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Reclassification of *Bracon mendocinus*, a gall-associated doryctine wasp, and description of a new closely related species of *Allorhogas* (Hymenoptera: Braconidae)

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Reclassification of *Bracon mendocinus*, a gall-associated doryctine wasp, and description of a new closely related species of *Allorhogas* (Hymenoptera: Braconidae)

Juan J. Martínez^{a*}, Alejandro Zaldivar-Riverón^b and Alberto G. Sáez^b

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One of the first reported gall-associated braconids, from 1910, *Bracon mendocinus* Kieffer and Jörgensen, is removed from the subfamily Braconinae and transferred to the doryctine genus *Allorhogas*, *A. mendocinus* (Kieffer and Jörgensen) comb. nov. A new species morphologically similar to *A. mendocinus*, *A. joergenseni* Martínez and Zaldivar-Riverón sp. nov., is also described. Additionally a neotype is designated for *B. mendocinus* Kieffer and Jörgensen. We base our conclusions on the morphological examination of recently collected specimens from central Argentina associated with galls on *Lycium chilense* (Solanaceae), as well as on the DNA variation at 28S ribosomal RNA and cytochrome oxidase subunit I (COI) mitochondrial DNA genes.

Keywords: Doryctinae; *Allorhogas*; galls; *Lycium chilense*; new combination; new species; barcoding

Introduction

In the parasitic wasp family Braconidae, one of the largest and more diverse families of Hymenoptera, association with galls is a rare strategy that may involve inquilinism (where the gall is only a habitat), parasitism of gallers, or cecidogenesis (i.e. phytophagy linked to gall formation). The few cases of gall association in braconids have been observed mainly in the subfamily Doryctinae (e.g. Mácido and Monteiro 1989; Infante et al. 1995; Ramírez and Marsh 1996; Marsh et al. 2000; Mácido et al. 1998; Pentado-Dias 2000; Martínez 2006), but they are also known to occur in some species of Mesostoinae (Austin and Dangerfield 1998; Oda et al. 2001).

The first reports of gall association in braconids are from the early twentieth century (Kieffer and Jörgensen 1910; Gahan 1912). In a study of gall insects from Argentina, Kieffer and Jörgensen (1910) described a doryctine genus with a single species, *Percnobracon stenopterus*, associated with galls of Fabaceae. These authors described eight other species that they assigned to the braconine genus *Bracon*, and which were associated with galls of Asteraceae, Fabaceae, Solanaceae and Chenopodiaceae. These eight species have been mostly neglected, remaining in the genus *Bracon* to date, although they were recently excluded from a key to species of *Bracon* from Argentina (Berta and Colomo 2000). Contemporary with Kieffer and Jörgensen (1910), Gahan

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(1912) also described the doryctine genus *Allorhogas* to include *Allorhogas gallicola* Gahan, a species apparently associated with oak galls in the USA.

Recently, one of us (J.J.M.) obtained three specimens that strongly resemble one of the gall-associated braconine species described by Kieffer and Jörgensen (1910), *Bracon mendocinus* Kieffer and Jörgensen. Two of these specimens were reared from galls of *Lycium chilense* (Solanaceae), the appearance of which is consistent with the galls from the same host plant species described and illustrated by Kieffer and Jörgensen (1910) and Jörgensen (1917). Unfortunately, most of Kieffer's collection is apparently lost (Gagné 1994). Jörgensen's collection on the other hand is deposited in the Museo de La Plata, Argentina, although it mostly comprises higher Hymenoptera and does not hold the types described in Kieffer and Jörgensen (1910). Therefore, we have not been able to compare the specimens that we collected with Kieffer and Jörgensen's type material. However, the original descriptions, including gall morphologies and host plant association records, allowed us to assign the specimens collected to *B. mendocinus*. Their morphological examination, supported by DNA sequences, prompted us to transfer *B. mendocinus* to *Allorhogas mendocinus* comb. nov., moving it from the subfamily Braconinae to the Doryctinae. Additionally, an undescribed species of *Allorhogas* that is morphologically similar to *A. mendocinus* is described and illustrated.

Material and methods

Specimens and terminology

All specimens were collected in the surroundings of Santa Rosa, La Pampa province, Argentina (36°37'03"S; 64°19'27"W), except one female, which was collected in Parque Luro, also from La Pampa (36°54'47"S; 64°15'42"W). Some specimens were collected with a net by sweeping the foliage of *L. chilense*, whereas others were reared from bud galls of the same plant species. Rearing was conducted by placing the galls individually in plastic tubes and leaving them at room temperature until the emergence of adult individuals. All specimens are deposited at the Museo Argentino de Ciencias Naturales (MACN). Morphological terminology follows that of Sharkey and Wharton (1997), and surface sculpture terminology is based on Harris (1979).

Molecular methods

Two gene fragments, from the nuclear 28S ribosomal DNA (including the second and third domain regions) and the mitochondrial cytochrome oxidase subunit I (COI) genes, were chosen as diagnostic loci for species identification. We sequenced 28S (around 650 base pairs) from both *A. mendocinus* and the undescribed species, whereas the standard barcoding gene COI (603 base pairs) was sequenced only for the undescribed species (we could not amplify COI from *A. mendocinus* despite numerous attempts). The sequences generated were analysed together with published sequences of three additional species of *Allorhogas* and four additional doryctine genera. All five of these genera are known to be gall-associated, and were recently described as closely related (Zaldivar-Riverón et al. 2007, 2008). We also included two species from the widespread genus *Heterospilus*, using *Heterospilus prosopidis* to root all the trees. A clade with the latter genus consistently appeared as the sister group of the clade with the gall-associated genera (Zaldivar-Riverón et al. 2007, 2008).

We used single hind legs as the source of genomic DNA for gene amplifications. The DNA extraction and polymerase chain reaction protocols, including primer sequences, are described in Zaldivar-Riverón et al. (2006). The COI sequences were aligned based on their translated amino acids. The 28S sequences were aligned based on the braconid secondary structure model proposed by Gillespie et al. (2005). The unalignable regions were delimited and excluded from the subsequent analyses.

Sequence divergences were calculated using the Kimura two-parameter model (Kimura 1980). Separate neighbour joining and maximum parsimony analyses were carried out for the COI and 28S datasets using PAUP* version 4.0b10 (Swofford 1998) to provide a graphic representation of the genetic divergences among the species examined.

Results and Discussion

As mentioned above, Kieffer's personal collection is presumably lost (Gagné 1994; Spies and Sæther 2004) so we cannot confirm the identification of our specimens based on direct comparisons with the type material. Nevertheless, a detailed examination of our collected specimens and their galls revealed that *B. mendocinus* Kieffer and Jörgensen actually represents an odd form of *Allorhogas*, with an extremely rugose cuticle in most of the head and mesosoma (see below).

Kieffer and Jörgensen's interpretation of *B. mendocinus* as a braconine and not as a doryctine is understandable if we think that the different doryctine genera reported to contain gall-associated species show disparate morphologies, and therefore, had often been placed in separate tribes (e.g. Labanini, Percnobraconini, Spathiini; Belokobylskij 1992) or even subfamilies (e.g. *Monitoriella* in the Hormiinae; Wharton 1993). In contrast, a recent molecular phylogenetic study that included species belonging to five gall-associated doryctine genera showed that they actually form a monophyletic group (Zaldivar-Riverón et al. 2007), which suggests that the independent evolution of gall association within the Braconidae is rarer than was initially understood (Wharton and Hanson 2005).

Our phylogenetic study examines the genetic distances among the *Allorhogas* species whose sequences are available, two of which are the focus of this paper. Figure 1 shows the neighbour joining phylograms obtained for both the 28S and the COI datasets, and the parsimonious substitutions relative to each branch. The 28S phylogram shows that *A. mendocinus* and the undescribed species (hereinafter named *A. joergenseni* sp. nov.) are closely related; however, their parsimonious differences are greater than those recovered for the other species of *Allorhogas*. In agreement with this, the corrected genetic distance between *A. mendocinus* and *A. joergenseni* for the 28S fragment is 2.88%, whereas among the five species of *Allorhogas* this distance ranges from 1.05 to 2.99% (Figure 1). Our genetic data therefore confirm that *A. mendocinus* and *A. joergenseni* sp. nov. represent distinct and probably sister evolutionary lineages. In relation to COI, the genetic distance between *A. joergenseni* sp. nov. and *Allorhogas* sp. 1 shows a similar degree of divergence compared to other gall-associated recognized species.

Systematics

Genus *Allorhogas* Gahan

Allorhogas Gahan 1912, p. 3.

Catolestes Brèthes 1922, p. 136; synonymized by Marsh (1993)

Type species: *Allorhogas gallicola* Gahan

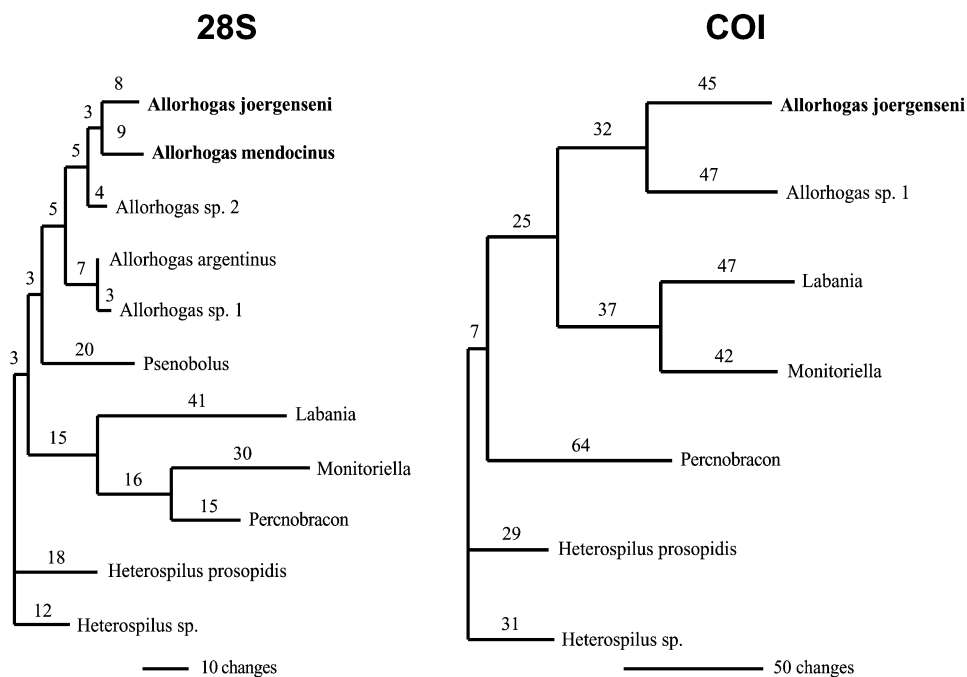


Figure 1. Phylograms obtained from neighbour joining separate analyses for the 28S and COI datasets, including all the available *Allorhogas* sequences, those of the other gall-associated braconids and *Heterospilus* as the outgroup. The two specimens investigated in this paper are indicated in bold type. The numbers above each branch indicate the observed parsimony changes.

Diagnosis

The concept of *Allorhogas* has been broadened in the past decade. Marsh (1993) redefined the boundaries of this genus by segregating a few parasitic species in the new genus *Parallorhogas* Marsh. This author also proposed the following five diagnostic characters to identify *Allorhogas*: (1) coriaceous mesopleuron, (2) excavated frons, (3) swollen male hind femur, (4) short ovipositor sheaths, and (5) association with plant galls and phytophagy. This concept of *Allorhogas* was followed in Marsh et al. (2000), but it has been subsequently modified in a revision of the Doryctinae of Costa Rica (Marsh 2002).

The genus *Allorhogas*, as defined in this study following Marsh (2002), can be distinguished from the remaining doryctine genera by its excavated frons and the slightly curved vein m-cu in the hind wing.

Biology

Allorhogas has been previously reported to be associated with galls on the plant families Bignoniaceae, Fabaceae and Melastomataceae (Macêdo and Monteiro, 1989; Macêdo et al. 1998; Marsh et al., 2000; Marsh, 2002). Here, based on the new combination, the genus is now known to be also associated with the family Solanaceae.

Allorhogas mendocinus (Kieffer and Jörgensen) comb. nov.

(Figures 2A,C,E, 3A,E, 4A,B)

Bracon mendocinus Kieffer and Jörgensen 1910, p. 414

Diagnosis

Allorhogas mendocinus can be distinguished from all other species of *Allorhogas* except *A. joergenseni* sp. nov. by the rugose head and mesoscutum and the obscured or weak notauli. Following Marsh's key to species of Costa Rica (Marsh 2002), the latter two species may be more related to *A. rugosus* Marsh, which has rugulose

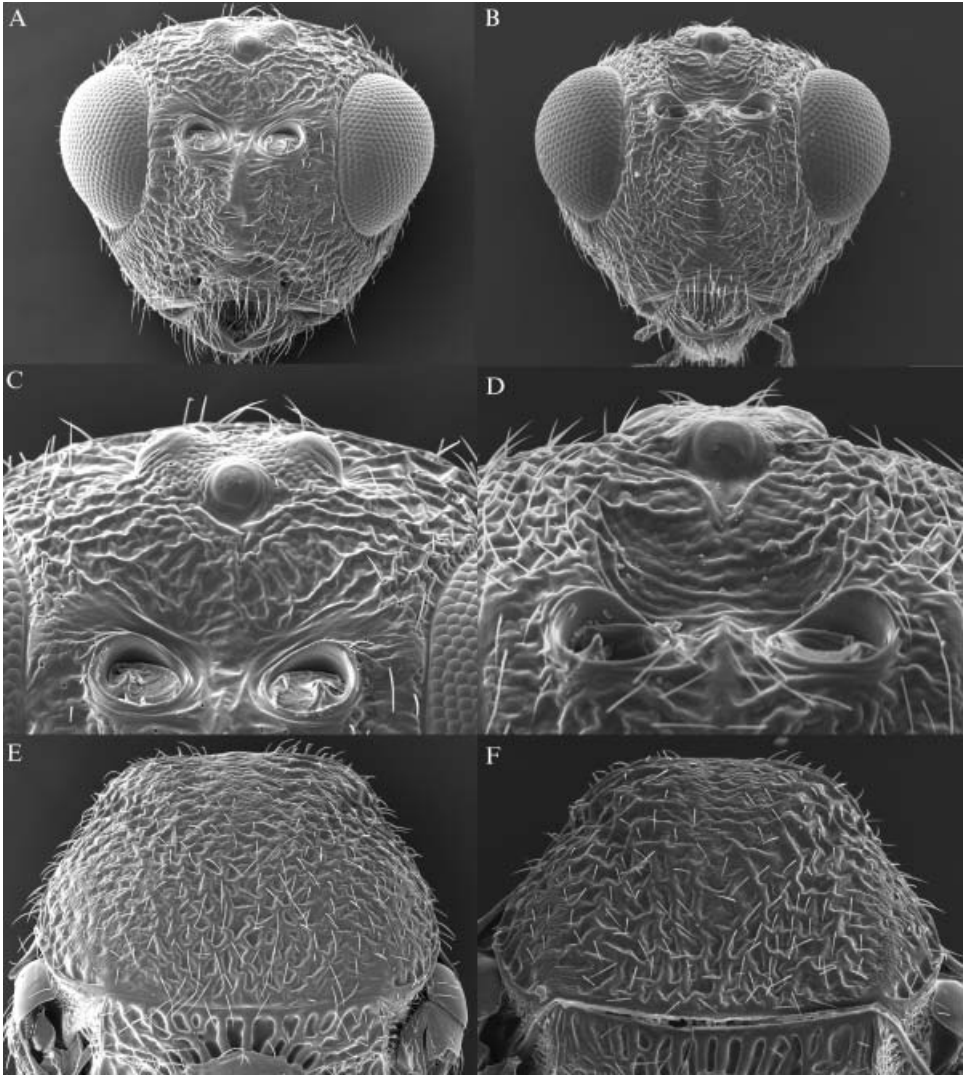


Figure 2 (A,C,E) *Allorhogas mendocinus*: (A) head in anterior view; (C) frons in anterior view; (E) mesoscutum in dorsal view. (B,D,F) *Allorhogas joergenseni* sp. nov.: (B) head in anterior view; (D) frons in anterior view; (F) mesoscutum in dorsal view.

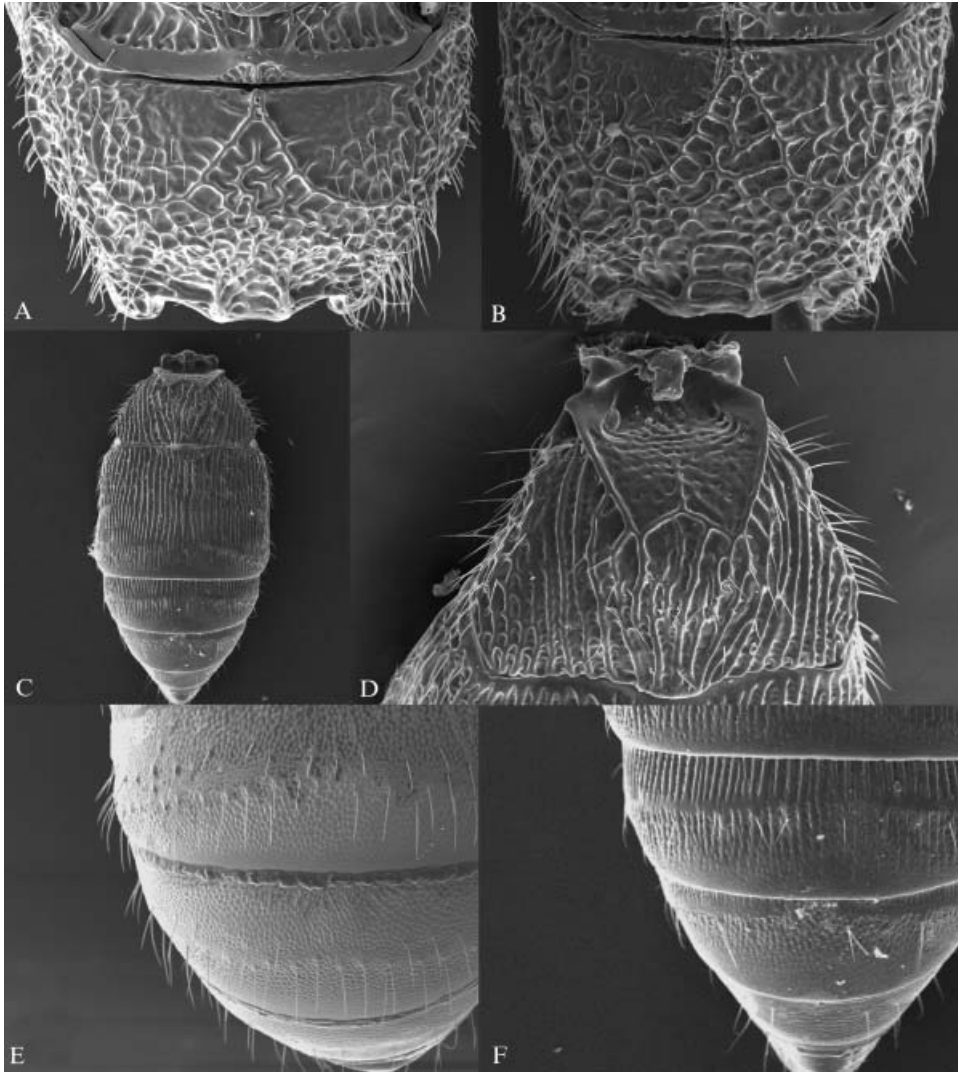


Figure 3 (A,E) *Allorhogas mendocinus*: (A) propodeum in dorsal view; (E) fourth and fifth metasomal terga in dorsal view. (B–D,F) *Allorhogas joergenseni* sp. nov.: (B) propodeum in dorsal view; (C) metasoma in dorsal view; (D) metasomal tergum I on dorsal and anterior view; (F) fourth and fifth metasomal terga in dorsal view.

mesonotal lobes at least along the notauli, although in the species treated here the sculpture is much coarser. Additionally, *A. rugosus* has bigger eyes (maximum diameter about three times the length of the malar space), honey brown in colour, and with inner orbits emarginated near the toruli. *Allorhogas mendocinus* is distinguished from *A. joergenseni* sp. nov. by its different metasomal sculpture. In *A. mendocinus*, the metasomal terga beyond tergum III are entirely coriaceous, whereas in *A. joergenseni* these are striate basally and weakly punctate to smooth apically. In addition, frons excavation is not as conspicuous in *A. mendocinus* as in *A. joergenseni*.

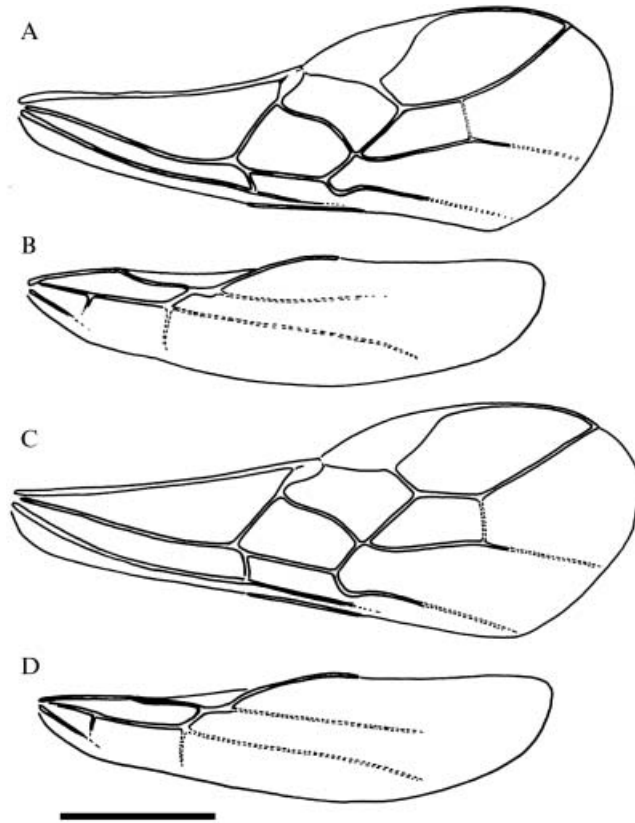


Figure 4 (A,B) *Allorhogas mendocinus*: (A) forewing; (B) hindwing. (C,D) *Allorhogas joergenseni* sp. nov.: (C) forewing; (D) hindwing. Scale: 0.5 mm.

Female

Body length 2.6 mm, forewing 1.9 mm.

Colour. Head and mesosoma orange-red, apex of antenna and metasoma beyond tergum I black, telotarsi darkened, forewing hyaline basally and very weakly infusate beyond vein M; veins brown, except veins C+SC+R, M+CU and 1-1A which are light brown to yellow; pterostigma brown, hindwing entirely hyaline.

Head. Transverse, about twice as wide as long, 18 antennomeres; occipital carina present and complete, reaching hypostomal carina; face, vertex and temples coarsely rugose (Figure 2A), except for an almost smooth narrow median line from clypeus to toruli; frons weakly excavated (Figure 2C); oral cavity small, shorter than malar space; eye moderate sized, 1.5 to 2 times the length of the malar space, with inner orbits uniformly rounded; temples narrow, shorter than eye width.

Mesosoma. Relatively short and compact, 1.5 to 1.7 times longer than high and about as high as wide. Pronotum rugose, pronotal collar not distinct, pronotal

furrow rugose. Mesoscutum (Figure 2E) transverse in dorsal view and strongly declivous anteriorly, 0.6 to 0.7 times as long as wide, anterior edge strongly directed anteriorly, apical face forming an acute angle with dorsal face in lateral view; coarsely rugose; notauli completely obscured by sculpture. Scutellum weakly acinose. Propodeum (Figure 3A) rugose–areolate, declivous posteriorly, without distinct carina or areola, with two somewhat more evident divergent carinae directed posteriorly and laterally from the median anterior edge. Mesopleuron rugose to acinose, subalar groove rugose, sternaulus half as long as mesopleuron.

Legs. Foretibia with a row of seven spines along the anterior margin, hind coxa mostly rugose with a small but distinct basal tubercule.

Wings. Forewing (Figure 4A) with pterostigma short and broad, second submarginal cell closed at apex; first subdiscal cell open apically; r shorter than 3RS; 2cu-a absent; RS+Ma sinuate; RS+Mb very short. Hindwing (Figure 4B) with vein m-cu nebulous and weakly curved towards wing apex.

Metasoma. Tergum I always wider than long, striate, anterior area clearly delimited by carinae and punctate; raised median area not clearly defined by carinae, basal sternal plate one-quarter to one-third the length of tergum I. Terga II and III striate, fused, line separating second and third terga weakly indicated laterally; remainder of terga entirely coriaceous (Figure 3E); ovipositor sheaths 0.25 times as long as metasoma.

Male

Essentially as in female, with 23 to 24 antennomeres.

Material examined

Argentina: Neotype female (MACN, here designated), La Pampa, Parque Luro, 22 February 2003, Martinez coll. Additional specimens: two males (MACN), La Pampa, Santa Rosa 20 March 2006, reared from galls of *L. chilense*, Martinez coll.

Biological observations

The new specimens assigned to *A. mendocinus* were reared from bud galls of *L. chilense* var. *chilense* (Figure 5B). These galls are identical to those described and illustrated by Jörgensen (1917) from the same plant species (Figure 5A). Although the last author mentioned the name *L. gracile*, this is a junior synonym of *L. chilense* var. *glaberrimum*. Galls on this plant species are oval, approximately 1 cm long, with a stiliform process that is about as long as the gall, and pubescent and green when fresh but brownish and almost glabrous when dry. The tissue surrounding the single pupal chamber is spongy in both mature and dry galls. As mentioned by Jörgensen (1917), galls are common during summer and it is possible that *A. mendocinus* produces more than one generation per year. Unlike the other gall-associated doryctines in the same locality (*Percnobracon* cf. *stenopterus*), which spend winter as

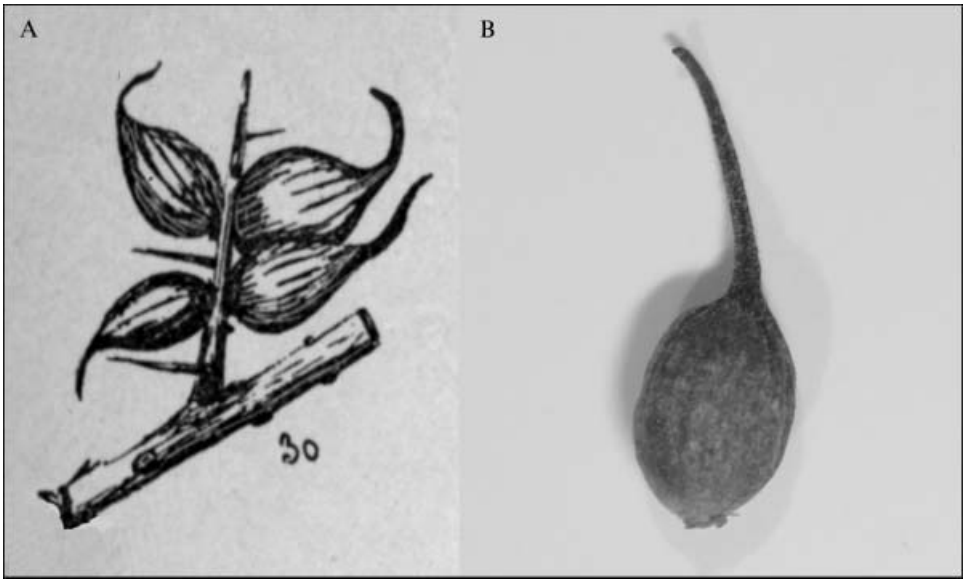


Figure 5 (A) Original illustration of galls on *Lycium chilense* from Jörgensen (1917); (B) gall found on *L. chilense*.

mature larvae within galls and the adults emerge in spring, adults of *A. mendocinus* emerge in late summer or early autumn.

In their study of gall insects from Argentina, Kieffer and Jörgensen (1910) proposed the name *Oligotrophus* (?) *lyciicola* for a hypothetical gall-inducing cecidomyiid (Diptera) species that could not be reared or observed within the galls, but that was assumed to be the host of *A. mendocinus* and other parasitic Hymenoptera. During the surveys made for this study, no adult cecidomyiid flies were reared from galls of *L. chilense* and no cecidomyiid larvae or pupae remains were observed within the pupal chambers. This, together with the current knowledge of gall induction by other species of *Allorhogas*, strongly suggests that *A. mendocinus* actually is the species that induces the galls on *L. chilense*. However, the absence of remains of the host after parasitoid emergence is known to occur in various parasitic species, and therefore further observations are needed to confirm the existence of the above cecidomyiid species.

Allorhogas joergenseni Martínez and Zaldivar-Riverón sp. nov.
(Figures 2B,D,F, 3B–D,F, 4C,D)

Diagnosis

As mentioned above, *A. joergenseni* sp. nov. is similar to *A. mendocinus*, but it can be distinguished by having a striate third metasomal tergum and the more conspicuous frons excavation.

Female

Body length 2.1–2.7 mm, forewing 1.6–2 mm.

Colour. Body orange-red, apex of antenna and metasoma darker, sometimes almost black, forewing hyaline basally and very weakly infuscate beyond vein M. Veins brown, except C+SC+R, M+CU and 1-1A, which are light brown to yellow, pterostigma brown, hind wing hyaline.

Head. Transverse, about twice as long as it is wide, 19 to 24 antennomeres; occipital carina present and complete, reaching hypostomal carina; face and vertex rugose (Figure 2B), temples rugose to weakly rugose in the smaller specimens, except for an almost smooth, fine median line from clypeus to toruli; frons excavated and weakly sculptured (Figure 2D), oral cavity small, shorter than malar space; eye moderate size, 1.5 to 2 times the length of the malar space; temples narrow, shorter than eye width.

Mesosoma. Relatively short and compact, 1.5 to 1.7 times longer than high and about as high as wide. Pronotum rugose, pronotal collar not distinct, pronotal furrow rugose or somewhat scrobiculate. Mesoscutum (Figure 2F) transverse in dorsal view and strongly declivous anteriorly, anterior face vertical in lateral view, 0.6 to 0.8 times as long as wide; coarsely rugose; notauli obscured by sculpture. Scutellum acinose. Propodeum (Figure 3B) rugose-areolate, declivous posteriorly, without distinct carina or areola, with two divergent carinae directed posteriorly and laterally from median anterior edge. Mesopleuron rugose to acinose, subalar furrow poorly indicated and rugose, sternaulus about half the length of mesopleuron.

Legs. Foretibia with a row of seven spines along anterior margin, hind coxa mostly rugose and with a small but distinct ventral tubercle.

Wings. Forewing (Figure 4C) with pterostigma short and broad. Second submarginal cell closed at apex; first subdiscal cell open apically; r shorter than 3RS; 2cu-a absent; RS+Ma sinuate; 2RS almost directly in line with m-cu, RS+Mb very short; hind wing (Figure 4D) with vein m-cu weakly curved towards wing apex.

Metasoma. Tergum I (Figure 3D) always slightly wider than long, striate, anterior area clearly delimited by carinae and punctate; dorsal raised median area not clearly defined by carinae. Terga II and III (Figure 3C) striate, fused, line separating second and third terga weakly indicated only laterally; remaining terga (Figure 3F) striate basally and smooth apically; ovipositor sheaths 0.25 times as long as metasoma.

Male

Essentially as in female, sometimes slightly smaller and lighter in colour, not so heavily sculptured, with notauli weakly indicated anteriorly.

Biology

Unknown. The specimens examined were collected with a net by sweeping the foliage of *L. chilense* and associated plant species.

Etymology

Named after Pedro Jörgensen, for his contribution to the knowledge of gall-associated insects in Argentina.

Material examined

Argentina: *Holotype female* (MACN). La Pampa, Santa Rosa, 26 July 2006, Martinez coll. *Paratypes*: Nine females (one coated for scanning electron microscopy) and three males, same data as holotype (MACN).

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Appendix

EMBL/GenBank accession numbers of the taxa employed in this study for the molecular phylogenetic analyses. Localities and voucher numbers of the specimens examined are listed in Zaldivar-Riverón et al. (2007).

Doryctinae: *Allorhogas mendocinus* (Kieffer and Jörgensen): 28S: EU871765; *Allorhogas joergenseni* Martínez and Zaldivar-Riverón sp. nov.: 28S: EU871764, COI: EU871763; *Allorhogas argentinus*: 28S: DQ498927; *Allorhogas* sp. 1: 28S: DQ649756, COI: DQ498959; *Allorhogas* sp. 2: 28S: EF645755; *Heterospilus prosopidis* Viereck: 28S: AY935469, COI: AY935396; *Heterospilus* sp. 2: 28S: DQ498926, COI: DQ498958; *Labania* sp.: 28S: DQ498928, COI: AY935397; *Monitoriella* sp.: 28S: AY935457, 28S: AY935387; *Percnobracon* cf. *stenopterus* Kieffer and Jörgensen: 28S: DQ498930, COI: DQ498960; *Psenobolus* sp.: 28S: DQ498929.