Sociobiology 62(2): 246-265 (June, 2015) DOI: 10.13102/sociobiology.v62i2.246-265

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - ANTS

Wasmannia Forel (Hymenoptera: Formicidae: Myrmicinae) in Argentina: Systematics and Distribution

F. Cuezzo[1], L.A. Calcaterra[2], L. Chifflet[3], P. Follett[4]

1 - Instituto Superior de Entomología Dr. A. Willink, Facultad de Ciencias Naturales e IML. CONICET, Tucumán, Argentina
2 - Fundación para el Estudio de Especies Invasivas-CONICET, Buenos Aires, Argentina
3 - Universidad de Buenos Aires-CONICET, Ciudad de Buenos Aires, Argentina
4 - USDA-ARS, Pacific Basin Agricultural Research Center, Hilo, Hawaii

Article History

Edited by
John Lattke, Universidad Nacional de Loja, Ecuador
Received 01 December 2014
Initial acceptance 11 February 2015
Final acceptance 02 March 2015

Keywords
Wasmannia longiseta n. sp., little fire ant, biogeography, taxonomy, phylogeny.

Corresponding author
Fabiana Cuezzo
Instituto Superior de Entomología
Dr. A. Willink, Facultad de Ciencias
Naturales e IML
Miguel Lillo 205, T4000JFE, San Miguel de Tucumán, Tucumán, Argentina
E-Mail: cuezzof@yahoo.com.ar

Abstract

The ant genus *Wasmannia* is endemic to the Neotropics, with 10 species occurring within the presumptive native range for the genus from Mexico to Argentina. Only the little fire ant, *Wasmannia auropunctata* is widely distributed being present from central-eastern Argentina to Bermuda, and has become infamous due to its recent worldwide expansion and status as an invasive pest. The objective of this work was to study the systematics and distribution of *Wasmannia* in its southern limit of distribution in Argentina. Out of the three species reported so far for Argentina, only *W. auropunctata* was found to be widely distributed, but abundant only in disturbed habitats mostly in the Northeast. Herein, the distribution of *Wasmannia auropunctata* is extended and its queen and male castes are redescribed, along with descriptions of gynandromorphs (specimens with left side of the head similar to a male and right side similar to a queen). *Wasmannia sulcaticeps* and *W. williamsoni* are much less common and widespread. *W. sulcaticeps*is mostly found in mountain forests in northwestern Argentina, whereas *W. williamsoni* is only found in shrublands and grasslands in central eastern Argentina, and most frequently in mountain grasslands. Both species overlap with *W. auropunctata*, which is more common in the lowlands, between approximately 400 and 1000 m elevation. The queen of *W. williamsoni* is described and queen and male of *W. sulcaticeps* are redescribed. A new species, *Wasmannia longiseta* n. sp. Cuezzo and Calcaterra, recently found in northeastern Argentina, is described based on worker morphology. *Wasmannia rochai* is recorded for the first time in Misiones, extending its distribution range from São Paulo (Brazil) to Misiones in northeastern Argentina. A key to the worker caste is provided. A cladistic analysis based on discrete and continuous morphological characters is presented as a first attempt to clarify the phylogenetic relationships between the known species of *Wasmannia.*

Introduction

The ant genus *Wasmannia* (Formicidae: Myrmicinae) was created by Forel in 1893. Initially, this genus was included in the tribe Ochetomyrmicini because its member species are very similar to those of the genus *Ochetomyrmex* Mayr (Fernández, 2003). One hundred and ten years later, Bolton (2003) included it in the tribe Blepharidattini, a sister group of the fungus growing ants, Attini s.s. (Shultz & Meier, 1995). However, Ward et al. (2015) recently synonymized the tribe Blepharidattini under Attini.

All the members of the previous tribe Blepharidattini can be recognized by the following characteristics: 1) mandibles with 5 or fewer teeth, 2) 11-segmented antenna with a terminal well-differentiated 2-segmented club, 3) clypeus broadly inserted between the frontal lobes, 4) propodeal spiracle low on the side of propodeum, and 5) no species cultivate fungus (as in the former Attini) (Longino & Fernandez, 2007).

For a long time, *Blepharidatta* Wheeler was considered the sister taxon of *Wasmannia* within the tribe Blepharidattini, but after the Ward et al. (2015) study, based on molecular data, *Allomerus* Mayr (previously considered within the tribe

Open access journal: http://periodicos.uefs.br/ojs/index.php/sociobiology
ISSN: 0361-6525

Solenopsidini, Fernández, 2007) is currently inferred as the most closely related genus. All three genera are now included in the tribe Attini (new sense). All species of *Wasmannia* are small ants that can be differentiated from *Blepharidatta* and*Allomerus* by 1) having shallow, always well-developed antennal scrobes, 2) posterior margin of the vertex not pronounced as lobes or teeth (as in *Blepharidatta)*, 3) petiolar node with a distinct anterior and dorsal face, and 4) irregularly striated head, at least in part, in full face view (Longino & Fernandez, 2007).

Besides these characters, the eight known species of *Allomerus* inhabit internal cavities of plants and have the propodeum unarmed to bidentate. The well-developed spines between the dorsal and posterior face of the propodeum, so typical of *Wasmannia*, are absent in *Allomerus*. The body of workers in *Allomerus* is always smooth and shining, resembling more a small *Solenopsis* than a worker of *Wasmannia*.

The genus *Wasmannia* is mostly endemic to the Neotropics, with ten species occurring from Argentina to Mexico, according to the last taxonomic review (Longino & Fernández, 2007). The little fire ant *Wasmannia auropunctata* Roger (1863) (LFA) is the most widely distributed species of the genus, being present from central-eastern Argentina north to the Caribbean and Bermuda (Wetterer & Porter, 2003). It has spread fairly recently throughout Pacific and Atlantic islands, and the Mediterranean region (e.g. Israel), and has become a serious pest in Hawaii and the Galapagos, disrupting agricultural practices and threatening wildlife (Foucaud *et al*., 2010).

Kusnezov (1952) hypothesized parthenogenetic reproductionby this species given the high prevalence of colonies containing only females, this was later confirmed by Fournier (et al., 2005). The LFA displays extraordinary reproductive polymorphism with both regular sexual and unusual clonal populations (Foucaud et al., 2007). This rare type of clonality was also recently reported for the invasive longhorn crazy ant *Paratrechina longicornis* (Latreille) (Pearcy *et al*., 2011). This unusual reproductive system is postulated to be responsible for unicoloniality, in which individuals from different nests form a large supercolony, an attribute that probably contributes to the success as an invader (Orivel et al., 2009).

Although numerous studies were conducted on the LFA in northern South America (Ulloa-Chacón & Cherix, 1990, de Souza et al., 1998, Foucaud et al., 2009, Orivel et al., 2009), little is known about populations at the southern limit of its native range (Kuznezov, 1952, Rey et al. 2012, Calcaterra et al., 2012).

Wasmannia rochai Forel (1912) is the second most widely distributed species of the genus, occurring from Guatemala to São Paulo, Brazil. Four other scarcely collected and little known species, *W. iheringi* Forel (1908), *W. lutzi* Forel (1908), *W. affinis* Santschi (1929), and *W. scrobifera* Kempf (1961), occur mostly with *W. auropunctata* and *W. rochai* in the Atlantic Forest of southeastern Brazil and/or the Amazon Forest in Brazil (Longino & Fernández, 2007).

At present, only three species of *Wasmannia* have been reported from Argentina: *W. auropunctata*, *W. sulcaticeps* Emery (1894), and *W. williamsoni* Kusnezov (1952). According to Longino & Fernández (2007), *W. sulcaticeps* and *W. williamsoni* are related endemic species that occur in the far southern range of the genus and, as stated by Kusnezov (1952), they could be the poorest competitors within the genus, whereas *W. auropunctata* appears to be the most successful and competitive species of the genus, with a pool of derived attributes and a wide distribution.

The main objectives of this work are to (1) update the distribution of *Wasmannia* in Argentina, (2) describe a new species for Argentina (*Wasmannia longiseta* n. sp.), and (3) study the phylogenetic position of the Argentinean species in relation to the rest of the genus.

Materials and methods

This study was conducted by examining specimens of *Wasmannia* deposited at the Instituto y Fundación Miguel Lillo (IFML) ant collection, Tucumán, Argentina, and new specimens collected during surveys carried out by L.A.C. and L.C. between 2008 and 2013 in northern and central Argentina. The new material examined, including types, was deposited in the IFML, and vouchers were deposited in the Fundación para el Estudio de Especies Invasivas (FuEDEI), Hurlingham, Buenos Aires, Argentina.

General terminology and abbreviations are based on Longino and Fernández (2007), Serna and Mackay (2010) and Serna et al. (2011). Measurements (in mm.) were taken using a Leitz stereoscope at 40x magnification.

HL: Head Length in full face view, measured on a straight line from the anterior margin of the clypeus to the frontovertexal margin of the head.

HW: Head Width in full face view, perpendicular to HL, excluding the compound eyes.

EL: Maximum Length of the compound Eye in dorsal view.

SL: Scape Length in dorsal view, excluding the radicule.

AD: Maximum Distance between frontal carinae.

WL: Weber's Length, measured on a straight line in lateral view of the mesosoma from the most anterior part of the prothorax to the postero-ventral angle of the propodeum, including the propodeal lobes.

PSL: Length of the Propodeal Spine in lateral view measured on an imaginary straight line from its insertion in the propodeum to the apical point of the spine.

PD: Peduncular Length, in lateral view, measured from the petiolar point of insertion in the mesosoma to the anterior face of the petiolar node.

PTL: Maximum Length of the petiole in dorsal view.

PPTL: Maximum Length of the Postpetiole in dorsal view.

PTW: Maximum Width of the Petiole in dorsal view.

PPTW: Maximum Width of the Postpetiole in dorsal view.

Indexes

CI: Cephalic Index (=HW/HL)

OI: Ocular Index (=EL/HL)

Phylogenetic analysis

A matrix was constructed with 46 morphological characters (12 continuous and 34 discrete). The genera *Allomerus*, *Blepharidatta*, *Cyphomyrmex* Mayr, and *Acromyrmex* Mayr, were selected as outgroups on the basis of previous studies (Schultz & Meier, 1995; Longino & Fernández, 2007; Ward et al., 2015). The ingroup includes all described species of *Wasmannia* (except *W. villosa*), together with the new species described in this work, *Wasmannia longiseta* n. sp.

Characters (see Table 1 for a list of the characters and explanations) were obtained from 1) recently collected material, 2) samples deposited in the IFML collection, and 3) literature reports (Wheeler, 1915; Kempf, 1965, 1967; Gonçalves, 1961; Wheeler & Wheeler, 1991; Snelling & Longino, 1992; Longino & Fernández, 2007). A new source of characters, provided by lineal morphometry, normally used to define ant taxa was also included in this phylogenetic approach. In the alpha taxonomic literature there is a vast amount of linear morphometric data that could be useful to infer phylogenetic relationships or, at least, to improve clade support, but they are seldom used. One possible reason are the numerous arguments against the use of continuous characters in phylogenetic reconstructions (Rae, 1998; Wiens, 2001); however, most objections relate to how best to encode those characters (Pimentel & Riggins,1987; Cranston & Humphries, 1988; Stevens,1991), rather than reasons for excluding them from the analysis (Goloboff et al., 2006).

Herein, continuous queen and worker character measurements are expressed as a range of values (minimum to maximum), except in those species whose descriptions are based on only one specimen (see Table 1). The data matrix of continuous characters for gynes and workers (characters 0-11) is shown in Appendix 1, whereas the data matrix of discrete morphological characters for workers (characters 12-45) is shown in Appendix 2.

The resulting character matrix was analyzed with TNT version 1.1 (Goloboff et al., 2008b) under parsimony with implicit enumeration (exact search) using combined data sets for discrete and continuous characters. The discrete character number 44 was considered additive, whereas the rest of the discrete characters were codified and analyzed as non-additive. Continuous characters are automatically considered as additive by TNT. To measure clade support, the original matrix was subjected to symmetric resampling (Goloboff et al., 2003b) with 1000 replicates,(P = 0.25) and cut = 25. Values of symmetric resampling are given as frequency differences (GC values).

Results

Updated list of Argentinean species of ***Wasmannia***
Wasmannia auropunctata Roger 1863
Wasmannia longiseta Cuezzo & Calcaterra **n. sp.**
Wasmannia rochai Forel 1912
Wasmannia sulcaticeps Emery 1894
Wasmannia williamsoni Kusnezov 1952

Key to workers of ***Wasmannia***

The key of Longino and Fernández (2007) to the worker caste of *Wasmannia* species was modified to include *W. longiseta* n. sp. together with all the other species (except *W. villosa*) as follows:

1- Petiolar node strongly quadrate in lateral view; petiolar peduncle about as long as node; setae on mesosomal dorsum simple and erect, color red brown to orange …... *auropunctata*
1'- Petiolar node never quadrate, more rounded; or clypeus strongly projecting and box-like and dorsal pilosity composed of a very short stubble; petiolar peduncle longer or shorter than node; color variable ....…………………………. 2

2- Petiolar peduncle longer than node in lateral view; mesosomal dorsum with long setae (length close to the length of the propodeal spine in lateral view) and gaster smooth and shiny, with abundant long (>1 mm), curved and whitish setae………………...…...………*W. longiseta* **n. sp.**
2'- Petiolar peduncle equal to node or shorter in lateral view; mesosomal dorsum with shorter setae, gaster frequently weakly punctate with fewer, scattered setae …………..…...……… 3

3- Scape strongly flattened; clypeus strongly projecting and box-like, sharply divided into equaldorsal and anterior faces that meet at a right angle; setae on mesosomal dorsum abundant, straight, filiform; very short propodeal spines, about same length as the setae on mesosomal............................*scrobifera*
3'- Scape not strongly flattened; clypeus not strongly box-like, rounded from posterior to anterior margins; setae on mesosomal dorsum longer and/or curved, clavate; propodeal spine length variable……... 4

4- First gastral tergite lacking erect setae; petiolar peduncle longer than node; dorsal setae on mesosoma and face thin, flexuous; color yellow orange ....*iheringi*
4'- First gastral tergite with abundant erect setae; petiolar peduncle equal to node or shorter; dorsal setae stiff to slightly clavate; color various……........…...................................... 5

5- Antennal scrobe narrow, not extending to side of head, ventral margin defined by preocular carina that runs from dorsal margin of eye to margin of vertex; side of head posterior to eye rounded 6
5'- Antennal scrobe broad and flat, extending to side of head, ventral margin formed by angular side of head posterior to eye 9

6- Face between frontal carinae with about 12 distinct longitudinal striae overlaying strong punctate sculpture; propodeal spiracle small, diameter less than width of base of propodeal spine (Argentina).. 7
6'- Face between frontal carinae with fewer and more irregular longitudinal rugae, overlaying opaque but not as strongly punctate sculpture; propodeal spiracle large and conspicuous, diameter about equal to width of base of propodeal spine........................ 8

7- Head width less than 0.50 mm; longitudinal striae on face very regular to margin of vertex; color yellow red; posterior face of petiole rounded, anterior face slightly angulate.......... *sulcaticeps*
7'- Head width greater than 0.54 mm; striae on face somewhat less parallel, becoming irregular near margin of vertex; color uniformly dark maroon, abdomen black; anterior and posterior face of petiolar node similarly rounded......................*williamsoni*

8- Dorsal setae on mesosoma and gaster straight to weakly curved, thin, not clavate; head relatively long, CI about 0.90; propodeal spines relatively long and upturned (Fig 1); eyes relatively larger (OI 0.26).. *sigmoidea*
8'- Dorsal setae on mesosoma curved and clavate; head relatively short, CI 0.95-1.00; propodeal spines short and directed posteriorly; eyes shorter (OI 0.21-0.24)............*rochai*

9- Postpetiole in dorsal view subquadrate to slightly trapezoidal, with widest portion anterior to midlength; postpetiolar dorsum strongly punctate and opaque; propodeal spines relatively long and stout, in dorsal view about as long as distance between their tips.. *lutzi*
9'- Postpetiole in dorsal view elliptical, widest portion at or posterior to mid length; postpetiolar dorsum weakly punctate, sublucid medially; propodeal spines shorter, in dorsal view shorter than distance between tips................................. *affinis*

Species accounts

Wasmannia auropunctata (Roger)

Worker (n=10): HL: 0.55-0.61; HW: 0.42-0.48; EL: 0.11-0.13;, SL: 0.35-0.40; AD: 0.20-0.27; PSL: 0.13-0.20; WL: 0.51-0.55; PD: 0.10-0.12; PTL: 0.12-0.15; PPTL: 0.10-0.12; PTW: 0.10; PPTW: 0.15-0.17; CI: 0.91-0.93; OI: 0.20-0.21.

Color reddish-yellow to orange brown, variable. Frons between frontal carinae punctate, covered with irregular striae. Only 5-6 striae reach vertexal margin of head. Occipital margin of head with short, curved setae. One curved and long seta present at posterior end of frontal carinae. There are three long hairs on each frontal carina, arranged longitudinally and curved inwards. Antenna with 11 segments. Shallow antennal scrobe, with sculpture similar to rest of head. Preocular carina runs along ventral margin of scrobe. Disc of clypeus striate. Clypeal striae weakly developed, running longitudinally. Masticatory margin of mandible with five teeth, no denticles and basal margin without teeth or denticles. Compound eye well developed, protruding from lateral margin of headin full face view. Malar space with 4-5 longitudinal irregular carinae. Vertexal margin straight. Promesonotum with 3-4 pairs of long, simple, and curved setae (length approx. 0.1 mm). Humeral angle well developed, without hairs. Mesosomal dorsum reticulate-punctuate. Propodeum with one pair of straight setae shorter than promesonotal setae. Long propodeal spines weakly curved inwards in dorsal view. In lateral view, propodeal spines shorter than or equal to length of petiole and posteriorly directed. Petiole rectangular, with 1-2 pairs of setae, similar in longitude to those of propodeum, anterior face well differentiated, forming a well defined angle with dorsal face. Mesosoma, petiole, and postpetiole, in lateral view, strongly spotted. Metapleural gland strongly developed, bulky. Posteropropodeal lobe rounded and well developed. Petiolar peduncle approximately of same length as petiole in lateral view. Very short acute spine present in anterior ventral face of peduncle. In dorsal view, petiole is long with rounded anterior edge, tapering towards apex. Postpetiole quadrate and wider than

Figs 1a-c. Queen of *Wasmannia auropunctata*. 1a, head in full-face view; 1b, profile; 1c, dorsal view.

Table 1. List of characters and states (only for discrete characters) used in the phylogenetic analysis.

Morphometric characters (0-11):

Queen (0-5)

0. WL: Weber Length
1. HW: Head Width
2. HL: Head Length
3. EL: Eye Length
4. CI: Cephalic Index
5. OI: Ocular Index

Worker (6-11)

6. WL: Weber Length
7. HW: Head Width
8. HL: Head Length
9. EL: Eye Length
10. CI: Cephalic Index
11. OI: Ocular Index

Discrete characters (12-45). States of each character is indicated between parentheses:

Worker

12. Antennal scrobe: shallow (0); deep (1); absent (2)
13. Antenal scrobe: narrow, not reaching the side of the head in full face view (0); very broad, forming a flat surface that extends from the frontal carinae to the side of the head (1); absent (2).
14. Frontal carina: placed far from the compound eye (0), close to the compound eye (1)
15. Frontal lobe: well developed, covering the malar space in dorsal view (0); poorly developed, not covering the malar space in dorsal view (1)
16. Sculpture between the frontal carinae with no more than 6 longitudinal and irregular striae (0); with 10 to 12 distinct longitudinal striae (1); reticulate (2); strongly punctate, with no striae or reticule (3); absent (4)
17. Shape of the frontovertexal corner: rounded (0); angulate (1)
18. Frontovertexal margin: straigth (0); weakly concave in the middle (1); strongly concave (2)
19. Sculpture of the antennal scrobe: absent (0); same to the rest of the head (1); quite different to the rest of the head (2)
20. Ventral margin of the antennal scrobe: not defined by the preocular carinae (0); completely defined by the preocular carinae (1); partially define by the preocular carinae (2); absent (3)
21. Antennal club: absent (0); present, with 2 segments (1); present, with 3 segments (2)
22. Palp formula: 4-2 (0); 3-2 (1)
23. Length of the mandible: Long (7 or more teeth) (0); short (no more than 5 teeth) (1)
24. Position of the dorsal mesosomal setae: erect (0), appressed (1)
25. Shape of the dorsal mesosomal setae: simple (0), weakly spatulate (1), strongly spatulate (2)
26. Length of the dorsal mesosomal setae: longer than 1.0 mm (0), shorter than 1.0 mm (1)
27. Promesonotal spines or boses: absent (0), present (1)
28. Propodeal spines: absent (0), present (1)
29. Length of the propodeal spines: absent (0), shorter than the distance between its apical tips (1), no more longer than ¼ of the distance between its apical tips (2), longer than twice the distance between its apical tips (3)
30. Petiolar peduncle: shorter than the length of the node in lateral view (0), about the same length of the node (1), longer than the length of the node in lateral view (2)
31. Petiolar anterior face: poorly defined, convex (0); well defined, convex (1); well defined, almost vertical (2)
32. Angle between the anterior and dorsal faces of the petiolar node in lateral view: as a cylinder, poorly defined (0); rounded (1); strongly quadrate (2)
33. Posterior face of the petiolar node in lateral view: absent (0); rounded, convex (1); vertical and angulate (2)
34. Shape of the postpetiole related with the petiole in dorsal view: normal, equal to (0), small (1), large (2)
35. Abdominal tergum IV (1^{st} of the gaster): slightly cover the sternum on the ventral surface of the gaster (0), not covering the sternum (1)
36. Sting: normal, well developed (0); vestigial (1)
37. Polymorphism: absent (0), present(1)
38. Larval profile (sensu Wheeler G. C. and J. Wheeler, 1976): pheidoloid (0), attoid (1)
39. Diameter of the propodeal spiracle: large and conspicuous, diameter about equal to width of base of propodeal spine (0); small, diameter less than width of the base of propodeal spine (1)
40. Shape of the subpetiolar spine: absent (0); short and rounded at the apical point (1); long and thin something sharp at the apical point (2)
41. Genal and postgenal sculpture: punctate (0), weakly rugoreticulate (1), strongly rugo-reticulated (2), punctate and with some weakly and irregular carinae (3), absent (4)
42. Gastral pilosity: absent (0), short (< than 1 mm) and abundant (1), long and abundant (2), long (more than 1 mm in length), sparced (3)
43. Post petiolar process: absent (0), present and rectangular (1)
44. Difference between worker and queen size given by therelationship of queen head width to worker head width: small, there is almost no differences in size (0); medium, queen relatively big compared with workers (1); big, worker much smaller and queen bigger (2)
45. Fungus-growing habit: present (0); absent (1).

long, in dorsal view. Gaster weakly punctuate, with long, curved setae, scattered along each segment.

Comments. This species is easily recognized by the strongly square shape of the petiolar node in lateral view, with a sharply defined dorsal and anterior face in worker and queen. As pointed out by Longino and Fernández (2007), there is considerable variation in the development of head sculpture and color.

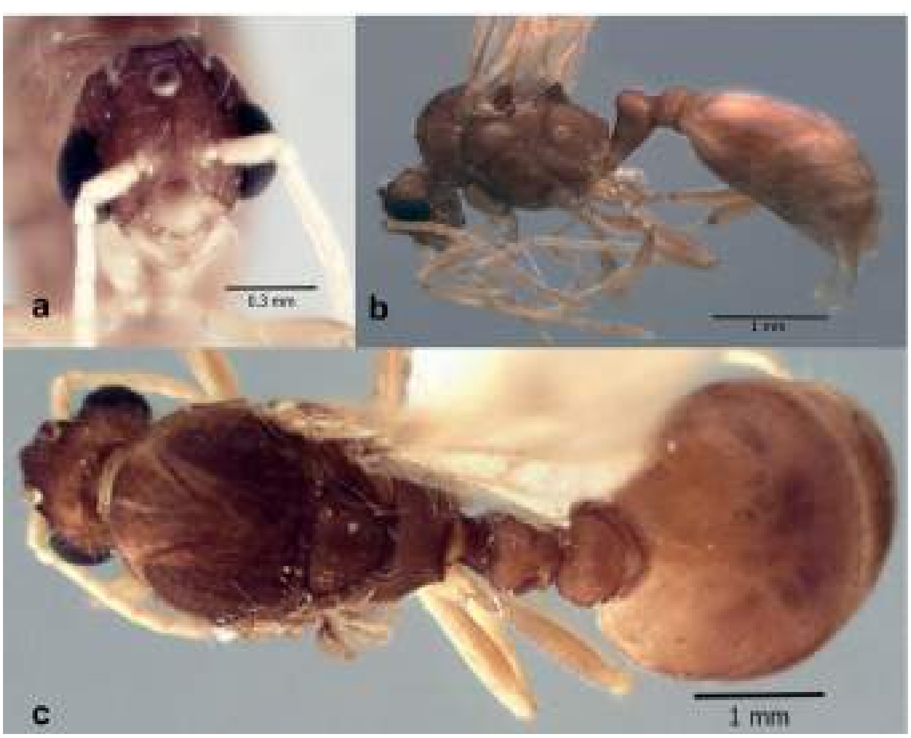
Gyne (n = 17): HL: 0.69-0.74; HW: 0.77-0.84; EL: 0.21-0.26; WL: 1.47-1.57.

Color and pilosity similar to worker. Head wider behind compound eyes. Scape barely reaches vertexal margin. Frontal carina separated by 10-12 longitudinal, poorly developed and irregular striae. Antennal scrobe deep and reticulate, with longitudinal carina that starts atventral margin of antennal torulus and almost reaches posterior margin of compound eye. Preocular carina runs along ventral margin of scrobe almost to occipital angle of head. Compound eye well-developed, located close to anterior margin of head, and protruding. Antena with 11 segments; apical club with two antennomeres. Mandibular dorsum with longitudinal, thin striae. Masticatory margin of mandible with five teeth. Malar space with three to four longitudinal striae. Disc of clypeus with more than 10 well developed, longitudinal striae. Pronotum poorly developed anterodorsally scutum encompasses more than half of mesosoma in dorsal view. Humeral angle rounded. Mesonotum dorsally striate, with thin, irregular striae and poorly developed. Axilla well developed, almost triangular and continuous in midline by narrow strip of integument. Middle area of scutellum with a deep, longitudinal groove. Anapleural sulcus completely divides anepisternum from the katepisternum. Anepisternum, katepisternum and metakatepisternum finely striate. Propodeal spine thick at its base. Propodeal lobe rounded. Fore and hind wings infuscate. Fore wing with three closed cells: costal, radial (=basal) and cubital (=subbasal). No closed discal cell. Hind wing with a closed radial cell and cubital cell, almost entirely delimited by veins. Hamuli composed by five hooks. Cinctus 1 and 2 well-developed. Petiolar peduncle longer than petiolar node in lateral view. Sterno-postpetiolar process sharp and short. Metasoma III weakly punctuate, covered with sparse, subdecumbent and thin setae.

Comments. Two sympatric sizes of gynes were described in Costa Rica on the basis of their head size (Longino & Fernández, 2007) and could represent either differences between cryptic species or intraspecific polymorphisms. Gyne variation in head size was not observed in Argentina. Argentinean queens were most similar to the small headed form found in Costa Rica, Jamaica, and Venezuela (Longino & Fernández, 2007). According to Kusnezov (1952), the worker size of populations of *W. auropunctata* from Misiones province differ from the size of workers found in other populations elsewhere in Argentina; however, we have not observed such variation.

Male (n = 10): HL: 0.6-0.68; HW: 0.55-0.62; EL: 0.27-0.32; WL: 1.32-1.57.

Head (Fig 2a) oval in full face view. Mandible falcate with four teeth. Antenna with 13 segments, last antennomere of funicle longer than the rest. Scape not reaching frontovertexal margin of head. Compound eye well developed, covering more than half of lateral side of head. Three well developed ocelli are present; lateral ocellus reaches frontovertexal margin of head. Area between ocellicarinulate. Several diagonal carinae present in malar space and clypeal disc. Clypeal disc covered



Figs 2a-c. Male of *Wasmannia auropunctata*. 2a, head in full-face view; 2b, profile; 2c, dorsal view.

with parallel longitudinal carinae. Axillae medially compressed on middle of mesonotum; anterior and posterior margins nearly parallel (Fig 2c). Fore and hind wing venation similar to queen. Petiolar node quadrate in profile, but with angles (anterior and posterior) not as strongly marked as worker (Fig 2b). Postpetiole narrowly attached to abdominal segment III. Abdominal sternum IX (=subgenital plate) medially projected as a triangle and distally rounded. Pygostyles well developed, one segmented. Telomere elongated, finger like, ventrally curved, longer than basimere, distal width 0.05 mm. Digitus and cuspis poorly developed. Digitus stout and strongly curved ventrally. Ventral margin of aedeagus denticulate.

Gynandromorphs (n = 2): HL: 0.70-0.75; HW: 0.70 (measured only in the specimen with a head shape similar to a normal male); EL: 0.32; SL (right scape): 0.50, (left scape): 0.25; WL: 1.60-1.62.

Diagnosis. These are unusual sexual caste specimens because the left side of their head and antennae are similar to those of a normal male, but the right side has the characteristics of a queen. In one specimen, both compound eyes are less developed than in a normal male, but larger than a queen´s eyes (EL: 0.325). In the second specimen (Figs. 3a-c) the left side of the head, including eyes and antennae, is similar to a male, while the right side is similar to a queen (Figs. 3a and 3c). In this specimen both antenna scrobes are well developed. In this last specimen, the left antenna is similar to a male and the right one has the same shape of the queen antenna. In both specimens, meso and metasoma are similar to a normal male (Figs 3b-c), with similar wing venation and a male external genitalia. The only difference noted in the genitalia is referred to the development of the telomere. In both gynandromorphs the telomere is more stout (distal width: 0.1 mm) than in a normal male (Fig 3c). Pygostyle is also longer than in a normal male.

Comments. The two specimens of gynandromorphs were found in a nest of *W. auropunctata* with putatively sexual castes reproducing clonally (see below), in Colón (32º14´S, 58º08´W), Entre Ríos province, Argentina. This is the first record of gynandromorphs occurring naturally in a LFA colony, however, additional gynandromorphs have been found recently in natural populations of *W. auropunctata* in São Sebastian, Brazil (LAC, unpublished data) and also found by F. Cuezzo in series of *W. auropunctata* collected by N. Kusnezov and deposited in IFML. Gynandromorphs previously have been found in clonal LFA colonies that were exposed to temperatures of more than 40°C in the laboratory (Olivier Rey, personal communication). They could have been induced in the laboratory during embryonic development by the effect of the extremely high rearing temperature. Gynandromorphism is common in Hymenoptera (ants: Jones & Phillips, 1985; bees: Wcislo et al., 2004). These sexual mosaics have been reported in more than 40 ant species (Jones &Phillips, 1985) but, to date, their production has only been explained in two cases: sub-lethally high breeding temperature in the pharaoh's ant, *Monomorium pharaonis* (L.) (Berndt & Kremer, 1982), and *Wolbachia* infections in the isopod *Armadillidium vulgare* (Rigaud & Juchault, 1993).

Figs 3a-c. Gynandromorph of *Wasmannia auropunctata*. 3a, head; 3b, profile; 3c, dorsal view.

Examined Material: Argentina: Tucumán: Capital, 09 Dec 1952, #8186 (IFML)1w, 58q, manual coll., N. Kusnezov; same loc, 16 Set 1950, #6125 (IFML), more than 100w, manual coll., N. Kusnezov; same loc, 20 Nov 1952, #8179 and #1848 (IFML), w, manual coll., N. Kusnezov; same loc, 06 May 1848, #1868 (IFML), w, q, manual coll.; N. Kusnezov; El Siambón, 26 May 1949, #4598 (IFML), w,q, manual coll, N. Kusnezov; El Cadillal, Trancas, 16 May 1948, #1928 (IFML), w, N. Kusnezov; Salinas, 16 Apr 1948, #1658 and # 1684 (IFML), w, N. Kusnezov; Río Cochuna, Concepción; 06 May 1948, #1886 and # 1850 (IFML), w, R. Golbach; San Ramón, Burruyacú, 10 May 1948, #1896 (IFML), w, R. Golbach; San Javier, 10 Dec 2005, #10005 (IFML), w, F. Cuezzo; Misiones: Loreto, 20 Jul 1949, #5140 (IFML), w, manual coll., N. Kusnezov; Esperanza, 02 Aug 1949, #5022 (IFML), w, N. Kusnezov; Salta: P.N. El Rey, feb-1953, # 8334 and #8333 (IFML), w, manual coll., N. Kusnezov; Chaco: Roque Sáenz Peña, 11 Jun 1948; #2545 (IFML), w, N. Kusnezov; Jujuy: near Ocloyas, 13 Dec 2009, WAS040-05, -06 and -02 (IFML), w,q, L.A. Calcaterra coll.; Tumbaya, 14 Dec 2009, WAS041-01 and -02 (IFML), w, q, m; L.A. Calcaterra coll.

Biogeography of *W. auropunctata* in Argentina. *W. auropunctata* is widely distributed in Argentina (Fig 4); however, it is common only in anthropic habitats, mostly in northeastern Argentina (Rey et al., 2012; L.A.C, unpublished data). Nests are usually found in urban areas under stones, around or inside tree trunks, and under sidewalks. *W. auropunctata* was found in Lozano (34º51´S, 59º03´W, 45m, Francisco Sola coll.) in Buenos Aires province, representing the southernmost record reported so far for this species (Fig 4). Unexpectedly, it was also found for the first time in the arid desert of the Monte ecoregion from Salta province to the locality of Anillaco (28°49'S, 66°56'W, Adriana Aranda coll.) in La Rioja province, and up to 2125 m elevation in the locality of Tumbaya (23º51'S, 65º28'W), Puna ecoregion, Jujuy province (Fig 4). *Wasmannia auropunctata* is uncommon in minimally disturbed native habitats where ant assemblages are typically more diverse compared with anthropic habitats (L.A.C., unpublished data). Though scarce in native forests in northern Argentina (L.A.C., unpublished data). *W. auropunctata* was only common in one type of agricultural habitat (banana plantations) in the Jujuy (Yungas) and Formosa (Chaco) provinces.

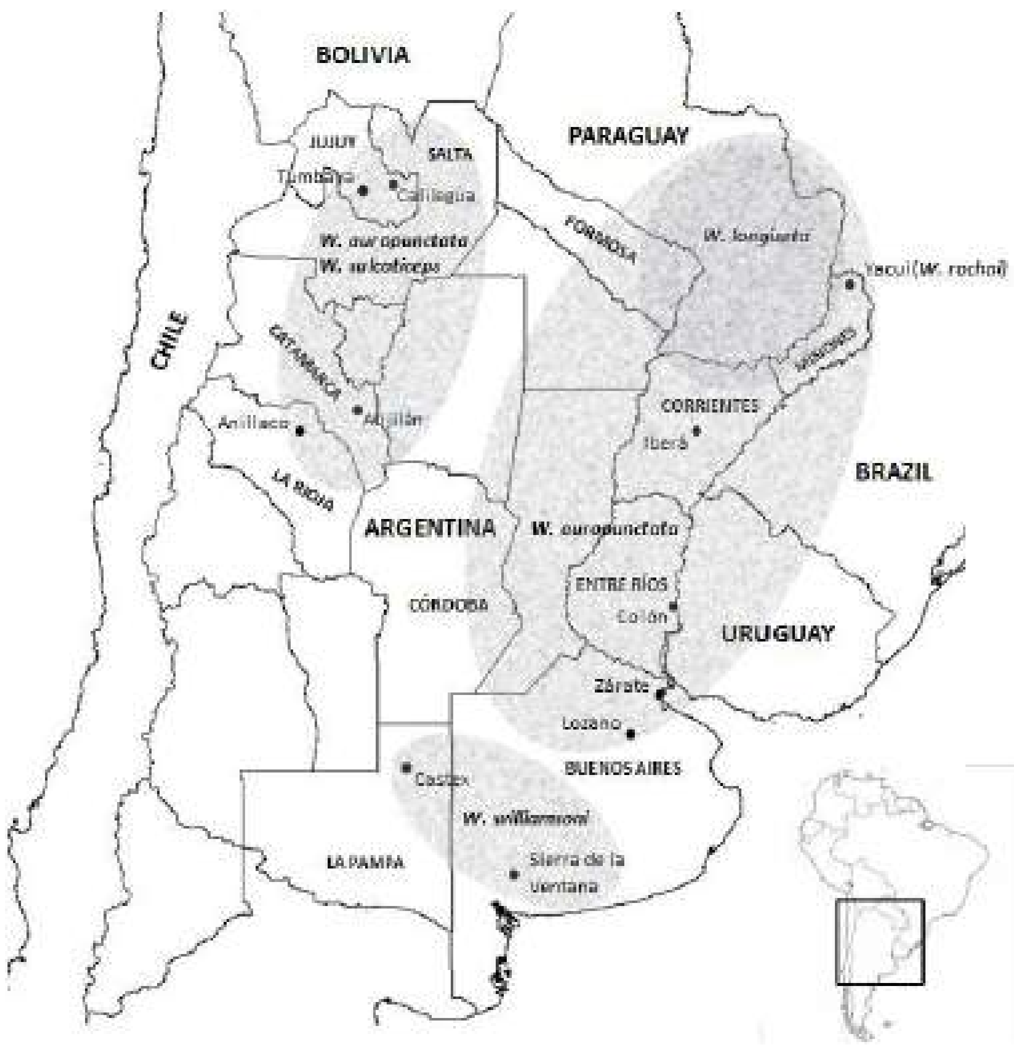


Fig 4. Main distribution regions of the five species of *Wasmannia* found in Argentina, including several sites mentioned in the text.

Wasmannia longiseta Cuezzo and Calcaterra n.sp.

Diagnosis (worker)**.** This species is recognized by the following combination of characters: 1) head in dorsal view reticulate; 2) Malar space and postgena also reticulate without longitudinal carina as in other spp. of *Wasmannia*, and 3) gaster smooth and shiny, with abundant long (>1 mm), curved and whitish setae.

Etymology. The name of the new species refers to the long whitish setae that are present on its gaster.

WorkerHolotype:HL: 0.50; HW: 0.42; EL: 0.10; SL: 0.40; AD: 0.25;PSL: 0.175;WL: 0.52; PD: 0.10; PTL: 0.10; PPTL: 0.12; PTW: 0.12; PPTW: 0.15; CI: 0.85; OI: 0.20. **Paratype workers** (n=2): HL: 0.50-0.52; HW: 0.42-0.45; EL: 0.10; SL: 0.40; AD: 0.25; PSL: 0.175;WL: 0.47-0.5; PD: 0.10-0.12; PTL: 0.10-0.17; PPTL: 0.12; PTW: 0.10-0.12; PPTW: 0.15; CI: 0.85-0.86; OI: 0.20.

Reddish-yellow head, mesosoma and anterior metasoma, with posterior half of first gastral segment and posteriorly dark brown. Frons between frontal carinae rugo-reticulate with irregular striae, 5-6 striae reach vertexal margin of head. Three long simple setae present on margin of each frontal carina separated by distance similar to or greater than length of hairs. Frontal carinae with three erect hairs, shorter than previous ones, arranged longitudinally along an imaginary line that runs along the anterior edges. The vertexal margin has six simple setae curved towards the frons (Fig 5a). Antenna with 11 segments. Antennal scrobe shallow with weak sculpture similar to rest of the head. Preocular carina runs along ventral margin of scrobe, reaching posterior margin of compound eye. Disc of clypeus with four longitudinal and well developed carinae. Each carina forked toward posterior margin of clypeus and with four simple setae with a similar length to those of frontal carina. Reticulate sculpture between frontalcarinae, both in clypeus and frons. Masticatory margin of mandible with five teeth, no denticlesand basal margin without teeth or denticles. Compound eye well developed, protruding from lateral margin of headin full face view. Malar space with 4-5 longitudinal and irregular carinae. Vertexal margin slightly concave medially. Promesonotum with 3-4 pairs of long, weakly spatulate and curved setae (length approx. 0.1 mm). Humeral angle strongly developed with long hair on angle. Mesosomal dorsum with three longitudinal carinae that intersect at irregular intervals forming weak grid that doesnot obscure stippling of integument. Propodeum with two pairs of curved setae shorter than promesonotal setae. Long propodeal spines, with length similar to t hairs of mesosomal dorsum. In lateral view, propodeal spines longer than length of petiole and posteriorly directed. In dorsal view propodeal spines diverge from one another. Metapleural gland strongly developed, bulky. Posteropropodeal lobe rounded and well developed. Petiole with three pairs of long setae (0.1-0.15 mm), anterior margin well differentiated, forming gentle curve with rest of petiolar profile. Mesosoma, petiole, and postpetiole in lateral view, strongly spotted. Petiolar peduncle longer than length of petiole in lateral view. Short acute spine present on anterior ventral margin of peduncle. In dorsal view petiole long with a rounded anterior edge, tapering forward; in lateral view, node of petiole with distinct anterior face not forming acute angle with dorsal margin (Fig 5b), posterior face of petiolar node weakly developed. In dorsal view, postpetiole ovaland barely wider than long. Gaster smooth and shiny, with abundant long (>1 mm), curved and whitish setae.

Figs 5a-c. Worker of *Wasmannia longiseta* n. sp. 5a, head in full-face view; 5b, profile; 5c, dorsal view.

Gyne and Male. Unknown.

Holotype worker. Argentina: Formosa, Parque Nacional Pilcomayo, 25º07´S, 58º11´W, 81m, 29 Jan 2009, #WAS 034-02, 1w (IFML), leaf-litter sample, L. Calcaterra. **Paratype workers** (= 2w): seccional Yacuí, Parque Nacional Iguazú, Misiones, 25º41´S, 54º26´W, 243m, 12 Dec 2008, 1w #WAS019-01 (IFML), leaf-litter sample, L. Calcaterra; 1w #WAS019-02, same data as previous individual (IFML). **Other worker examined**: Corrientes, Santa Isabel stream, route 12, km 1169, near Berón de Astrada, 27º28´S, 57º29´W, 75m, 30 Jan 2009, #Was 037, 1w (IFML), leaf-litter sample, L. Calcaterra (FuEDEI).

Comments: No other species of *Wasmannia* shows the particular set of characters described in the diagnosis. This species is morphologically similar to *W. affinis* and *W. lutzi* in several aspects (cephalic sculpture and general shape of the petiole), but differs in the number of setae in the vertexal margin, which is fewer in *W. affinis* and *W. lutzi*. These two species have a petiolar peduncle shorter than the length of the petiole in lateral view.

Geographical distribution. This species is known only from secondary forest habitats of the Chaco and Paranaense phytogeographical provinces (Cabrera & Willink, 1980) present in Formosa, Corrientes, and Misiones provinces in northeastern Argentina and probably in Paraguay (Fig 4). A similar species was found by Alex Wild (*Wasmannia* alw02) in Amambay, Canindeyú, Concepción, and Ñeembucú (Paraguay). All these collecting sites represent a continuous occurrence area centered on 25ºS and 57ºW and located in the ecotone between the Chaco and Atlantic Forest ecoregions. More surveys are necessary to determine in which of these two ecoregions it is more common.

Wasmannia rochai Forel
(See illustration in Longino & Fernández, 2007)

Worker (n=3) HL:0.45-0.50; HW:0.43-0.50; EL: 0.10-0.11; SL:0.35-0.37; AD:0.22-0.25; PSL:0.07-0.10; WL: 0.45-0.54; PD: 0.07-0.10; PTL: 0.10-0.12; PPTL:0.12; PTW:0.07; PPTW:0.12-0.15; CI: 0.96-0.99; OI:0.21-0.24.

Lectotype worker measurements, 1w (from Longino & Fernández, 2007, not examined): WL: 0.54; HW: 0.50; HL: 0.50; EL: 0.11; CI: 0.99; OI: 0.22.

Color reddish-yellow to orange. Frons, between frontal carina, punctuate with irregular striae weakly marked, reaching the vertexal margin of the head. Occipital margin of the head with short, curved setae. Frontal carina with four long hairs arranged longitudinally along an imaginary line that runs along the anterior edges and curves. Antenna with 11 segments. Antennal scrobes shallow with sculpture similar to rest of head but without striae. Punctuate sculpture more defined laterally on head in full face view. Ventral margin of scrobe weakly developed. Disc of clypeus with several weakly developed striae anteriorly divergent. Masticatory margin of mandible with five teeth, no denticles and basal margin without teeth or denticles. Compound eye well developed, protruding from lateral margin of headin full face view. Malar space with 5-7 longitudinal irregular carinae. Vertexal margin straight with median notch. Promesonotum with four pairs of long, clavate, and curved setae (length approx. 0.1 mm). Humeral angle well developed with one long and curved hair. Mesosomal dorsum rugose with 6-8 longitudinal carinae strongly developed on anterior half of pronotum. Propodeum with one pair of curved setae shorter than those of promesonotum. Short propodeal spines, divergent in dorsal view. In lateral view, propodeal spines shorter than length of petiole and posteriorly directed, with wide base. Petiole triangular, with 1 pair of long, curved setae, similar in longitud to those of promesonotum, anterior margin well differentiated, joining rest of profile in a curve, profile without defined ridge or angle. Mesosoma, petiole, and postpetiole in lateral view, strongly spotted. Metapleural gland strongly developed, bulky. Propodeal lobe rounded and well developed. Petiolar peduncle shorter than petiole in lateral view. Long, acute spine ispresent on anterior ventral margin of peduncle. In dorsal view petiole with rounded anterior edge. In dorsal view postpetiole square and wider than long with four long and curved setae disposed in a middle line. Gaster feebly punctuate, with long curved setae, scattered along each segment.

Examined material:Argentina, Misiones, seccional Yacuí (25º41´S, 54º26´W, 243m) of the Parque Nacional Iguazú, 11-Dec-2008, 3 w, L. Calcaterra coll. (IFML); **Mexico, iv.5.38, no specific loc, 3w, N.K. ident, (IFML);** all the studied material was compared with syntype photographs available in the web-page: www.evergreen.edu/ants/AntsofCostaRica (ver. 17.set.2010). No queen material was available for examination.

Male unknown

Comments. The main characters to easily recognize workers of *W. rochai*, and separate this species from other of *Wasmannia*, are the presence of curved and clavate hairs on the dorsum of the mesosoma, short propodeal spines with a wide base, and a strong and well developed spine in the anteroventral part of the petiole. This species has been recorded from Costa Rica to São Paulo State, Brazil (Longino & Fernández, 2007). We extend its distribution north to Mexico and south to the seccional Yacuí (25º41´S, 54º26´W, 243m) of the Parque Nacional Iguazú, Misiones, Argentina. This species co-occurred with *W. longiseta* n. sp. in a secondary rainy subtropical forest belonging to the Paranaense phytogeographical province (Atlantic Forest ecoregion). This species is not as behavioral aggressive as *W. auropuntata* but is considered as a pest, particularly in the cocoa plantations of the southeast and southwest regions of Bahia State, Brazil (Souza et al., 2009).

Wasmannia sulcaticeps Emery

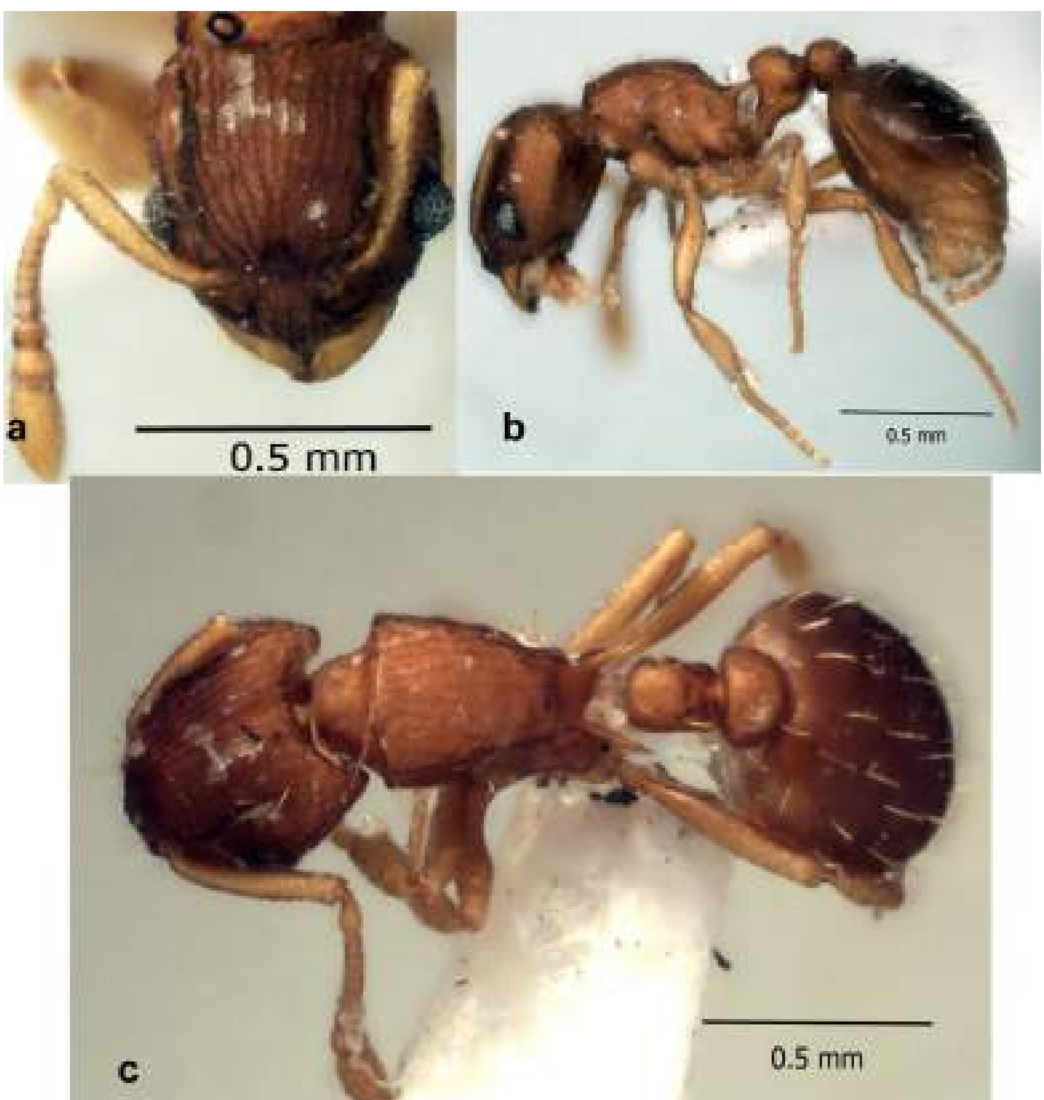
Worker (n = 12): HL: 0.50-0.60; HW: 0.45-0.53; EL: 0.10-0.13; SL: 0.35-0.45; AD: 0.28-0.33; PSL:0.10; WL:

0.55-0.63; PD: 0.10; PTL: 0.10-0.20; PPTL: 0.13-0.15; PTW: 0.15; PPTW: 0.20-0.23; CI: 0.88-0.90; OI: 0.20-0.22.

Color variable from dark brown to yellowish brown in the workers of the same nest. Area between frontal carinaerugo-reticulatewith some regular carinae (8-10) reaching the frontovertexal margin. Malar space with four well developed longitudinal carinae. Antenna with 11 segments. Scrobe shallow and foveate. The ventral margin of scrobe formed by preocular carina which reaches frontovertexal margin. Clypeus with eight well-developed not bifurcated longitudinal carinae, the four central carinae reach posterior margin of clypeal disc and continue anteriorly. Sculpture between carinae foveate, bothonclypeal disc andfrons. Masticatory margin of mandible with 5 teeth and no denticles, basal margin smooth and without teeth. Vertexal margin weakly concave to straight, with six erect setae curved anteriorly, the two outer hairswith length similar to innermost and located on frontovertexal corner.Compound eye well developed, protruding from lateral margin of headin full face view. Promesonotum with eight longitudinal and irregular carinae. Propodeal spines long and straight, posteriorly directed. Propodeal declivity foveate. Petiole with two pairs of long setae weakly spatulatehairs; anterior margin distinct, forming a curve with the rest of the petiole. Anterior face not separated from dorsum nor defined by an angle. Petiole and postpetiole stronglyfoveate.Petiolelonger than wide in dorsal view; postpetiolewider than long and with rounded corners. Petiolar peduncle shorter than length of petiole in lateral view, with small anteroventral spine.First tergum of gasterfinely striate, with abundant, whitish, long and curved setae,thickenedatits apex.

Gyne (n = 1, dealate): HL: 0.63; HW: 0.59; EL: 0.19; WL: 0.80; CI: 0.93; OI: 0.28.

Color and pilosity similar to worker. Head wider behind compound eyes. Scape barely reaches vertexal margin. Frontal carinae separated by 10-12 longitudinal, strong, and very regular striae. Antennal scrobe well developed and punctuate, longitudinally crossed by carina that starts in ventral margin of antennal torulusand almost reaches posterior margin of compound eye. Preocular carina forming the ventral margin of antennal scrobe, this carina runs almost to occipital angle.



Figs 6a-c. Worker of *Wasmannia sulcaticeps*. 6a, head in full-face view; 6b, profile; and 6c; dorsal view.

Compound eye well-developed, bulky. Antennae with 11 segments, terminal club with two antenomeres. Dorsal surface of mandible with longitudinal thin striae. Masticatory margin of mandible with five teeth. Malar space rugo-reticulate. Disc of clypeus longitudinally striate, well developed, similar to striae between frontal carinae. Pronotum poorly developed antero-dorsally, so that scutum in dorsal view encompasses more than half of mesosoma. Humeral angle well developed, angulate, not rounded. Mesonotal dorsumwith more than 20 strong, longitudinal and very regular striae. Axilla well developed, almost triangular and medially continuous by a narrow strip of integument. Scutellum strongly striate. Anapleural sulcus completely separates anepisternum from katepisternum, but sulcus weakly impressed. Anepisternum, katepisternum and metakatepisternum finely striate. Propodeal spine short and thick at base. Propodeal lobe acute. Cinctus 1 and 2 well-developed. Petiolar peduncle about same length as petiolar node in lateral view. Sterno-postpetiolar process shaped as blunt and short spine. Metasoma 3 weakly punctate and covered with abundant and subdecumbent, thin setae.

Male (n = 1): HL: 0.52; HW: 0.47; EL: 0.22; WL: 0.92.

Dark brown, with yellowish mandibles, antennae and legs. Head rectangular in full face view. Mandible triangular with five teeth. Antenna with 13 segments, last antennomere of funicle longest. Scape not reaching frontovertexal margin of head. Compound eye well developed, covering half of lateral side of head. Three ocelli well developed; lateral ocellus reaching frontovertexal margin of head. Area between ocelli with 4-5 strongly impressed rugae. Malar space reduced, crossed by two strong longitudinal carinae. Rest of head in full face view punctuate and crossed by longitudinal and thin striae. Clypeal disc with several parallel and longitudinal carinae. Fore wing with three closed cells, plus open radial cell. Pterostigma present. Hind wing with one basal closed cell. Hamuli with 4 hooks. Peduncle short. Petiolar node triangular in profile with blunt apex and no dorsal margin. Abdominal sternum IX (=subgenital plate) medially projecting as triangle and distally rounded. Pygostyle well developed, one segmented. Telomere short and thick. Digitus and cuspis not observed.

Comment: Because of the scarcity of material (only one male and one dealate gyne could be studied) the descriptions of alates of *W. sulcaticeps* must be considered as provisional.

Examined material: Argentina: Catamarca: Alijilán, 28º94´S, 65º27´W, 690m, #003 (1w), #008 (2w), #010 (1w), #019 (1w), leaf-litter sample, L. Calcaterra, 24 Oct 2008; Corrientes: Reserva Natural Iberá (Iberá Provincial Park), Ea. El Rincón del Socorro (6 w), 28º35´S, 57º14W, pitfall traps, Y. Di Blanco, 22 Mar 2008; Jujuy: Yala, #741, 1w, 1 dealate q, 1m, N. Kusnezov coll.; Parque Nacional Calilegua, 23°44´S, 64º51´W, 750 m, #181 (1w), leaf-litter sample, L. Calcaterra, 28 Oct 2008; Salta: Metán, 26-i-56, N.K. coll., 1 queen (IFML), Tucumán: N. Kusnezov coll., 22-Xii-1958; Parque Provincial La Florida, 27°15´S, 65°41´W, 920 m, (1w), manual collection, L. Chifflet, 11 Dec 2013.

Geographical distribution. *Wasmannia sulcaticeps* was mostly found in mountain forests in northwestern Argentina (Yungas ecoregion), overlapping with *W. auropunctata* generally between 400-700 meters of altitude in secondary forests, such as the Parque Nacional Calilegua (Jujuy) and Parque Provincial La Florida (Tucumán) (Fig 4). Additional individuals of this species were also found for the first time in secondary forest in the Catamarca province and in lowlands in a secondary gallery forest in the Reserva Natural Iberá, in the Corrientes province (Fig 4).

Wasmannia williamsoni Kusnezov

Worker (n = 20): HL: 0.55-0.60; HW: 0.48-0.53; EL: 0.10-0.13; SL: 0.38-0.43; AD: 0.28-0.35; PSL:0.10- 0.12; WL: 0.50-0.63; PD: 0.10-0.13; PTL: 0.15-0.20; PPTL: 0.10-0.15; PTW: 0.13-0.15; PPTW: 0.18-0.23; CI: 87-88; OI: 18-22.

Reddish-brown with gaster slightly darker than rest of body, sometimes slightly darker than *W. auropunctata*. Head in dorsal view with erect, short (<0.05 mm) and abundant setae.

Head between frontal carinae, from posterior margin of the clypeal disc to the frontovertexal margin covered with very regular longitudinal carinae (approx. 10-12). Carinae present in malar space. Disc of clypeus bears more than 6 longitudinal and irregular carinae. Antennal scrobe with a short medial longitudinal carina that barely exceeds posterior margin of compound eye. Ventral margin of antennal scrobe defined by preocular carina that reaches frontovertexal margin. Antennal scape fails to reach frontovertexal margin. Antenna with 11 segments. Compound eye well developed, protruding from lateral margin of head in full face view. Frontovertexal corner bears long, curved seta at each side. Humeral angle acute, strongly developed. Pro- and mesonotum with 8-10 longitudinal carinae. Propleura with four longitudinal carinae and foveolate, sometimes weakly developed, meso and metapleura foveolate, without carinae. Rounded epicnemial process well developed. Dorsal and lateral sides of propodeum foveolate. In lateral view propodeal spine with wide base. Propodeal spine length less than petiole in lateral view. In dorsal view propodeal spine joined by curved line. Metapleural gland well developed and bulky, protruding beyond mesosomal profile. Propodeal lobe well developed, foveolate and almost rectangular with round angles. Short peduncle. Petiole in dorsal view slightly narrower than postpetiole, both heavily foveolate. In lateral view petiolar node rounded. Sterno-postpetiolar process well developed with short spine. Metasomal tergite 3 (fourth abdominal segment) weakly reticulate. Gaster covered with long, weakly curved and sparse hairs.

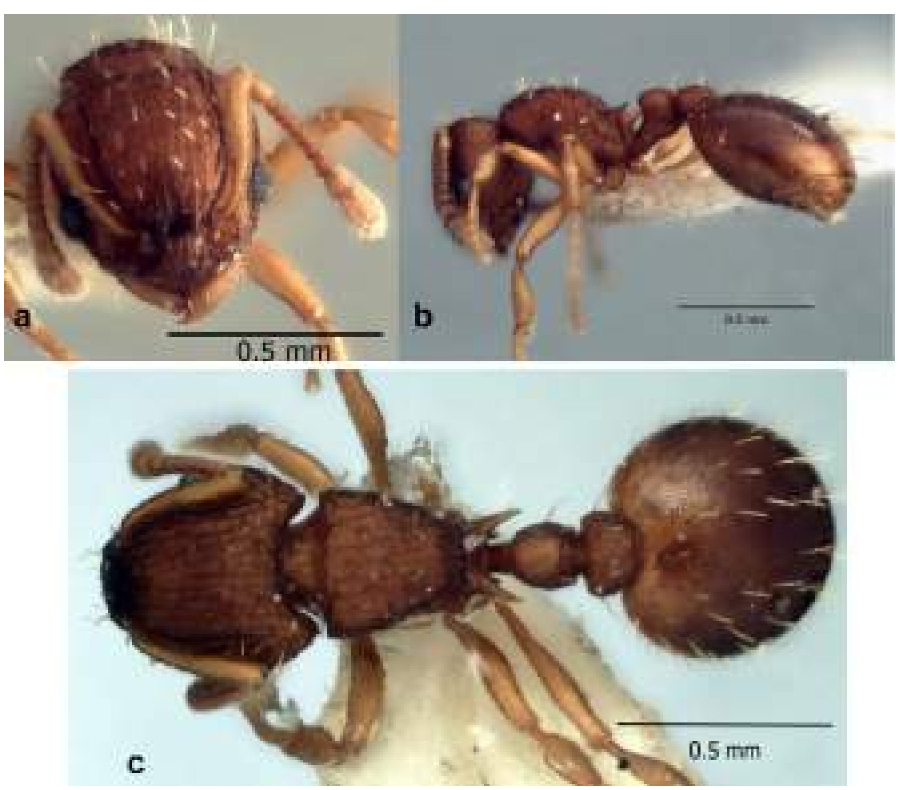
Gyne (n = 1).HL: 0.62, HW: 0.57, EL: 0.15, WL: 0.72, CI: 0.91, OI: 0.24.

Dealate. Color dark brown. Head slightly wider behind compound eyes. Scape does not reach vertexal margin. More than 14 longitudinal, strongly marked and irregular striae present between frontal carinae. Antennal scrobe deep and punctuate, crossed longitudinally by preocular carina originating from ventral margin of antennal torulus and almost reaches posterior margin of compound eye. Antennal scrobe delimited ventrally by carina that reaches occipital angle. Well-developed compound eye located closest to anterior margin of head. Antennae with 11 segments, terminal club with 2 antenomeres. Dorsal surface of mandible with 2-3 longitudinal fine striae. Masticatory margin of mandible with five teeth. Discal surface of clypeus with 7-8 well developed longitudinal estriae. Pronotum poorly developed antero-dorsally, scutum in dorsal view encompasses more than half of mesosoma. Humeral angle obtuse, strongly marked. Mesonotum dorsally with irregular and well developed striae. Axilla not well developed. Scutellum poorly developed, punctuate without median longitudinal groove. Anapleural sulcus barely visible, incomplete. Anepisternum, katepisternum and metakatepisternum punctuate. Propodeal spine narrow at base. Propodeal lobe rounded. Cinctus 1 and 2 well-developed. Petiolar peduncle shorter than petiole in lateral view. Sterno-postpetiolar process forms sharp and short spine. Metasomal tergum 3 weakly punctate and covered with sparse and subdecumbent, fine setae.

Male. Unknown.

Examined Material: Syntype worker. Argentina: La Pampa, General Pico, 07 Jun 1950, #6066, 1 w, N. Kusnezov coll (IFML). **Other examined material**: Argentina: La Pampa, Castex, 35º56´S, 64º16´W, 219 m, 04 May 2011, 20w, L. Chifflet coll, hand coll., under stone; Macachín, 37º04´S, 63º, 30´W, Jan-Mar 2012, 1w, C. Ramos coll, pitfall traps; Buenos Aires, Sierra de la Ventana, Parque Provincial Ernesto Tornquist, 38º05´S, 62º00´W, 815-1025 m, Jan-Mar 2012, 3w, S. Santoandre coll, pitfall traps, 38º05´S, 62º00´W, 400 m, 10 Apr 2013, 1♀, L. Chifflet coll, handing collection, under stone; Coronel Suárez, 37º09´S, 62º03´W, Jan-Mar 2012, 1w, Olavarría, 36º43´S, 60º16´W, Jan-Mar 2012, 1w, C. Ramos coll, pitfall traps (FuEDEI).

Comments: This species was only known from its type locality in Castex (Espinal ecoregion), La Pampa, in central Argentina. A new survey was conducted during 2011 to search forits presence in Buenos Aires and La Pampa provinces. However, its presence could only be confirmed 59 years after its discovery by a small colony found under a stone next to a Caldén tree (*Prosopis caldenia*) scrubland in Castex. The collecting site was located in the ecotone between the Pampeana and Espinal ecoregions. Unfortunately, gynes or males were not found. In 2012, a few workers of this species were captured by C. Ramos in three pitfall traps placed in Olavarría and Coronel Suárez in southern Buenos Aires and Macachín in western La Pampa province, and by S. Santoandre in six pitfall traps placed between 436-1025 m elevation in the Parque Provincial Ernesto Tornquist, next to the locality of Sierra de la Ventana, also in southern Buenos Aires. A new survey was conducted in these sites in 2013 to try to collect sexuals of this species. Fortunately, two small colonies (one of them containing a queen) were manually found under small stones at 412 and 536 m elevation in the park Tornquist. This protected area is located in the Austral district of the Pampeana ecoregions (Cabrera & Willink,1980). The climate in this mountainous region is temperate, with higher humidity in the inter-mountains areas. Annual rainfall ranges between 500 - 800 mm (De Fina, 1992). The mean temperature in summer and winter is of 20.5 and 8°C, respectively; the absolute maximum temperature in summer is of 40°C, while in winter frosts are frequent and it occasionally snows.



Figs 7a-c. Worker of *Wasmannia williamsoni*. 9a, head in full-face view; 9c, profile; and 9c, dorsal view.

Figs 8a-c. Queen of *Wasmannia williamsoni*. 10a, head in full-face view; 10b, profile; 10c, dorsal view.

Phylogeny of *Wasmannia*

Only one tree was obtained under implicit enumeration (Fig 9). L = 93.648, CI=0.718, and RI = 0.613, which showed a low level of homoplasy. The cladistic analysis treating each dataset (continuous or discrete characters) separately could not resolve all the relationships between the species of *Wasmannia*, resulting in a polytomous tree.

The analysis shows that the clade [*Blepharidatta* + *Allomerus* + *Wasmannia*] proposed by Ward et al. (2015) based on molecular data is extremely well supported (GC= 91) by morphological data. *Wasmannia* is as a monophyletic group, defined by the following synapomorphies: worker: antennal scrobe with sculpture (character 19) and postpeciolar shape (character 34).

Although the cladogram shows high resolution for the genus, group support was relatively low for some clades within the genus. The clades: [*W. sigmoidea* + *W. rochai*], [*W. lutzi*+ *W. longiseta* + *W. affinis*], [*W. longiseta*+ *W. affinis*], and [*W. sulcaticeps* + *W. williamsoni*] show GC values close to 50 (Fig 9).

W. longiseta was recovered as the sister group of *W. affinis* with high support, with *W. lutzi* as the sister group of this clade. The entire clade [*W.lutzi* + *W. longiseta* + *W.affinis*] is defined by the following synapomorphies: queen ocular index (character 5); worker head width (character 7); worker eye length (character 9); reticulate sculpture between frontal carinae (character 16, state 2); long subpetiolar spine (character 40, state 2), and reticulated genae and postgenae (character 42, state 2). *W. longiseta* is supported as a terminal by two characters: presence of feeble spatulate and long setae on the mesosoma (Character 25, stae 1) and long setae (>1 mm) in the first gastral tergum (character 42, state 3). The clade [*W. sigmoidea* + *W. rochai*] was supported by a morphometric character: gyne ocular index (character 5), and two morphological characters: the shortness of petiole (character 30, state 0) and gastral pilosity (character 43, state 1). The clade [*W. sulcaticeps* + *W. williamsoni*] had a lower support value (=48) and it is based on only one synapomorphy: a small propodeal spiracle (character 39, state 1).

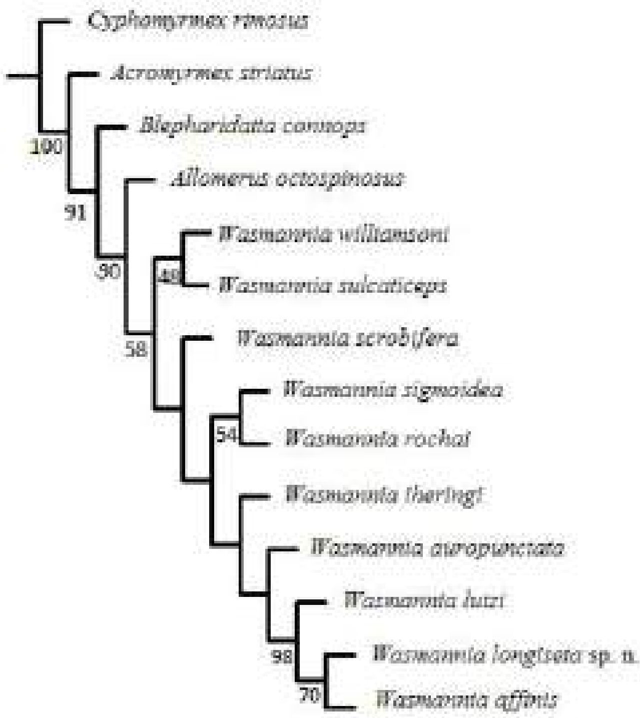


Fig 9. The singlemost parsimonious cladogram obtained under implicit enumeration (Length = 93.648, CI = 0.718, RI = 0.619). Numbers below nodes represent support values as frequency differences, only those values close to GC=50 are shown.

Discussion

The only species widely distributed in Argentina is the little fire ant, *W. auropunctata,* while the other four recorded species are rare and/or inconspicuous. The distribution of the *W. auropunctata* known from previous studies by Kusnezov (1952), Kempf (1972), Cuezzo (1998), and Fuentes et al.(1998) (Buenos Aires, Entre Ríos, Córdoba, Santa Fe, Corrientes, Chaco, Formosa, Tucumán, Jujuy, Salta and Misiones) was extended in this work to the provinces of Santiago del Estero, Catamarca, and La Rioja. *W. auropunctata* was not found in natural/native habitats of the Monte ecoregion, nor in the Patagonian ecoregion (L.A.C., unpublished data). The finding of *W. auropunctata* in Lozano (southern Buenos Aires province, 34º51´S) extends the known range 100 km further south than previously recorded in northeastern Buenos Aires (Reserva Natural Otamendi; 34º13'S) (Fuentes et al., 1998).

The wide distribution and relatively high abundance of *W. auropunctata* could be explained by the fact it has the largest and most fecund queen within the genus (Kusnezov, 1952; Longino & Fernández, 2007). However, the higher abundance of *W. auropunctata* in disturbed habitats, mostly in central-eastern Argentina, seems to be more related with the fact that sexual castes are produced almost exclusively by clonal reproduction (clonal populations) in this region (Rey et al. 2012, LAC, unpublished data).

All individuals collected in Argentina morphologically identified as *W. auropunctata* were genetically grouped in clade B within *W. auropunctata* (as defined by Mikheyev & Mueller, 2007), which shares genetic similarities with several populations from the invasive range (e.g. Israel, New Caledonia, and Western Africa) (Rey et al. 2012, LAC, unpublished data).

Interestingly, molecular evidence revealed that clonal populations present in the floodplain of the Paraná River in the locality of Zárate (Buenos Aires, Fig 4) are the putative source population of the *W. auropunctata* introduction in Israel. Clonal queens from Israel display a multilocus microsatellite genotype similar to that found in queens from Zárate; the Israeli clonal males also display a multilocus haploid genotype remarkably similar to the clonal males found in Zárate. As in the Israeli population, this Argentinean clonal population seems to be more adapted to low temperatures than those clonal populations present in tropical regions (Rey et al., 2012).

The finding of clonal populations of *W. auropunctata* up to 2125 m elevation in the locality of Tumbaya, Jujuy, was surprising because it had been previously found only up to approximately 1070 m elevation (Wetterer & Porter, 2003). The discovery of *W. auropunctata* in the Puna ecosystem (Tumbaya, Jujuy) under extremely cold and dry conditions (annual rainfall 179 mm and mean and minimum temperatures of 8.1ºC and -8ºC in July, the coldest month, De Fina, 1992) was unexpected. According to Kusnezov (1952), *W. auropucntata* was not able to resist prolonged drought. However, our finding supports laboratory evidence that clonal populations present in Argentina are strongly adapted to very low temperatures and probably also to low levels of humidity in environments such as the Puna. This record represents both the highest altitude and the most severe natural environmental conditions reported so far for this species.

The other four species found in Argentina (*W. sulcaticeps*, *W. rochai*, *W. williamsoni*, and *W. longiseta* n. sp.) were much less common than *W. auropunctata*, and they were mostly present in natural and/or disturbed habitats. *W. sulcaticeps* was recorded for the first time for Corrientes and Catamarca provinces; it was previously known only from Buenos Aires, Santa Fé, Córdoba, Tucumán, Salta, and Jujuy provinces (Cuezzo, 1998; Vittar & Cuezzo, 2008). Although intensive surveys were conducted at multiple sites and in different biogeographic regions of Argentina, *W. williamsoni* was only found in central-eastern Argentina, suggesting it may be a relict endemic species. *W. williamsoni* was more common in the Parque Provincial Ernest Tornquist. This park protects several rare and endemic species of the Ventania mountainous system (Sellés-Martínez, 2001), which originates from the Tertiary period (around 22 million years ago). This could be the case of *W. williamsoni*, which is mostly restricted to this region and seems to show very small populations confined mainly to a specific habitat type. According to Longino & Fernández (2007), *W. williamsoni* and *W. sulcaticeps* are two related species that occur at the far southern limit of distribution of the genus and, as stated by Kusnezov (1952), could be the most primitive members of the genus, acting in the present as relicts. It is important to note that both species overlapped with *W. auropunctata* (more commonly in the lowlands) between approximately 400 and 1000 m elevation.

The cladistic analysis shows that the genus *Wasmannia* is monophyletic and sister to the genus *Allomerus*. Only four clades within the genus *Wasmannia* were strongly supported. One of them showed that the new species found in northeastern Argentina (*W. longiseta* n. sp.) is the sister species of *W. affinis*, while *W. lutzi* is the sister species of this latter clade. The clade [W. *lutzi* +*W. longiseta* + *W. affinis*] is characterized by sharing a unique development of the antennal scrobe. *Wasmannia affinis* and *W. lutzi* are, according to Longino and Fernádez (2007), related species distributed from São Paulo to Paraná states in southeastern Brazil, the neighboring region to where *W. longiseta* n. sp. occurs.

Another well supported clade was [*W. rochai* + *W. sigmoidea*]. These are two allopatric species; *W. rochai* is known to occur from Guatemala to São Paulo state in Brazil, now extending its southern limit of distribution to northeastern Argentina, whereas the current reported range of *W. sigmoidea* is smaller and apparently restricted to the Caribbean region (Guiana, Antilles St. Vincent, Grenada, Puerto Rico, Costa Rica, and Venezuela) (Longino & Fernández 2007). In St. Vincent, *W. sigmoidea* can co-occur with *W. auropunctata* (Kuznezov, 1963). However, this species was recently reported from several surveys conducted by Brazilian researchers in northeastern Brazil (e.g. in the state of Bahia), and thus both species can co-occur at least in this region as well.

W. sulcaticeps and *W. williamsoni* were resolved as sister species with relative high support, which is concordant with Longino and Fernández (2007) who suggested that these are two closely related species. The size of workers of both species (*W. sulcaticeps* and *W. williamsoni*) is similar and much larger than workers of other known species of *Wasmannia*. The hypothesis presented by Kusnezov (1952), which mentioned that these species may be primitive members of the genus, is partially supported by this analysis.

The position of *W. auropunctata* in relation to the other species of the genus could not be well clarified. Although the most parsimonious tree places *W. auropunctata* as a sister group of [*W. longiseta* + *W. affinis* + W. *lutzi*], this grouping is not well supported by symmetric resampling. New studies based in further sources of characters (such as molecular) will be useful to clarify the relationships that are not well supported in the analysis here presented.

The morphometric characters used in this work, rarely used by myrmecologists as a source of phylogenetic information, have proved to be useful in resolving the relationships of species within the genus and in adding support to several clades.

Acknowledgements

We thank to the students Sonia Cabrera and Leonardo Ramirez for their field assistance, and Santiago Santoandre, Carolina Ramos, Francisco Sola, Julieta Fillol, and Adriana Aranda Rickert, who provided exemplars of *Wasmannia* species included in this study. We also thank three anonymous reviewers for the critical view of this article. This research was partly funded by USDA-ARS-Pacific Basin Agricultural Research Center, USDA-ARS-South American Biological Control Laboratory (now FuEDEI); the National Scientific and Technical Research Council (CONICET, Argentina) and the project 26/G413 CIUNT, Universidad Nacional de Tucumán.

References

Berndt, K.P. &Kremer, G. (1982). Heat Shock-Induced Gynandromorphism in the Pharaoh's Ant *Monomorium pharaonis* (L.). Experientia, 38:798–799.

Bolton, B. (2003). Synopsis and Classification of Formicidae. Memoirs of the American Entomological Institute, 71: 1-370.

Cabrera, A.L. & A. Willink, A. (1980). Biogeografía de América Latina. Segunda edición. *Monografía 13, serie biología. Programa Regional de Desarrollo Científico y Tecnológico, Organización de los Estados Americanos*. 122 pp. + 1 map.

Calcaterra, L.A., Coulin, C., Briano, J.A. & Follett, P.A. (2012). Acute Exposure to Low Dose Radiation Disrupts Reproduction and Reduces Longevity in *Wasmannia auropunctata* (Hymenoptera: Formicidae) Queens. Journal of Economic Entomology, 105: 817-822.

Cranston, P.S. & Humphries, C.J. (1988). Cladistics and Computers: a Chironomid Conundrum? Cladistics, 4: 72-92. http://dx.doi.org/10.1111/j.1096-0031.1988.tb00469.x

Cuezzo, F. (1998). Formicidae. In *Biodiversidad de Artrópodos de la Argentina*. Morrone, J.J. & S. Coscarón Eds. La Plata. Argentina, 1998: pp. 452-462.

De Fina, A.L. (1992). Aptitud Agroclimática de la República Argentina. Academia Nacional de Agronomia y Veterinária. 402 pp.

De Souza, A.L.B., Delabie, J.H.C. & Fowler, H.G. (1998). *Wasmannia* spp. (Hym. Formicidae) and Insect Damage to Cocoa in Brazilian Farms. Journal of Applied Entomology, 122: 339-341.

Emery, C. (1894). Studi Sulle Formiche della Fauna Neotropica. VI-XVI. Bulletino della Societá Entomologica Italiana, 26: 137-241.

Fernández, F. (2003). The Myrmicine Ant Genera *Ochetomyrmex* Mayr and *Tranopelta* Mayr (Hymenoptera: Formicidae). Sociobiology, 41: 633-661.

Fernández, F. (2007). The Myrmicine Ant Genus *Allomerus*

Mayr (Hymenoptera: Formicidae).Caldasia, 29: 159-175.

Fournier, D., Estoup, A., Orivel, J., Foucaud, J., Jourdan, H., Breton, J., & Keller, L. (2005). Clonal Reproduction by Males and Females in the Little Fire Ant. Nature, 435: 1230-1234. doi: 10.1038/nature03705.

Foucaud, J., Fournier, D., Orivel, J., Delabie, J., Loiseau, A., Le Breton, J., Kergoat, G. & Estoup, A. (2007). Sex and Clonality in the Little Fire Ant. Molecular Biology and Evolution, 24: 2465-2473. doi: 10.1093/molbev/msm180.

Foucaud, J., Orivel, J., Fournier, D., Delabie, J.H.C., Loiseau, A., Le Breton, J., Cerdan, P., & Estoup, A. (2009). Reproductive System, Social Organization, Human Disturbance, and Ecological Dominance in Native Populations of the Little Fire Ant, *Wasmannia auropunctata*. Molecular Ecology, 18: 5059-5073.http://dx.doi.org/10.1111/j.1365-294X.2009.04440.x.

Foucaud, J., Orivel, J., Loiseau, A., Delabie, J.H.C, .Jourdan, H., Konghouleux, D., Vonshak, M., Tindo, M.,Mercier, J.-L., Fresneau, D., Mikissa, J.-B., McGlynn, T., Mikheyev, A.S.,Oettler, J. &Estoup, A.(2010). Worldwide Invasion by the Little Fire Ant: Routes of Introduction and Eco-Evolutionary Pathways. Evolutionary Applications, 3: 363-374. doi: 10.1111/j.1752-4571.2010.00119.x.

Forel, A. (1893). Formicides de I'Antille St. Vincent, Récoltées par Mons. H. H. Smith. Transactions of the Entomological Society of London, 1893: 333-418.

Forel, A. (1908). Ameisen aus São Paulo (Brasilien), Paraguay etc. gesammelt von Prof. Herm. v. Ihering, Dr. Lutz, Dr. Fiebrig, etc. Verh.der Kaiserlich-Königlichen Zool.-Bot. Ges. in Wien, 58: 340-418.

Forel, A. (1912). Formicides Néotropiques. Part IV. 3me sous-famille Myrmicinae Lep. (suite). Memoires de la Société Entomologique de Belgique, 20: 1-32.

Fuentes, M.B., Cuezzo, F. & Di Iorio, O. (1988). Ant Species of the Natural Reserve of Otamendi, Buenos Aires, Argentina (Hymenoptera: Formicidae). Giornale Italiano di Entomologia, 9: 97-98.

Goloboff, P.A., Farris J.S., Källersjö, M., Oxelmann, B., Ramirez,M., and Szumik, C. (2003). Improvements to Resampling Measures of Group Support. Cladistics, 19: 324-332. 10.1111/j.1096-0031.2003.tb00376.x.

Goloboff, P.A., Mattoni C.I., Quinteros, A.S. (2006). Continuous Characters Analyzed as Such. *Cladistics* 22: 589-601. http://dx.doi.org/10.1111/j.1096-0031.2006.00122.x.

Goloboff, P.A., Farris, J.S., Nixon, K.C. (2008). TNT (Tree analysis using new technology) (BETA) ver. 1.1. Published by the authors, Tucumán, Argentina.

Goncalves, C.R. (1961). O Genero *Acromyrmex* no Brasil (Hym. Formicidae). *Studia Entomol.*(N. S.) 4: 113-180.

Jones, S.R., & Philips, S.A. Jr. (1985). Gynandromorphism in the Ant *Pheidole dentate* Mayr (Hymenoptera: Formicidae). *Proc. Entomol. Soc. Wash*. 87: 583–586.

Kempf, W.W. (1961). A Survey of the Ants of the Soil Fauna in Surinam (Hymenoptera: Formicidae). *Stud.Entomol.* 4: 481-524.

Kempf, W.W. (1965). A Revision of the Neotropical Fungus-Gowing Ants of the Genus *Cyphomyrmex* Mayr. Part II. Group of *rimosus* (Spinola) (Hym. Formicidae). *Studia Entomol.* 8: 161-200.

Kempf, W.W. (1967). Three New South American Ants (Hym. Formicidae). *Studia Entomol.* 10: 353-360.

Kusnezov, N. (1952). El género *Wasmannia* en la Argentina (Hymenoptera, Formicidae). *Acta Zool. Lilloana*, 10: 173-182.

Longino, J.T. & Fernández, F. (2007). Taxonomic Review of the Genus *Wasmannia*. In: Snelling, R.R., B.L. Fisher, and P.S. Ward (eds). Advances in Ant Systematics (Hymenoptera: Formicidae): homage to E. O. Wilson – 50 years of contributions*.Mem. Am. Entomol. Inst.* 80: 271-289.

Mikheyev, A. & Mueller, U. (2007). Genetic Relationships BetweenNative and Introduced Populations of the Little Fire Ant *Wasmannia auropunctata.Diver.& Distrib*. 13: 573-579. http://dx.doi.org/10.1111/j.1472-4642.2007.00370.x.

Orivel, J., Grangier, J., & Foucaud, J. (2009). Ecologically Heterogeneous Populations of the Invasive Ant *Wasmannia auropunctata*within its Native and Introduced Ranges. *Ecol. Entomol*. 34:504-512.

Pearcy, M., Goodisman, M.A.D. & Keller, L.(2011). Sib Mating without Inbreeding in the Longhorn Crazy Ant. *Proc. R. Soc. B*, 278: 2677–2681.http://dx.doi.org/10.1098/rspb.2010.2562.

Pimentel, R.A. & Riggins, R. (1987). The Nature of Cladistic Data. Cladistics, 3: 201-209. doi: 10.1111/j.1096-0031.1987.tb00508.x.

Rae, T.C. (1998). The Logical Basis for the Use of Continuous Characters in Phylogenetic Systematics. Cladistics, 14: 221-228. doi: 10.1111/j.1096-0031.1998.tb00335.x.

Rey, O., Estoup, A., Vonshak, M., et al. (2012). Where do adaptive shifts occur during invasion? A multidisciplinary approach to unravelling cold adaptation in a tropical ant species invading the Mediterranean area. Ecology Letters, 15:1266–1275. doi: 10.1111/j.1461-0248.2012.01849.x.

Rigaud, T.& Juchault, P. (1993). Conflict between Feminizing Sex Ratio Distorters and an Autosomal Masculinizing Gene in the Terrestriael Isopod *Armadillidium vulgare* Latr. Genetics 133: 247-252.

Roger, J. (1863). Die neu aufgeführten Gattungen und Arten meines Formiciden-Verzeichnissesnebst Ergänzung einiger früher gegebenen Beschreibungen. Berliner entomologische Zeitschrift, 7: 131-214.

Santschi, F. (1929). Nouvelles fourmis de la République Argentine et du Brésil. An. Soc. Cient. Arg.107: 273-316.

Schultz, T.R. & Meier, R. (1995). A Phylogenetic Analysis of the Fungus-Growing Ants (Hymenoptera: Formicidae: Attini) Based on Morphological Characters of the Larvae. Systematic Entomology, 20: 337-370. doi: 10.1111/j.1365-3113.1995.tb00100.x.

Sellés-Martínez, J. (2001). The Geology of Ventania (Buenos Aires Province, Argentina). Journal of Iberian Geology, 27: 43-69.

Serna, F.& Mackay, W. (2010). A Descriptive Morphology of the Ant Genus *Procryptocerus* (Hymenoptera: Formicidae). Journal of Insect Science, 10 (111):1-36. doi: 10.1673/031.010.11101.

Serna, F., Bolton, B. & Mackay, W. (2011). On the Morphology of *Procryptocerus*. Some Comments and corrigenda. Zootaxa 2923: 67-68.

Snelling, R.R. & Longino, J.T. (1992). Revisionary Notes of the Fungus Growing Ants of the Genus *Cyphomyrmexrimosus*Group (Hymenoptera: Formicidae: Attini). In Quintero, D. & A. Aiello (Eds.) *Insects of Panamá and Mesoamerica: selected studies*. Oxford University Press, Oxford. 692 pp.

Souza, A.L.B., Tavares, M.G., Serrao, J.E., & Delabie, J.H.C. (2009). Genetic Variability of Native Populations of *Wasmannia* Forel (Hymenoptera: Formicidae) and their Biogeographical Implications. Neotropical Entomology, 38:376-383.

Stevens, P.F. (1991). Character States, Morphological Variation, and Phylogenetic Analysis: a Review. Systematic Botany, 16: 553-583. doi: 10.2307/2419343.

Ulloa Chacón, D. & Cherix, D. (1990). The Llittle Fire Ant *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae). Pp. 281-289. In: Vander Meer, R. K., Jaffe, K. & Cedeno, A.(eds). *Applied Myrmecology: a World Perspective*: 741 pp. Westview Press, Boulder,Colorado, USA.

Vittar, F. & Cuezzo, F. (2008). Hormigas (Hymenoptera: Formicidae) de la Provincia de Santa Fe, Argentina. Revista de la Sociedad Entomologica Argentina, 67: 175-178.

Ward, P.S., Brady, S.G., Fisher, B.L. & Schultz, T.R. (2015). The evolution of Myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). Systematic Entomology, 40: 61-81. doi: 10.1111/syen.12090.

Wheeler, G.C. & Wheeler, J. (1976).Ant larvae: Review and synthesis. Entomological Society of Washington,108 pp.

Wheeler, G.C.& Wheeler, J.(1991).The Larva of *Blepharidatta* (Hymenoptera: Formicidae). Journal of the New York Entomological Society, 99: 132-137.

Wheeler, W.M.(1915). Two New Genera of Myrmicinae Ants from Brazil. Bulletin of the Museum of Comparative Zoology, 7: 482-491.

Wcislo, W.T., González, V.H. & Arneson, L.(2004). A Review of Deviant Phenotypes in Bees in Relation to Brood Parasitism, and a Gynandromorph of *Megalopta genalis* (Hymenoptera: Halictidae). Journal of Natural History, 38: 1443–1457. doi: 10.1080/0022293031000155322.

Wiens, J.J. (2001). Character Analysis in Morphological Phylogenetics: Problems and Solutions. Systematic Biology, 50: 689-699.http://dx.doi.org/10.1080/106351501753328811.

Wetterer, J.K.& Porter, S.D. (2003).The Little Fire Ant, *Wasmannia auropunctata*: Distribution, Impact, and Control. Sociobiology, 42: 1-41.

Appendix 1. Matrix of continuous morphometric characters (0-11) of all the known species of *Wasmannia* (except *W. villosa*) and the taxa used as outgroups (*Acromyrmex striatus*, *Cyphomyrmex rimosus*,*Blepharidatta conops*, and *Allomerus octoarticulatus*).

Species	0	1	2	3	4	5	6	7	8	9	10	11
Acromyrmex_striatus	1.125-2.850	2.125-2.175	1.650-1.775	0.325-0.400	1.287-1.225	0.196-0.225	2.475-2.550	1.975-2.250	1.675-1.825	0.325-0.350	1.179-1.232	0.178-0.208
Allomerus octoarticulatus	?	?	?	?	?	?	0.600-0.630	0.490-0.540	0.540-0.590	?	0.91	?
Cyphomyrmex_rimosus	1.250	0.700	0.775	0.225	0.903	0.290	0.825-1.000	0.600-0.625	0.675-0.750	0.125-0.175	0.833-0.888	0.185-0.233
Blepharidatta_conops	?	?	?	?	?	?	1.230	0.930	1.120	0.130	0.830	0.116
Wasmannia_auropunctata	1.130-1.190	0.770-0.840	0.690-0.740	0.210-0.260	0.300-0.350	0.580-0.620	0.510-0.550	0.420-0.480	0.550-0.610	0.110-0.130	0.910-0.930	0.200-0.210
Wasmannia_rochai	1.080-1.200	0.680-0.750	0.640-0.700	0.200-0.240	1.050-1.070	0.310-0.340	0.450-0.540	0.430-0.500	0.450-0.500	0.100-0.110	0.960-0.990	0.210-0.240
Wasmannia_sigmoidea	0.820-0.860	0.580-0.610	0.620-0.650	0.200-0.210	0.890-0.970	0.320-0.330	0.560-0.610	0.490-0.520	0.550-0.580	0.140-0.150	0.890-0.910	0.260-0.262
Wasmannia_scrobifera	0.670-0.700	0.540-0.560	0.600-0.610	0.160-0.170	0.880-0.940	0.270-0.280	0.560	0.520	0.520	0.150	0.990	0.290
Wasmannia_iheringi	0.860-0.880	0.600-0.620	0.610-0.630	0.160-0.180	0.983-0.984	0.260-0.290	0.630-0.635	0.490-0.570	0.530-0.560	0.110-0.130	0.870-1.060	0.200-0.240
Wasmannia_affinis	1.160	0.740	0.720	0.160	1.010	0.220	0.460-0.480	0.420-0.450	0.460-0.480	0.100-0.110	0.920-0.950	0.200-0.230
Wasmannia_longiseta n. sp.	?	?	?	?	?	?	0.470-0.500	0.425-0.450	0.500-0.520	0.100	0.850-0.860	0.200
Wasmannia_lutzi	1.150	0.760	0.690	0.190	1.100	0.270	0.560	0.490	0.550	0.100	0.890	0.190
Wasmannia_sulcaticeps	0.800	0.590	0.630	0.180	0.930	0.280	0.570-0.625	0.480-0.550	0.550-0.600	0.100-0.125	0.859-0.872	0.210-0.220
Wasmannia_williamsoni	0.725	0.575	0.625	0.150	0.912	0.24	0.570-0.625	0.480-0.550	0.550-0.600	0.100-0.150	0.850-0.950	0.217-0.182

Appendix 2. Matrix of discrete characters (12-43) for all the known species of *Wasmannia* (except *W. villosa*) and the taxa used as outgroups: *Acromyrmex striatus*, *Cyphomyrmex rimosus*,*Blepharidatta conops*, and *Allomerus octoarticulatus.*

Species	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Acromyrmex_striatus	0	1	1	1	1	2	0	1	0	0	0	1	0	1	1	1	0
Allomerus octoarticulatus	2	2	0	1	4	0	1	0	0	2	1	1	0	0	0	0	0
Cyphomyrmex_rimosus	1	1	1	0	3	1	1	1	2	0	0	1	1	2	1	1	0
Blepharidatta_conops	1	1	0	0	0	1	2	0	1	1	1	1	0	0	0	0	1
Wasmannia_auropunctata	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	0	1
Wasmannia_rochai	0	0	0	1	0	0	1	2	1	1	1	1	0	0	0	0	1
Wasmannia_sigmoidea	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	0	1
Wasmannia_scrobifera	0	0	1	1	1	0	0	1	2	1	1	1	0	0	1	0	1
Wasmannia_iheringi	0	0	0	1	0	0	1	1	3	1	1	1	0	0	0	0	1
Wasmannia_affinis	0	0	0	1	2	0	1	2	0	1	1	1	0	0	0	0	1
Wasmannia_longiseta	0	0	0	1	2	0	1	1	2	1	1	1	0	1	0	0	1
Wasmannia_lutzi	0	0	0	1	2	0	1	1	0	1	1	1	0	0	0	0	1
Wasmannia_sulcaticeps	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	1
Wasmannia_williamsoni	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	1

Appendix 2. Matrix of discrete characters (12-43) for all the known species of *Wasmannia* (except *W. villosa*) and the taxa used as outgroups: *Acromyrmex striatus*, *Cyphomyrmex rimosus*,*Blepharidatta conops*, and *Allomerus octoarticulatus* (Continued).

Species	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Acromyrmex_striatus	0	0	1	1	2	1	0	1	1	-	0	0	1	0	0	0	3
Allomerus octoarticulatus	0	1	1	1	1	2	1	0	0	0	-	1	4	2	0	1	1
Cyphomyrmex_rimosus	0	0	0	0	1	2	1	1	0	1	-	0	0	1	0	0	0
Blepharidatta_conops	3	2	0	0	0	1	0	1	0	1	-	0	0	1	0	0	1
Wasmannia_auropunctata	2	1	2	2	2	0	0	0	0	0	0	1	1	1	0	2	1
Wasmannia_rochai	1	0	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1
Wasmannia_sigmoidea	1	0	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1
Wasmannia_scrobifera	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	1
Wasmannia_iheringi	2	2	1	1	1	0	0	0	0	0	0	1	1	0	0	1	1
Wasmannia_affinis	1	1	1	1	1	0	0	0	0	0	0	2	2	2	0	0	1
Wasmannia_longiseta	2	2	1	1	1	0	0	0	0	0	0	2	2	3	0	0	1
Wasmannia_lutzi	2	1	1	1	1	0	0	0	0	0	0	2	3	2	0	0	1
Wasmannia_sulcaticeps	2	0	1	1	1	0	0	0	0	0	1	1	1	1	0	?	1
Wasmannia_williamsoni	2	2	1	1	1	0	0	0	0	0	1	1	1	1	0	?	1