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New insights on the biology and larval morphology of Neotropical Mesostoinae (Hymenoptera, Braconidae): *Hydrangeocola llaollin* sp. nov. an endoparasitoid of *Centrodiplosis crassipes* (Diptera, Cecidomyiidae)

Juan José Martínez [a, b, *], Bárbara M. Corró Molas [b], Fernando Diez [a, b], Laura Gabriela Cornejo [a, b]

[a] Consejo Nacional de Investigaciones Científicas y Técnicas, (CONICET), Argentina
[b] Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Uruguay 151, L6300, Santa Rosa, La Pampa, Argentina

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ABSTRACT

The Southern Hemisphere subfamily Mesostoinae (Hymenoptera: Braconidae) includes, in most cases, species associated with plant galls, although the details regarding their biological traits are largely unknown. In this contribution, *Hydrangeocola llaollin* sp. nov. is described based on specimens that develop as larval endoparasitoids of *Centrodiplosis crassipes* (Diptera: Cecidomyiidae) in stem galls on *Lycium chilense* (Solanaceae). The mature larva of a Neotropical mesostoine wasp is described here for the first time and is compared with the only known larva from Australia. Larval morphology is entirely congruent with features typical of endoparasitoid species, which together with male genital features clearly relates *Hydrangeocola* with the South American genus *Andesipolis*, but separates it from the Australian phytophagous genus *Mesostoa*. These findings reveal the relevance of larval and male genital characters for our comprehension of the relationships among representatives of this poorly known braconid subfamily.

1. Introduction

The braconid genus *Hydrangeocola* Brèthes was originally proposed to include one species reared from galls on *Hydrangea serratifolia* (Hydrangeaceae) in Chile (Brèthes 1927). Later, several species were described from the *Nothofagus* (Fagales: Nothofagaceae) forests of Chile and Argentina (Fischer 1968; Papp 1992), with no additional biological information. Currently, the genus *Hydrangeocola* includes ten valid species known only form these humid forests of Southern South America (Yu et al. 2012). The placement of the genus *Hydrangeocola* within the subfamiliar and tribal classifications of the family Braconidae has been conflictive. Brèthes (1927) and Fischer (1968) placed it in the subfamily Hormiinae. Similarly, Papp (1992) included it in the Hormiini within the subfamily Exothecinae. Whitfield (1992) proposed the tribe Hydrangeocolini for the Neotropical genera *Hydrangeocola* and *Aspilodemon* Fischer, within the subfamily Hormiinae. In the Manual of the New World genera of Braconidae (Wharton et al. 1997), the genus was included in the chapter of the subfamily Hormiinae (Whitfield & Wharton 1997). More recently, in two independent phylogenetic analyses based on molecular evidence, both *Hydrangeocola* and *Aspilodemon*, as well as the puzzling genus *Andesipolis* Whitfield & Choi, were related to the Australasian gall-associated subfamily Mesostoinae (Zaldivar Riverón et al. 2006; Sharanowski et al. 2011), this criterion has been followed in the recent revision of *Andesipolis* (Shimbori et al. 2017). The biological traits of members of Neotropical mesostoines are poorly understood. The subfamily, as it is currently defined (Quicke 2015), includes species generally associated with plant galls in Australia and South America. One Australian species, *Mesostoa kerri* Austin & Dangerfield, is known to induce stem galls on *Banksia marginata* (Proteaceae) (Austin & Dangerfield 1998), being one the few known

* Corresponding author. Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Uruguay 151, L6300, Santa Rosa, La Pampa, Argentina.
E-mail address: jjmartinez@exactas.unlpam.edu.ar (J.J. Martínez).

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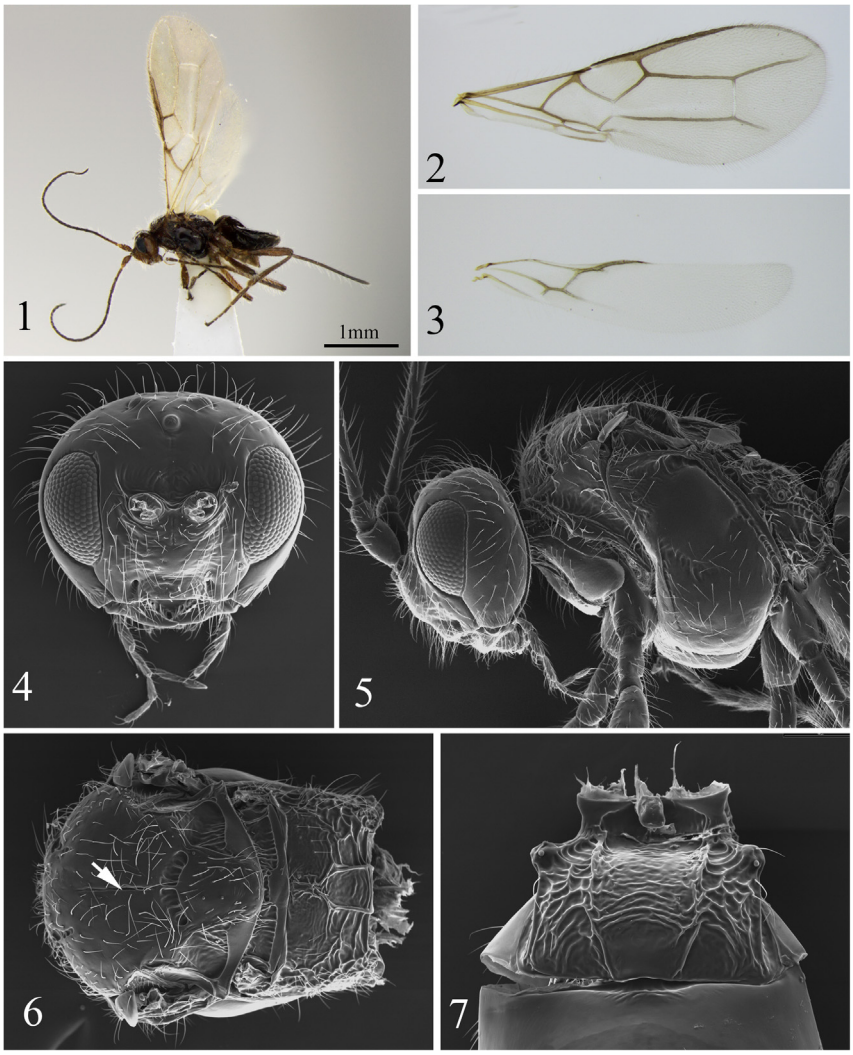
phytophagous braconids, together with some seed-feeding species of *Bracon* (Flores et al. 2005; Ranjith et al. 2016) and species in the Neotropical gall-associated doryctine lineage (Zaldivar-Riveron et al. 2007, 2014). Among Neotropical mesostoines, gall association has been mentioned for species in the genera *Hydrangeocola* and *Aspilodemon* (Brèthes 1927; Oda et al. 2001). Representatives of *Andesipolis*, have been reported as koinobiont gregarious parasitoids of an unidentified pyralid (Lepidoptera) larvae concealed in plant tissues (Townsend & Shaw 2009).

In unrelated studies on gall associated insects from Argentina, Kieffer & Jörgensen (1910) described three gall midge species (Diptera: Cecidomyiidae) inducing galls on species of *Lycium* (Solanaceae), now included in the tribe Centrodiplosini. During recent studies on the gall associated insects from central Argentina, it was possible to locate galls entirely congruent with the ones induced by *Centrodiplosis crassipes* (Diptera: Cecidomyiidae) as described and illustrated in Kieffer & Jörgensen (1910) and Jörgensen (1917). From these galls, together with the inducer, it was possible to obtain specimens of an undescribed parasitoid species of the genus *Hydrangeocola*. The objectives of this work are: 1) to formally describe the new species of *Hydrangeocola,* and 2) to provide new information on the biology and larval morphology of *Hydrangocola* and compare it with the scarce available information of this poorly known braconid subfamily.

2. Material and methods

Galls containing mature larvae were collected in suburban areas of Santa Rosa city, in La Pampa province, Argentina. This small population of gall bearing *Lycium* was observed during two growing seasons in order to recognize the time of the season in which mature larvae and pupae are present inside the galls. Some galls were dissected to obtain mature larvae and pupae, while others were kept in jars covered with commercial tissue paper until adult emergence. Larval and adult cecidomyiids were fixed in 80% ethanol and mounted following Gagné (1989, 1994). Adult cecidomyiids were keyed to genus following Gagné (1994) and Maia (2014) and compared with the original description (Kieffer & Jörgensen 1910), since no type material is available for study (Gagné 1994; Spies & Sæther 2004). Braconid adult morphological terms follow Sharkey & Wharton (1997), surface sculpture terminology follows Harris (1979), larval morphology follows Čapek (1970) and male genital morphology follows Belokobylskij et al. (2004) and Žikič et al. (2011). Male genitalia and larvae were digested in a solution of KOH ca. 10% and mounted in permanent microscopic slides following the same technique used for Cecidomyiidae. Some adults and larvae were covered with a gold-palladium coating and observed with a Scanning Electronic Microscope belonging to the Museo Argentino de Ciencias Naturales



Figs. 1–7. *Hydrangeocola llaollin* sp. nov., female. 1, habitus of females; 2, forewing; 3, hind wing; 4, head in anterior view; 5, head and mesosoma in lateral view; 6, mesosoma in dorsal view; 7, first metasomal tergite in dorsal view.

"Bernardino Rivadavia" (Buenos Aires); previously, larvae were critically point dried.

All material is deposited in the Entomology Division of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN).

3. Results

INSECTA
HYMENOPTERA
BRACONIDAE
Genus *Hydrangeocola* Brèthes
Hydrangeocola Brèthes 1927: 195
Kephalosema Fischer 1968: 792, synonymized by Wharton 1988: 344.
Type species: *Hydrangeocola espinosai* Brèthes, (MACN, examined)

Diagnosis. This remarkable genus is characterised by the following combination of charcters: Head cubical to transverse in dorsal view; ocellar triangle equilateral; eyes almost glabrous, with a few scattered and very short setae; malar suture present and deep; labrum concave and exposed; occipital carina present and complete, postgenal bridge narrow; maxillary palpus 5 segmented, labial palpus 3 segmented; pronotum not visible in dorsal view; mesoscutum with notauli present only anteriorly, and with a median deep pit or furrow on posterior half; precoxal sulcus present, prepectal and postpectal carinae present; propodeum with basolateral areas and with areola, sometimes poorly defined anteriorly; forewing with pterostigma very long and narrow, but distinguishable; second submarginal cell closed, long and wide; first subdiscal cell closed apically; first metasomal tergite relatively short and broad, basal sternal plate short; remaining metasomal terga smooth and unsculptured. Body covered with long and erect setae. Ovipositor sheaths at least as long as hind tibia, usually longer.

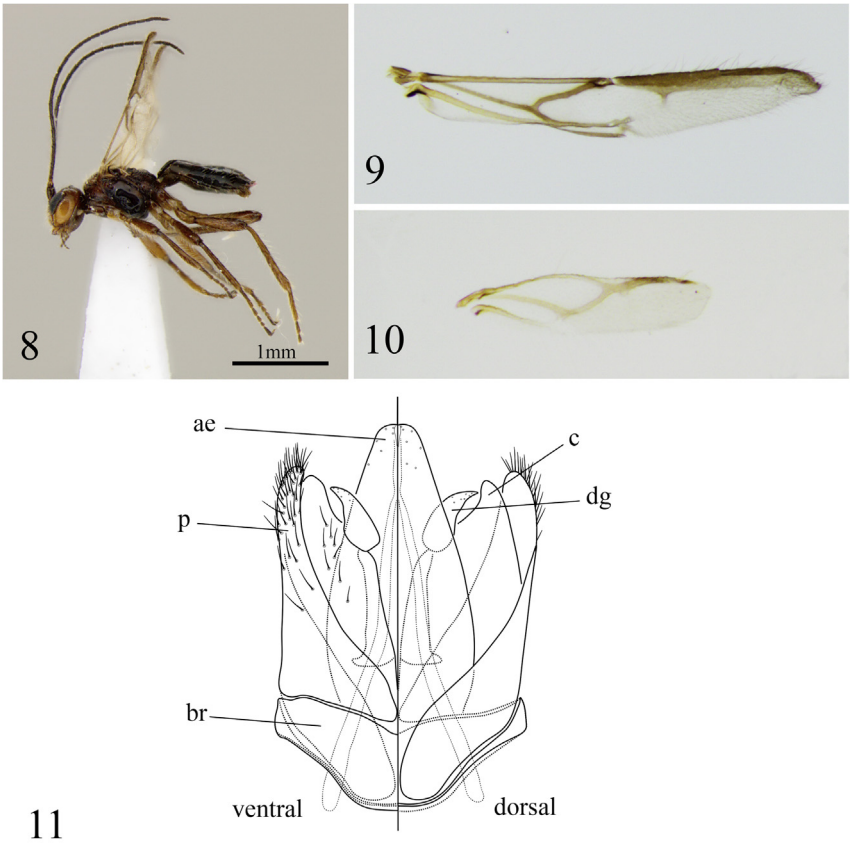
Hydrangeocola llaollin Martínez sp. nov.

Diagnosis. *Hydrangeocola llaollin* runs to *H. transversa* Papp in the key to species provided by Papp (1992) due to its transverse head in dorsal view, almost two times wider than long. It can be easily distinguished by the very distinct areolation on propodeum, without lateral carinae. The new species is the only species of the genus with known brachypterous males. Also, the new species is associated with galls from xeric environments in central Argentina, instead of the temperate humid forests in which all other members of the genus were collected.

Description.

Female. Body length 2.0–2.1 mm (Fig. 1), fore wing 2.5–2.6 mm (Fig. 2). Colour: Mostly uniformly dark reddish brown, with slightly lighter head, legs, base of antennae and ovipositor sheaths; wings hyaline, veins brown.

Head in dorsal view 0.6–0.7 times as long as wide, and 0.8 times as high as wide in anterior view (Fig. 4). Head mostly smooth and shining, except for two lines of irregular rugosities running from toruli to clypeus, also some weak rugae present on the lower half of the frons and on the genae adjacent to mandibular articulations. Eye 1.3 times higher than wide. Malar suture present and distinct (Figs. 4 and 5), malar space height/eye height ratio 0.3. Temple/eye length ratio (dorsal view) 0.6. Antenna with 20–21 flagellomeres, first flagellomere 5.5 times longer than wide and 1.3 times longer than second. Mesosoma 1.3 times longer than wide and 1.2 times



Figs. 8–11. *Hydrangeocola llaollin*, male. 8, habitus in lateral view; 9, fore wing; 10, hind wing; 11, genitalia. References: *ae*, aedeagus; *br*, basal ring; *c*, cuspis; *dg*, digitus; *p*, paramere.

longer than high. Pronotal groove deep, and irregularly rugose, pronotal collar indstinct, pronotum not visible in dorsal view. Propleuron smooth. Mesoscutum transverse, 0.5 times as long as wide. Notauli present only anteriorly, slightly rugose-scrobiculate, lobes of mesoscutum smooth and shining, except for a distinct and deep median furrow running through posterior half (Fig. 6). Scuto-scutellar suture present but weak. Prescutellar sulcus with one distinct median carina and several (4–5) poorly defined carinae at each side. Scutellar disc trapezoidal in shape and largely smooth. Mesopleuron smooth; precoxal sulcus weakly scrobiculate, running along anterior half of mesopleuron; subalar sulcus weak and irregularly rugose anteriorly, turning deep and smooth posteriorly, where it continues to meet the posterior mesopleural sulcus, which is deep and complete. Metanotum medially smooth and flat. Metapleuron weakly rugose. Propodeum with two smooth or very weakly sculptured basolateral areas, these areas are delimited by irregular and uncontinuous carinae. Posteriorly, a subpentagonal areola is distinct (Fig. 6); anteriorly, it continues as an irregular longitunidal carina reaching the anterior margin of propodeum. Posterolateral areas of propodeum irregularly rugose.

Forewing (Fig. 2) 2.6 times longer than wide; pterostigma long and slender, distinctly longer than R1. 3RSa almost six times longer than r and about as long as 3RSb. Second submarginal cell big and wide, 2.6 times longer than its maximum width. Hind wing (Fig. 3) vein M+CU 3.7 times longer than M and 2.5 times longer than r-m.

Legs. Hind femur 4.2 times longer than wide and 0.8 times as long as hind tibia, tarsal claws simple.

Metasoma. First metasomal tergum 0.9 times longer than apically wide; with two poorly defined carinae running longitudinally throughout its entire length delimiting three longitudinal areas (Fig. 7); the median one slightly rugose, and apically almost smooth; the lateral areas more coarsely rugose, spiracular tubercules present. Remaining metasomal terga smooth and shining. Ovipositor sheaths 2.3 times longer than hind femur.

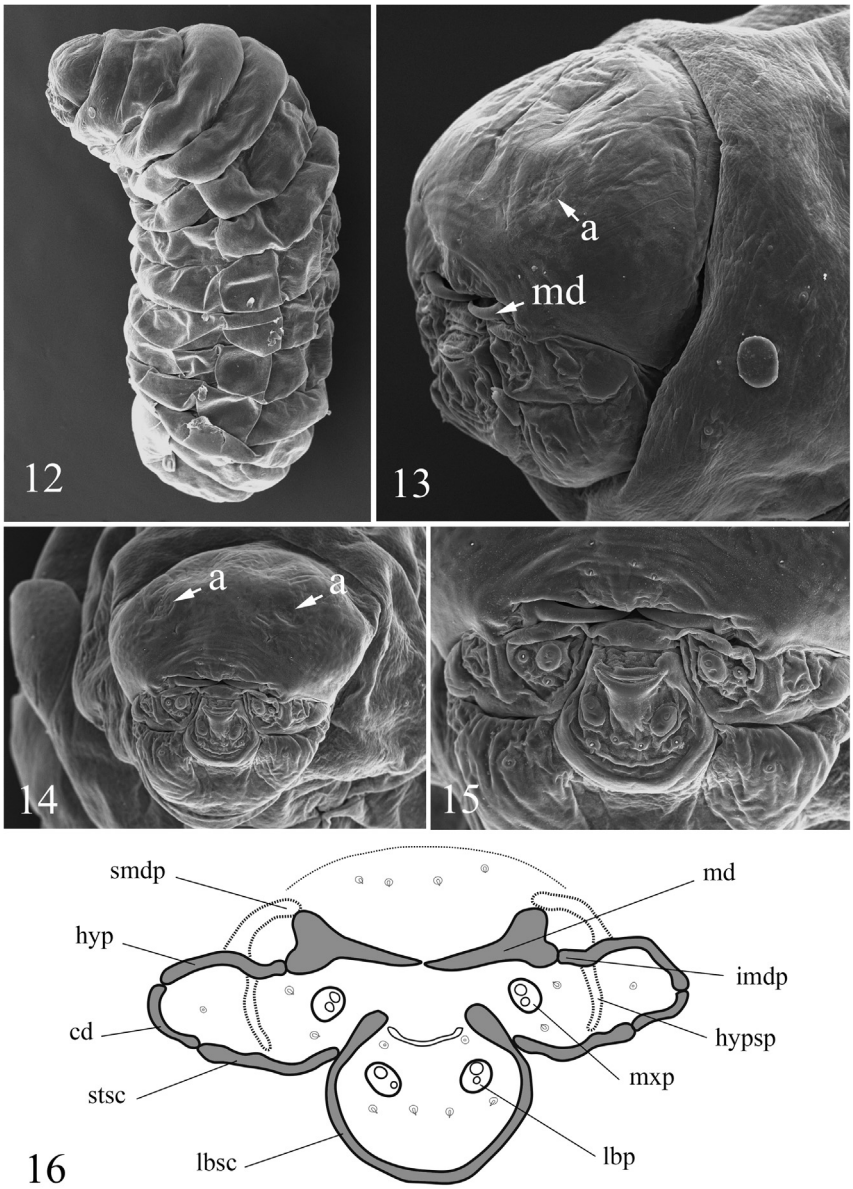


Fig.. 12–16. *Hydrangeocola llaollin*, mature larva. 12, habitus in lateral view; 13, head in anterolateral view; 14, head in anterior view; 15, detail of the cephalic structures; 16, scheme showing the mandibles and perioral sclerites. References: *cd*, cardo; *hyp*, hypostoma; *hypsp*, hypostomal spur; *imdp*, inferior mandibular process; *lbp*, labial palp; *lbsc*, labial sclerite; *md*, mandible; *mxp*, maxilary palp; *smdp*, superior mandibular process; *stsc*, stipital sclerite.

Male. Body length 2.0–2.1 mm (Fig. 8). Similar to female, sometimes with head and legs lighter in colour. Wings reduced (Figs. 9 and 10), fore wing about 0.6 times as long as total body length, only with veins C+SC+R, M+CU, 1A, M, CU and pterostigma distinguishable. Male genitalia (Fig. 11): Basal ring relatively short, dorsally extremely narrowed; parameres densely and evenly setose, long, slightly surpassing both the digitus and cuspis; volsella with cuspis well developed, longer than digitus.

Pupa (Fig. 21) without relevant features.

Mature larva 2.5 mm long (Figs. 12 and 20) with the head and thoracic segments in an obtuse angle with respect to the abdominal segments (Fig. 12). Larval cuticle smooth, largely devoid of microsculpture. Head with discoidal antennae (Figs. 13–14); mandibles sharp and toothless, but distinctly widened basally (Figs. 15 and 16); labial and stipital sclerites well developed, hypostomal spur present but slightly sclerotised; epistoma incomplete, represented by a shallow unsclerotised furrow; pleurostoma short, superior mandibular process slightly sclerotised, inferior mandibular process distinctly sclerotised and pigmented. Labial and maxillary palpi with two or, occasionally, three sensilla.

Distribution: Known only from the type locality in La Pampa, Argentina.

Material examined: Holotype female, ARGENTINA, La Pampa, Santa Rosa, Ea. La Malvina, -36.618275, -64.329324, 17-VIII-2008, from stem galls on *Lycium chilense*, Martínez col. Paratypes: 16 females and six males, same data as holotype; two males, same data as holotype except date, 22-III-2008; 11 females, Argentina, La Pampa, Santa Rosa, Laguna Don Tomás, -36.618272, -64.324311, 02-VIII-2009, from stem galls on *L. chilense*, Martínez col.; five mature larvae, same data as holotype except date, 10-XI-2009.

Etymology. The specific epithet refers to the common name given to the host plant species – *L. chilense* – from which this species was reared.

Biological observations. *C. crassipes* induces multilocular galls (larvae in individual chambers) on stems of *L. chilense* (Fig. 17). The galls described in this work are entirely congruent with the ones described and illustrated by Kieffer & Jörgensen (1910) and Jörgensen (1917). The abnormal tissue induced is the superficial cortical parenchyma located next to the peridermis (Fig. 18). In October the first mature larvae can be observed (Fig. 19) and in late October pupae are present inside the galls, and the first adults begin to emerge. Most adults emerge during November. Based on our observations, *C. crassipes* has one generation per year. We were not able to locate eggs on the stems but based on the original description (Kieffer & Jörgensen 1910) and our observations of adult emergence, females oviposit in stems in late spring or early summer. Immature larvae probably spend autumn and winter inside the stems remaining largely inactive until the following spring, when larvae become fully developed. In a few occasions, a mature cecidomyiid larva was observed inside galls collected in winter, thus the details of the host's life cycle are still obscure. Members of *H. llaollin* behave as endoparasitoids of *C. crassipes* within stem galls on *L. chilense*. In

Fig.. 17–21. 17, *Lycium chilense* with a stem gall; 18, detail of the gall; 19, three larvae of the host, *Centrodiplosis crassipes*; 20, mature larva of *Hydrangeocola llaollin*; 21, pupa of *H. llaollin*.

many occasions, it was possible to observe immobile cecidomyiid larvae containing an immature unidentified endoparasitoid larva. In other cases, gall chambers were occupied by a mature *Hydrangeocola* larva or pupa with no recognizable host remains (Figs. 20 and 21). Endoparasitoidism was confirmed by dissecting one gall containing a mature larva of *Hydrangeocola* entirely covered by the cuticle of a *C. crassipes* third instar larva. The spatula of the host's larva was identified when extracting the larva of *H. llaollin*.

4. Discussion

In the original description of *C. crassipes*, four parasitoid species were described: two pteromalid species, one eurytomid and one braconid, *Bracon lycii* Kieffer & Jörgensen, which probably belongs in the gall associated genus *Allorhogas* Gahan. The presence of a species of *Hydrangeocola* attacking *Centrodiplosis* not only represents a new and interesting host-parasitoid association, but also has important biogeographical implications. Currently all described

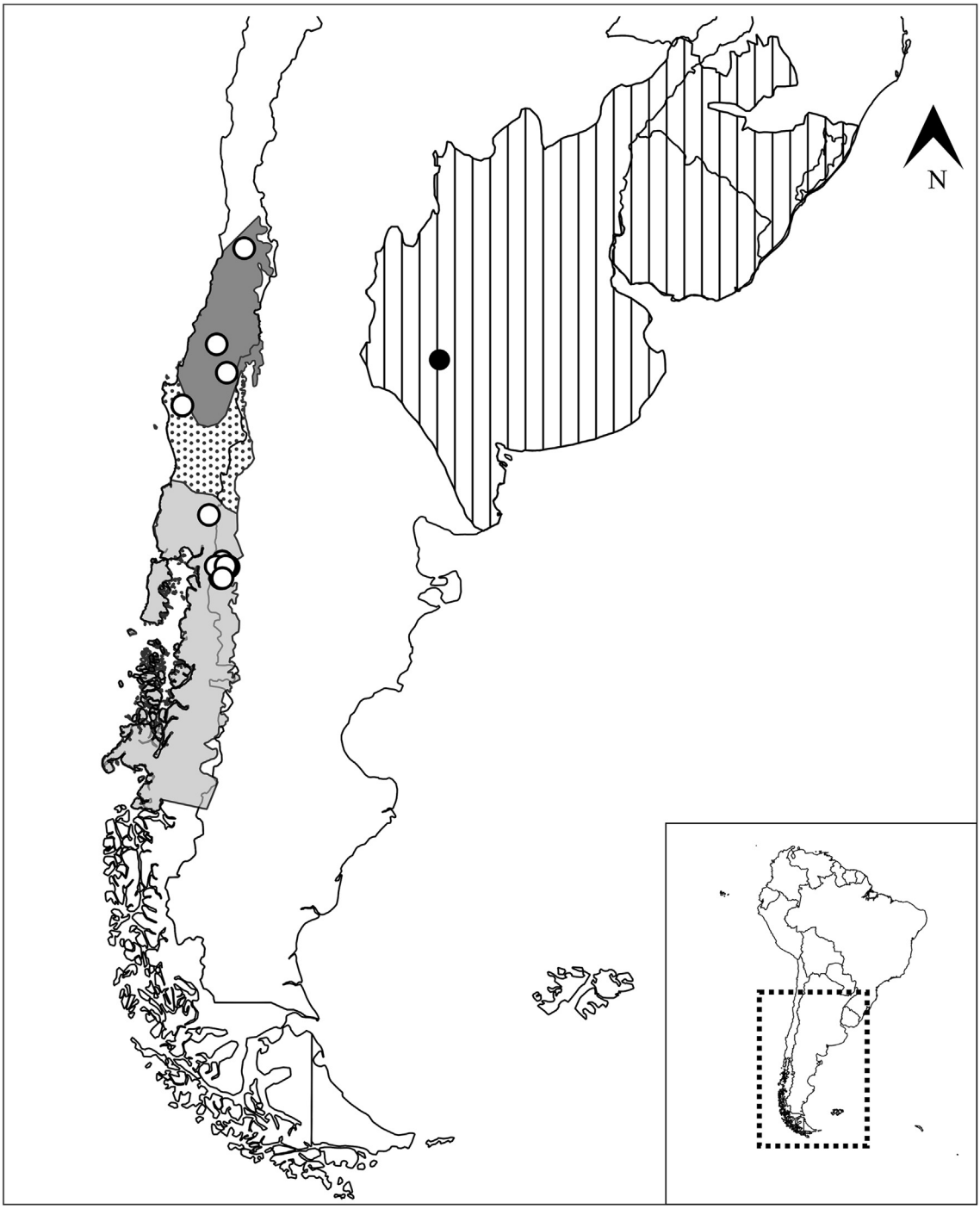


Fig. 22. Known distributional records of the genus *Hydrangeocola*. White circles: *Hydrangeocola* spp., previous records of species of the genus in *Nothofagus* and *Araucaria* forests (dark grey: Santiagan province, dotted: Maule province, light grey: Valdivian Forest province; as in Morrone 2015); black circle: type locality of *H. llaollin* in the Pampean province (Morrone 2014).

species of *Hydrangeocola* were collected in tempterate humid forests of the Andean Region (*sensu* Morrone 2015) in Argentina and Chile. The species described in this work is associated with a very common shrub from xeric landscapes widely distributed in central and western Argentina, in the Pampean province of the Chacoan dominion (Morrone 2014) (Fig. 22).

Larval morphology of mesostoine wasps is largely unknown. The only species with known mature larva is *Mesostoa austini*, whose larval instars develop in galls of *Banksia* sp. (Proteaceae) in Australia. Larval morphology of *M. austini* was briefly described based on the cephalic structures of the holotype's larval exuvia (Quicke & Huddleston 1989) and is characterized by its robust mandibles, probably used to feed on plant tissues. The larva of *H. llaollin*, on the other hand, is consistent with the typical endoparasitoid braconid larva with sharp mandibles and discoidal antennae. Similarly, male genital morphology of species of Mesostoinae is poorly known. The male genitalia of *H. llaollin* undoubtedly relates both *Hydrangeocola* and *Andesipolis* (Whitfield et al. 2004) but differs considerably with the morphology described for *M. austini*. *Andesipolis* and *Hydrangeocola* present distinctly large parameres and cuspis, both surpassing the digitus, whereas in *M. austini* parameres are shorter than digitus and the cuspidal process is indistinct.

The position of *Hydrangeocola*, *Aspilodemon* and *Andesipolis* in Mesostoinae has been accepted by various authors based on molecular evidence (Belshaw & Quicke 2002; Zaldivar Riverón *et al.* 2006; Sharanowski et al. 2011; Quicke 2015), however, this relationship is not supported by distinct morphological synapomorphies. These results were questioned by Townsend & Shaw (2009) in their description of *Andesipolis yanayacu*, a gregarious koinobiont parasitoid of a pyralid moth. These authors suggested a close relationship of *Andesipolis* with Rhysipolinae, arguing that members of the Mesostoinae are gall inducers. Although many members of Mesostoinae are associated with plant galls, their condition of gall makers, parasitoids or inquilines is not clearly understood. The only species for which phytophagy and gall induction is considered demonstrated is the Australian species *M. kerri* Austin & Dangerfield (Austin & Dangerfield 1998; Quicke 2015). Biological data regarding the Neotropical genera *Hydrangeocola* and *Aspilodemon* are scarce and consist only of the association with some galls, without further details. The ectoparasitoid condition of *Aspilodemon* was proposed based on circumstantial evidence but not on direct observation (Oda et al. 2001). Based on our findings, both biological and morphological evidences relate *Hydrangeocola* with *Andesipolis* and *Aspilodemon*, but it is still difficult to relate these Neotropical genera with Australian mesostoines based only on morphological evidence. The finding of *H. llaollin* as the first confirmed gall associated endoparasitoid species among Neotropical Mesostoinae reveals more complex biological interactions of members of the subfamily as it is currently defined.

Acknowledgments

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