Cynipidae, Cynipini). *Zootaxa*, 5617, 1–195. <https://doi.org/10.11646/zootaxa.5617.1.1>
- García-Martíñón, R. D., Equihua-Martínez, A., Estrada-Venegas, E. G., & Pujade-Villar, J. (2024). Una nueva especie mexicana de *Andricus* inductora de agallas tumorales en *Quercus crassipes*. *Southwestern Entomologist*, 49, 1–11.
- Harris, R. (1979). A glossary of surface sculpturing. State of California, Department of Food and Agriculture, *Occasional Papers in Entomology*, 28, 1–31.
- Ide, T., & Koyama, A. (2023). The formation of a rolling larval chamber as the unique structural gall of a new species of cynipid gall wasps. *Scientific Reports*, 13, 18149. <https://doi.org/10.1038/s41598-023-43641-6>
- Liljeblad, J., & Ronquist, F. (1998). A phylogenetic analysis of higher-level gall wasp relationships (Hymenoptera: Cynipidae). *Systematic Entomology*, 23, 229–252. <https://doi.org/10.1046/j.1365-3113.1998.00053>

- Martínez-Romero, A., Cuesta-Porta, V., Equihua-Martínez, A., Estrada-Venegas, E. D., Barrera-Ruiz, U. M., Cibrián-Tovar, D. et al. (2022). Aportación al conocimiento de las especies de Cynipini (Hymenoptera: Cynipidae) en los estados mexicanos. *Revista Mexicana de Biodiversidad*, 93, e933998. <https://doi.org/10.22201/ib.20078706e.2022.93.3998>
- Melika, G. (2006) Gall wasps of Ukraine. Cynipidae. *Vestnik Zoologii*, 21, 1–300.
- Melika, G. & Abrahamson, W. G. (2002). Review of the world genera of oak cynipid wasps (Hymenoptera: Cynipidae: Cynipini). In G. Melika, & C. Thuróczy (Eds.), *Parasitic wasps: evolution, systematics, biodiversity and biological control* (pp. 150–190). Budapest: Agroinform.
- Melika, G., Nicholls, J. A., Abrahamson, W. G., Buss, E. A., & Stone, G. N. (2021). New species of Nearctic oak gall wasps (Hymenoptera: Cynipidae, Cynipini). *Zootaxa*, 5084, 001–131. <https://doi.org/10.11646/zootaxa.5084.1.1>
- Melika, G., Pujade-Villar, J., Nicholls, J. A., Cuesta-Porta, V., Cooke-McEwen, C., & Stone, G. N. (2021). Three new Nearctic genera of oak cynipid gall wasps (Hymenoptera: Cynipidae: Cynipini): *Burnettweldia* Pujade-Villar, Melika and Nicholls, *Nicholliella* Melika, Pujade-Villar and Stone, *Disholandricus* Melika, Pujade-Villar and Nicholls; and re-establishment of the genus *Paracraspis* Weld. *Zootaxa*, 4993, 1–81. <https://doi.org/10.11646/zootaxa.4993.1.1>
- Nieves-Aldrey, J. L. (2001). *Fauna Ibérica, Vol. 16*. Hymenoptera: Cynipidae. Madrid: Consejo Superior de Investigaciones Científicas.
- Nixon, K. C. (1993a). The genus *Quercus* in Mexico. In R. Bye, T. P. Ramamoorthy, A. Lot, & J. Fay (Eds.), *Biological diversity of Mexico: origins and distribution* (pp. 447–458). Nueva York: Oxford University Press.
- Nixon, K. C. (1993b). Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names. *Annales des Sciences Forestières*, 50, 25–34. <https://doi.org/10.1051/forest:19930701>
- Nixon, K. C. (2008). *Quercus*. In *Flora of North America @ eFloras*. Missouri Botanical Garden, St. Louis, MO y Harvard University Herbaria, Cambridge, MA. Retrieved on September 15, 2020 from: http://www.efloras.org/florataxon.aspx?flora_id=landtaxon_id=127839
- Pujade-Villar, J., Romero-Rangel, S., Chagoyán-García, C., Equihua-Martínez, A., & Estrada-Venegas, E. G. (2010). A new genus of oak gallwasps, *Kinseyella* Pujade-Villar & Melika, with a description of a new species from Mexico (Hymenoptera: Cynipidae: Cynipini). *Zootaxa*, 2335, 16–28. <https://doi.org/10.11646/zootaxa.2335.1.2>
- Pujade-Villar, J., Equihua-Martínez, A., & Estrada-Venegas, E. G. (2014). Actualización del conocimiento de los Cynipidae mexicanos que producen agallas en encinos (Hymenoptera: Cynipidae: Cynipini). *Entomología Mexicana*, 13, 559–564.
- Pujade-Villar, J., & Ferrer-Suay (2015). Adjudicació genèrica d'espècies mexicanes d'ubicació dubtosa descrites per Kinsey i comentaris sobre la fauna mexicana (Hymenoptera: Cynipidae: Cynipini). *Butlletí de la Institució Catalana d'Historia Natural*, 79, 7–14.
- Pujade-Villar, J., Equihua-Martínez, A., Estrada-Venegas, E. G., & Chagoyán-García, C. (2009). Estado del conocimiento de los Cynipini (Hymenoptera: Cynipidae) en México: perspectivas de estudio. *Neotropical Entomology*, 38, 809–821. <https://doi.org/10.1590/S1519-566X2009000600015>
- Pujade-Villar, J., Pérez-Torres, B. C., Coombes, A. J., Aragón-García, A., Rodríguez-Acosta, M., López-Olguin, J. F. et al. (2024). Description of the first species of gall wasp (Hym., Cynipidae: Cynipini) on *Quercus grahamii* (Fagaceae). *Zootaxa*, 5403, 369–376. <https://doi.org/10.11646/zootaxa.5403.3.6>
- Pujade-Villar, J., Melika, G., & Cuesta-Porta, V. (2025). Structure and function of oak gall wasps. In D. C. de Oliveira, & R. M. S. dos Santos Isaías (Eds), *Plant galls* (pp. 313–347). Cham, Switzerland: Springer.
- Ronquist, F., Nieves-Aldrey, J. L., Buffington, M. L., Liu, Z., Liljeblad, J., & Nylander, J. A. A. (2015). Phylogeny, evolution and classification of gall wasps: the plot thickens. *Plos One*, 10, 1–40. <https://doi.org/10.1371/journal.pone.0123301>
- Ronquist, F., & Nordlander, G. (1989). Skeletal morphology of an archaic cynipoid, *Ibalia rufipes* (Hymenoptera: Ibalidae). *Entomologica Scandinavica*, 33, 1–60
- Stone, G. N., & Cook, J. M. (1998). The structure of cynipid oak galls: patterns in the evolution of an extended phenotype. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265, 979–988. <https://doi.org/10.1098/rspb.1998.0387>
- Stone, G. N., Schönrogge, K., Atkinson, R. J., Bellido, D., & Pujade-Villar, J. (2002). The population biology of oak gall wasps (Hymenoptera: Cynipidae). *Annual Review of Entomology*, 47, 633–668. <https://doi.org/10.1146/annurev.ento.47.091201.145247>
- Uotila P. (2011). *Quercus*. In *Euro + Med Plantbase-the information resource for Euro-Mediterranean plant diversity*. Retrieved on November 12, 2024 from: <http://www.europlusmed.org>
- Valencia, A. S. (2004). Diversidad del género *Quercus* (Fagaceae) en México. *Boletín de la Sociedad Botánica de México*, 75, 33–53. <https://doi.org/10.17129/botsoci.1692>
- Yoder, M. J., Mikó, I., Seltsmann, K. C., Bertone, M. A., & Deans, A. R. (2010). A gross anatomy ontology for Hymenoptera. *Plos One*, 5, e15991. <https://doi.org/10.1371/journal.pone.0015991>
- Zavala, F. (1998). Observaciones sobre la distribución de encinos en México. *Polibotánica*, 8, 47–64.