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TAXONOMIC REVIEW OF THE GENUS *WASMANNIA*

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ABSTRACT

The Neotropical ant genus *Wasmannia* is reviewed and a key is provided to all *Wasmannia* species. By far the most common species is *W. auropunctata*, native to the Neotropics and becoming a serious pest ant when introduced elsewhere. Although *W. auropunctata* is variable, there is no evidence that it is composed of multiple cryptic species. Queen size is dimorphic in Costa Rica, but the taxonomic and biological significance of this is unknown. Other species of *Wasmannia* are rare and inconspicuous. The following taxonomic changes are made: *W. australis* Emery 1894, *laevifrons* Emery 1894, *obscura* Forel 1912, *pulla* Santschi 1931, *nigricans* Emery 1906, and *rugosa* (Forel 1886) are synonymized under *auropunctata* (Roger 1863); *W. weiseri* Forel 1912 is synonymized under *sulcaticeps* Emery 1894. There is a negative relationship between queen size and worker size among *Wasmannia* species. *Wasmannia auropunctata* has the greatest difference, which may contribute to its ecological success.

Key words: Hymenoptera, Formicidae, Myrmicinae, *Wasmannia auropunctata*, invasive ants, taxonomy, Neotropics.

INTRODUCTION

The genus *Wasmannia* is endemic to the Neotropics. Its most famous member is *W. auropunctata*, the "little fire ant". This species does very well in synanthropic habitats throughout the Neotropics and has been introduced to tropical locales throughout the world, where it often becomes a severe pest ant. Other species in the genus are few, and all of them are uncommon relative to their famous relative. Twenty-one available names have accumulated in the taxonomic literature, but there has never been a synthetic review of the genus. Kusnezov (1952) characterized the *Wasmannia* species of Argentina, but no other work has focused on the taxonomy of the genus. The purpose of this report is to provide a revised key, taxonomic commentary, and natural history notes on all species in the genus. Particular emphasis is placed on the occurrence of the genus in Costa Rica, where extensive inventory work has been carried out.

Wasmannia was established in 1893 by Forel. The most recent ant classification (Bolton, 2003) places *Wasmannia* in the tribe Blepharidattini, within the attine tribe group. Bolton proposes as an autapomorphy for the attine tribe group the "anterior clypeal margin with a broad anteclypeal apron or flange that fits tightly over basal margins of mandibles and is at an angle to outline of clypeus proper (not a direct continuation of median clypeus). Anteclypeal apron of different sculpture/texture from median portion of clypeus." Within this tribe group there are two tribes: Attini (the fungus-growing ants) and Blepharidattini. Workers of Attini are differentiated from the Blepharidattini by (1) the fungus-growing habit; (2) masticatory margin of mandibles longer than basal margin, usually with 7 or more teeth (secondarily reduced to 5 teeth in some groups); and (3) the 11-segmented antennae gradually incrassate. In contrast, the Blepharidattini (1) do not culture fungi; (2) have relatively shorter mandibles, the masticatory margin with 5 or fewer teeth and subequal in length to the basal margin; and (3) the 11-segmented antennae have a discrete 2-segmented club. Additional blepharidattine characters described by Bolton are clypeus broadly inserted between the frontal lobes and the propodeal spiracle low on the side of the propodeum. The Blepharidattini contains two genera, *Blepharidatta* and *Wasmannia*. *Blepharidatta* have very strongly developed antennal scrobes, the upper margin of which is prolonged posteriorly so that the posterolateral margins of the vertex are drawn out as posteriorly directed teeth or lobes, the anterior margins of the frontal lobes project forward almost to the anterior margin of the clypeus, and the petiolar node is long, low, and without differentiated anterior face. In *Wasmannia*, the antennal scrobes are shallow and never so strongly developed; the posterolateral margins of the vertex are not produced as lobes or teeth; the frontal lobes do not project forward; and the petiolar node is always well-developed, with a distinct anterior face.

In practice, *Wasmannia* may be confused with some species of *Ochetomyrmex*. For example, the face of *O. semipolita* is very similar to *Wasmannia* (Fernandez, 2003). *Ochetomyrmex* have less developed antennal scrobes, the clypeal apron is lacking, and there is a slightly impressed mesonotal suture which is never present in *Wasmannia*. In addition, *Wasmannia* lacks a bifurcated carina on the ventral surface of the petiole, a character present in *Ochetomyrmex*, *Tranopelta*, and other myrmicines (Fernandez, 2003).

METHODS

The following terminology and abbreviations are used:

HL: head length; perpendicular distance from line tangent to rearmost points of vertex margin to line tangent to anteriormost projections of clypeus, including anterior flange, in full face view.

HW: head width; maximum width of head in face view, including eyes if they project beyond the sides of the head.

EL: eye length, measured along maximum diameter.
WL: Weber's length; viewing mesosoma in lateral profile, distance from approximate inflection point, where downward sloping pronotum curves into anteriorly projecting neck, to posteroventral propodeal lobes.
CI: cephalic index; HW/HL.
OI: ocular index; EL/HL.

Collections are referred to by the following acronyms:

MHNG: Muséum d'Histoire Naturelle, Geneva, Switzerland.
MZSP: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
NHMB: Naturhistorisches Museum, Basel, Switzerland.
NMW: Naturhistorisches Museum, Vienna, Austria.

TAXONOMIC SYNOPSIS

Wasmannia affinis Santschi 1929. Brazil (Paraná).
Wasmannia auropunctata (Roger 1863). Throughout Neotropics, introduced elsewhere.
= *atomum* (Santschi 1914).
= *australis* Emery 1894. **NEW SYNONYMY**
= *glabra* Santschi 1931.
= *laevifrons* Emery 1894. **NEW SYNONYMY**
= *obscura* Forel 1912. **NEW SYNONYMY**
= *panamana* (Enzmann 1947).
= *pulla* Santschi 1931. **NEW SYNONYMY**
= *nigricans* Emery 1906.. **NEW SYNONYMY**
= *rugosa* (Forel 1886). **NEW SYNONYMY**
Wasmannia iheringi Forel 1908. Brazil (Espirito Santo), Peru, Costa Rica.
Wasmannia lutzi Forel 1908. southeastern Brazil.
Wasmannia rochai Forel 1912. Brazil to Costa Rica.
Wasmannia scrobifera Kempf 1961. Surinam, Costa Rica.
Wasmannia sigmoidea (Mayr 1884). Guianas, Antilles (St. Vincent; Puerto Rico), Costa Rica.
Wasmannia sulcaticeps Emery 1894. Argentina.
= *bruchi* Santschi 1919. TL: Argentina.
= *weiseri* Forel 1912. TL: Argentina. **NEW SYNONYMY.**
Wasmannia villosa Emery 1894. Brazil (Rio Grande do Sul).
Wasmannia williamsoni Kusnezov 1952. Argentina.

KEY TO WORKERS

(The worker of *Wasmannia villosa* is unknown.)

1a. Petiolar node strongly quadrate in lateral view, with nearly vertical anterior face and forming sharp right angle with dorsal face (Fig. 1); petiolar peduncle about as long as node; setae on mesosomal dorsum erect, long, about 0.1 mm or longer; 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; color red brown to orange ....*auropunctata*
1b. Petiolar node more rounded, with sloping anterior and posterior faces, and without sharply differentiated dorsal face **or** clypeus strongly projecting and box-like and dorsal pilosity

composed of a very short stubble; petiolar peduncle longer or shorter than node; antennal scrobe various; color various 2

2a. Scape strongly flattened; clypeus strongly projecting and box-like, sharply divided into equal dorsal and anterior faces that meet at a right angle; setae on mesosomal dorsum abundant, straight, filiform, short (about 0.04 mm long), forming a stubble; propodeal spines very short, about same length as setae on mesosomal dorsum ....*scrobifera*
2b. Scape more terete, less flattened; clypeus not strongly box-like, rounded from posterior to anterior margins; setae on mesosomal dorsum longer and/or curved, clavate; propodeal spines various 3

3a. First gastral tergite lacking erect setae; petiolar peduncle longer than node (Fig. 1); dorsal setae on mesosoma and face thin, flexuous; color yellow orange ....*iheringi*
3b. First gastral tergite with abundant erect setae; petiolar peduncle equal to node or shorter; dorsal setae stiff to slightly clavate; color various.. 4

4a. 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 5
4b. Antennal scrobe broad and flat, extending to side of head, ventral margin formed by angular side of head posterior to eye 8

5a. 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) 6
5b. 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... 7

6a. 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*
6b. 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 faces of petiolar node similarly rounded...*williamsoni*

7a. 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*
7b. Dorsal setae on mesosoma curved and clavate; head relatively short, CI 0.95-1.00; propodeal spines short and directed posteriorly (Fig. 1); eyes shorter (OI 0.21-0.24) ....*rochai*

8a. 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 robust, in dorsal view about as long as distance between their tips .... *lutzi*
8b. Postpetiole in dorsal view elliptical, widest portion at or posterior to midlength; postpetiolar dorsum feebly punctate, sublucid medially; propodeal spines shorter, in dorsal view shorter than distance between tips .... *affinis*

KEY TO QUEENS

1a. Body covered with abundant, long, appressed pilosity; propodeal spine robust, short, forming nearly a right angle; length about 4 mm .... *villosa*
1b. Pilosity erect; propodeal spine long or short but usually more spiniform, acute; length various 2

2a. Clypeus strongly projecting and box-like, sharply divided into equal dorsal and anterior faces that meet at a right angle...*scrobifera*
2b. Clypeus not strongly box-like, rounded from posterior to anterior margins............................ 3

3a. Head width less than 0.65 mm 4
3b. Head width greater than 0.65 mm... 7

4a. Petiolar peduncle longer than node ....*iheringi*
4b. Petiolar peduncle about as long as node 5

5a. Mesosomal dorsum almost uniformly punctate, with faint longitudinal striae on mesonotum; striae on face weak...*sigmoidea*
5b. Mesosomal dorsum strongly longitudinally striate, on both mesonotum and scutellum; striae on face strong.. 6

6a. Cephalic striae continuous, not mixed with other sculpture; color yellow red; posterior face of petiole rounded, anterior face slightly angulate... *sulcaticeps*
6b. Cephalic striae mixed, appearing rugo-reticulated at least near vertex margin; color uniformly dark maroon, abdomen black; anterior and posterior faces of petiolar node similarly rounded...*williamsoni*

7a. Antennal scrobe broad and flat, extending to side of head, ventral margin formed by angular side of head posterior to eye; outer margin of frontal carinae not strongly convex, diverging at level of ocelli; propodeal spines spiniform, longer than width at base; anteroventral postpetiolar teeth short, inconspicuous.. 8
7b. Antennal scrobe narrow, side of head rounded, ventral margin of scrobe defined by preocular carina that runs from dorsal margin of eye to margin of vertex **or** ventral margin not defined; frontal carinae, propodeal spines, and ventral postpetiolar teeth variable 9

8a. Head in face view strongly trapezoidal, with widest portion of head behind eyes; rugae on face fading posteriorly, weak on cephalic dorsum near margin of vertex .... *lutzi*
8b. Head in face view less trapezoidal, widest across eyes; rugae on face continuing to margin of vertex .... *affinis*

9a. Antennal scrobe a distinct longitudinal trough, with defined ventral margin; propodeal spines subtriangular, about as long as wide at base; head width more than 0.75 mm ....*auropunctata*
9b. Antennal scrobe weakly impressed, ventral margin not defined; propodeal spines spiniform, longer than width at base; head width about 0.75 mm or less ....*rochai*

SPECIES ACCOUNTS

Wasmannia affinis Santschi
Table 1

Wasmannia affinis Santschi, 1929: 300, fig. 25, 26. Holotype worker: **Brazil**, Paraná, Rio Negro (Reichensperger) [NHMB] (*examined*).
Wasmannia sigmoidea Mayr (part): Mayr, 1887: 622.

Taxonomic comments

Wasmannia affinis and *lutzi* are two related species from southeastern Brazil. They share a unique development of the antennal scrobe. The scrobe is very broad, forming a flat surface that extends from the frontal carinae to the side of the head. The side of the head is somewhat angular posterior to the eye. The preocular carina is faint and does not form the ventral border of the scrobe. In contrast, all other species of *Wasmannia* have a more narrow scrobe that does not reach the side of the head in full face view. The ventral margin of the scrobe is limited by the preocular carina or, in cases where the carina is faint or absent, where it would be if it extended posterior to the eye. The side of the head behind the eye is rounded. The expanded scrobe is also present in the queen of *lutzi*, resulting in a strongly trapezoidal head shape, such that the head is broader behind the eyes than across them. *Wasmannia affinis* differs from *lutzi* in (1) the propodeal spines are shorter, and (2) in dorsal view, the postpetiole is elliptical with rounded sides, and the widest point is at or behind the midlength.

Mayr described *W. sigmoidea* in 1884, based on specimens from Cayenne (see below). Later (Mayr, 1887) he identified a series of specimens from Santa Catarina state in Brazil as *W. sigmoidea*. One of us (JTL) examined these Santa Catarina specimens (they have a variety of labels, some indicating they are from Santa Catarina and collected by Hechko, some just saying "Brazil 188," and some erroneously labeled as types of *sigmoidea*). The workers in the series are all very uniform and we suspect they are from a single original collection. These workers are not *sigmoidea*, but instead match the holotype of Santschi's *affinis*.

In addition to the material above, we have examined three collections from Santa Catarina and São Paulo states in Brazil.

Wasmannia auropunctata (Roger)
Fig. 1, Table 1

Tetramorium auropunctatum Roger, 1863: 182. Syntype worker, queen, male: **Cuba** (*not examined*). Combination in *Ochetomyrmex*: Forel, 1886; in *Wasmannia*: Forel, 1893. Description of larva: Wheeler, G.C. & Wheeler, J., 1954: 444.
Ochetomyrmex auropunctatus var. *rugosus* Forel, 1886: xlix. Syntype worker: **Guatemala**, Retalhuleu (Stoll) [MHNG] (*examined*). Combination in *Wasmannia*: Forel, 1901: 128. Description of queen, male: Santschi, 1929: 299. **NEW SYNONYMY**.
Wasmannia auropunctata var. *australis* Emery, 1894: 193. Syntype worker: **Brazil**, Rio Grande do Sul (v. Ihering). **NEW SYNONYMY**.
Wasmannia auropunctata var. *laevifrons* Emery, 1894: 193. Syntype worker: **Bolivia**, Coroico, Chulumani Yungas (Balzan). **NEW SYNONYMY**.
Wasmannia auropunctata var. *nigricans* Emery, 1906: 160. Syntype worker: **Paraguay**, Tacurú Pucú. **NEW SYNONYMY**.
Wasmannia auropunctata var. *obscura* Forel, 1912: 1. Syntype worker: Dibulla, Burithaka and Don Diego, Sierra Nevada de Santa Marta, **Colombia** (Forel); Ceará, **Brazil** (Diaz da

Rocha); Santos, **Brazil** (Dr. Ris) [MHNG] (Dibulla and Ceará syntypes *examined*, Ceará worker here designated **LECTOTYPE**). **NEW SYNONYMY**.

Xiphomyrmex atomum Santschi, 1914: 370. Syntype worker: **Gabon**, Libreville (Silvestri) [NHMB] (*examined*). Combination in *Wasmannia*, and variety of *auropunctata*: Santschi, 1916:504. Junior synonym of *auropunctata*: Wheeler, 1922: 912.

Wasmannia glabra Santschi, 1931: 272. Syntype queen: **French Guiana**, St. Laurent du Moroni (Le Moult) [NHMB] (*examined*). Junior synonym of *auropunctata*: Kempf, 1964:66.

Wasmannia auropunctata st. *pulla* Santschi, 1931: 272. Syntype worker: **Panama**, France Field, 9 May 1930 (A. Bierig) [NHMB] (*examined*). **NEW SYNONYMY**.

Hercynia panamana Enzmann, J. 1947: 44, pl. 5. Syntype worker, queen: Panama. Junior synonym of *auropunctata*: Brown, 1948: 102.

Taxonomic comments

Workers of *W. auropunctata* have a strongly quadrate petiolar node. The anterior face of the node is sharply differentiated from both the peduncle and the dorsal face of the node, meeting both at nearly right angles, and forming a strongly step-like profile. This is a highly distinctive feature that easily distinguishes *auropunctata* workers from all other *Wasmannia* species. Within the species there is abundant variation in the strength of sculpturing and coloration, and this has engendered the naming of nine infraspecific forms in addition to the nominotypical. We have never been able to discover evidence of discrete forms among the workers of *auropunctata*, either in sympatry or allopatry; the variation appears continuous. Three of the forms have already been synonymized by others: *atomum*, *glabra*, and *panamana*. We have been able to examine types of three additional forms—*obscura*, *pulla*, and *rugosa*—and they fall well within our concept of *auropunctata*. The remaining forms—*australis*, *laevifrons*, *nigricans*—we have not examined, but the published descriptions give no indication that they are beyond the range of variation of *auropunctata*. We have synonymized them, following the philosophy that taxa should be synonymized unless evidence of distinctness is obtained.

The above synonymy does not assure that there is no genetic structuring, and perhaps species-level differences, within the broad concept of *auropunctata*. There may even be distinct sympatric species. In Costa Rica, there appear to be two size classes of queens (Fig. 2). Queens with smaller heads include ten from various sites in Costa Rica, including La Selva Biological Station and the Peñas Blancas Valley, one from Jamaica, and one from Venezuela. Queens with large heads are all from the Atlantic slope of Costa Rica. Three are from La Selva (two from different Winkler samples of sifted leaf litter from the forest floor, one from a small nest under an epiphyte mat in an old treefall) and one is an alate queen found in a *Cecropia* sapling near Volcan Arenal. Thus the small-headed and big-headed forms are broadly sympatric in Costa Rica. Among the small-headed queens four are definitively associated with workers from the same colony, and among the big-headed queens one is associated with workers. Others have workers doubtfully associated (together in the same Winkler sample). We can discern no differences in workers associated with the two types of queens. The cause of the two size classes of queens is unknown, but could reflect either differences between cryptic species or intraspecific polymorphism.

An aberrant worker form is frequently encountered in large samples of *W. auropunctata*. These aberrant workers have the head grossly swollen. The entire head is more spherical than normal, as if the head were inflated like a balloon. The rest of the body is little different from a normal worker. These aberrant workers are occasionally encountered in Winkler samples that contain hundreds or thousands of *auropunctata* workers.

Natural History

Wasmannia auropunctata is a widespread pest ant (Clark *et al*., 1982; De Souza *et al*., 1998; Fabres & Brown, 1978; Jourdan, 1997; Lubin, 1984; Ulloa Chacón & Cherix, 1990; Williams, 1994; Wetterer & Porter, 2003). In its presumed native range it occurs from Argentina to Mexico (Kempf, 1972; Wetterer & Porter, 2003). Its introduced range includes the Galapagos Islands, West Africa (Gabon, Cameroon, and possibly the Republic of Congo and the Democratic RepubIic of Congo), Melanesia (New Caledonia, Solomon Islands, Vanuatu, and possibly Tuvalu), Polynesia (Wallis and Futuna and Hawaii), parts of the US (Florida and possibly California), and subtropical Atlantic islands (the Bahamas and Bermuda) (Wetterer & Porter, 2003). It is widespread on Caribbean islands, but it is unclear whether these are long-term native populations or recent introductions (Wetterer & Porter, 2003).

The species is remarkably catholic in its habitat preference. It is common in habitats ranging from wet to dry and from early successional to mature. In an elevational gradient of mature wet forest on the Atlantic slope of Costa Rica (the Barva Transect, from La Selva Biological Station to 2000m elevation on the slope of Volcan Barva) it is abundant at 50m and 500m elevations, but nearly absent at 1070m (Table 2). In the lowland habitats where it is abundant, it occurs in leaf litter on the forest floor and at all levels in the vegetation.

Although it occurs frequently in samples from mature forest habitats in Costa Rica, it is never so abundant in those habitats that it is noticeable as a pest or appears to be displacing other native species (Tennant, 1994; McGlynn & Kirksey, 2000; pers. obs.). In contrast, in certain agricultural habitats (banana plantations) and in parts of the tropics where it has been introduced it becomes super-abundant, with negative impacts on native species and human comfort (Clark *et al*., 1982; Wetterer & Porter, 2003). In dry-forest fragments in Colombia there is a negative correlation between *W. auropunctata* abundance and overall ant diversity (Armbrecht & Ulloa Chacón, 2003). Where introduced in New Caledonia it invades dense native forest and displaces native ants (Le Breton *et al*., 2003). Behavioral tests and cuticular hydrocarbon analysis show that *W. auropunctata* is multicolonial in its native range in Brazil, unicolonial where introduced in New Caledonia (Errard *et al*., 2002).

The sting of *Wasmannia* is noteworthy. These are extremely tiny ants, barely visible in the field. When the senior author first began studying ants in Costa Rica, he was at first puzzled about *Wasmannia*. By literature accounts *Wasmannia* was reputed to have a terrible sting, but he had been collecting them for months in Corcovado National Park without ever experiencing the famous sting. One day he was collecting from a populous nest and some workers made it up to the soft skin of his inner forearm and began to sting. The sting was definitely noticeable, about as severe as a fire ant (i.e., *Solenopsis geminata*) but inordinately strong for an ant that could barely be seen! Workers are so small they cannot sting through the thicker skin of the hands.

Surprisingly, the chemical and toxicological nature of the venom of *W. auropunctata* has not been investigated. Howard *et al*. (1982) discovered an alkylpyrazine compound in the mandibular glands, which acted as an attractant to conspecifics and a repellent to heterospecifics. They speculated that the workers might apply the mandibular gland product as an irritating secretion, augmenting the defensive properties of the venomous sting. It would be interesting to investigate whether the venom alone is the powerful agent in this small ant, or if the strong burning sensation is a synergetic effect of venom plus mandibular gland product.

Nests can be almost anywhere: in rolled leaves or dead sticks in the leaf litter, under stones, in rotten wood, in hollow stems suspended above the ground, in ant-plant domatia, and under epiphytes. Workers are omnivorous scavengers and predators and can rapidly recruit to food. Colonies are polygynous and it is never clear where colony boundaries are. Dozens of dealate queens may be found together in nests. Males are rare but do occasionally occur.

Wasmannia iheringi Forel
Fig. 1, Table 1

Wasmannia iheringi Forel, 1908: 359. Syntype worker, queen: **Brazil**, São Paulo (v. Ihering) [MHNG] (*examined*).

Comments

Prior to this report *W. iheringi* was known only from the type specimens. Forel's description and specimen labels indicate the specimens were collected in São Paulo by von Ihering. The types also bear a pencil label with "2265." Luederwaldt (1926) referred to *W. iheringi*, stating "Mr. E. Garbe found in Espirito Santo a small nest, constructed of fine carton ["serragem fina"], on a leaf of *Cecropia*. N. 2.265." Given the match of the collection numbers We assume these represent a single collection. We also presume Luederwaldt's data are more accurate than Forel's. Kempf (1972) lists only the type locality for the range of *W. iheringi*, suggesting it remained known only from the types at the time of his Neotropical catalogue.

Surprisingly, this species has been discovered in Costa Rica, where it inhabits the canopy of lowland rainforest on the Atlantic slope. Morphologically the Costa Rican specimens are identical to the types. It has been collected at La Selva Biological Station, at 500m elevation on the Barva Transect, and at the old Carrillo station at 600m in Braulio Carrillo National Park. The quantitative sampling by the ALAS project shows it to be a moderately abundant component of the arboreal fauna (Table 2).

One nest has been observed, at La Selva Biological Station in Costa Rica. The nest was on the undersurface of a single leaf of a fuzzy-leaved *Guarea* growing along a stream. A 2cm long felt-like carton roof covered a portion of the leaf between two veins. The nest contained 27 adult workers, one dealate queen, four adult males, and brood of various sizes. This observation is similar to Garbe's collection from southeastern Brazil, suggesting a specialized nesting behavior that is the same in both Costa Rica and southeastern Brazil.

On another occasion at La Selva the species was observed in a patch of old second growth forest comprised of medium to large trees over abandoned cacao. A small patch was being felled for an experiment at La Selva and collecting was carried out in these newly-felled trees. A dense aggregation of workers and two dealate queens were found on a branch of a felled *Coussapoa*, suggesting that colonies can be polygynous.

Alate queens were collected at blacklights at La Selva in October 1991.

We have also examined workers in Erwin's fogging samples from Tambopata, Peru. The species is now known from three widely separated localities, but it is unknown whether these are disjunct populations or a result of undersampling in intervening regions.

Wasmannia lutzi Forel
Table 1

Wasmannia lutzi Forel, 1908: 357. Syntype worker, queen, male: **Brazil**, São Paulo (Lutz) [MHNG] (*examined*).

See under *W. affinis*.

Wasmannia rochai Forel
Fig. 1, Table 1

Wasmannia rochai Forel, 1912: 1. Syntype worker: Ceará, **Brazil** (Diaz da Rocha) [MHNG] (*examined*, one worker here designated **LECTOTYPE**).

Comments

Wasmannia rochai occurs widely in the mainland Neotropics, from Guatemala south to São Paulo state in Brazil. The syntype workers from Ceará are slightly larger than workers from Panama and Costa Rica, but with similar proportions. The differences between *rochai* and *sigmoidea* are subtle but consistent. Compared to *sigmoidea*, *rochai* is smaller, with a relatively shorter and broader head. The propodeal spines are shorter and are directed posteriorly, instead of upturned in *sigmoidea*. The setae on the face, mesosoma, and gaster are more curved, appearing shorter than the setae of *sigmoidea* because of the greater curvature. They are also more clavate, swelling noticeably at the tips.

In some specimens of *rochai* the outer margin of the antennal scrobe is weakly defined, approaching the condition seen in *affinis* and *lutzi*. However, the face sculpture of *rochai* is always much more feeble than the coarse reticulate rugose sculpture on *affinis* and *lutzi*.

Kempf (1972) recorded the range of *rochai* as Panama, the Guianas, Trinidad, and six Brazilian states from Ceará south to São Paulo. Given the prior uncertainty of species differences among *affinis, lutzi*, *rochai*, and *sigmoidea*, earlier determinations should be treated cautiously pending reexamination of existing material. We have examined material from Guatemala, Costa Rica, Venezuela, and Brazil (Amazonas, Bahia, Ceará, and São Paulo states).

This species appears to be rare in Costa Rica, although its superficial similarity to *W. auropunctata* may result in its being overlooked in a sea of the latter species. Only two Costa Rican collections are known: Phil Ward collected workers and a dealate queen (PSW#7628) in a recent treefall at Carara Biological Reserve. The senior author collected a lone dealate queen in a canopy tree at Sirena in Corcovado National Park. The species has been collected multiple times on Barro Colorado Island in Panama, where it is a relatively common part of the canopy ant fauna (Mike Kaspari pers. comm.).

Wasmannia scrobifera Kempf
Fig. 1, Table 1

Wasmannia scrobifera Kempf, 1961: 512, figs. 14, 15. Holotype worker: Poeroe man kemisa, **Surinam** (van der Drift).

Comments

Kempf described this species from a single worker. Numerous collections are now known from Costa Rica, and we have also seen material from Colombia and Brazil (Bahia and Matto Grosso states).

In Costa Rica, this species is infrequently encountered. It inhabits mature lowland rainforest in the Atlantic lowlands. It has been collected in Winkler samples of sifted litter from the forest floor at Hitoy Cerere Biological Reserve, Casa Plastico near Rara Avis, the 500m site on the Barva Transect, and La Selva Biological Station. Quantitative sampling by the ALAS project reveals it to be a low density species occurring most often in fogging samples, and less often in Winkler and Berlese samples of forest floor litter (Table 2). Dinah Davidson collected it in a *Piper* plant at La Selva. Mary Cornelius, an OTS student, found a nest in a leaf domatium of an ant-plant (*Tococa*, Melastomataceae) at Tortuguero, but it contained only workers and brood. Grant Gentry found small carton nests under leaves at La Selva (pers. comm.). Workers have been collected from the stomachs of dendrobatid frogs in the Chocó region of Colombia. These results suggest that the species may nest in the low arboreal zone yet forage in the leaf litter on the forest floor.

Wasmannia sigmoidea (Mayr)
Fig. 1, Table 1

Tetramorium sigmoideum Mayr (in Radoszkowsky), 1884: 33. Syntype worker: Cayenne, **French Guiana** (Jelski) [NMW] (*examined*, one worker here designated **LECTOTYPE**). Combination in *Wasmannia* and description of queen and male: Forel, 1893:386.

Comments

Wasmannia sigmoidea is the second oldest name in the genus and to date has been poorly characterized. It has never been satisfactorily differentiated from other species in the genus, particularly *rochai*. Forel (1884) identified material from St. Vincent Island in the Antilles as *W. sigmoidea*, and described the queen and male. We have not been able to examine the workers of this collection, but the queens match queens of *sigmoidea* from Puerto Rico and Costa Rica.

Kempf (1972) gives the range of *sigmoidea* as Guianas, Antilles St. Vincent, Grenada, and Santa Catarina state of Brazil. The Guianas are listed because of the type locality in French Guiana and some Surinam specimens he tentatively identified as *sigmoidea* (Kempf 1961). The St. Vincent record is based on Forel's publication. We do not know the basis of the Grenada record. The Santa Catarina record is based on a published record by Mayr (1887), which is a misidentification of specimens of *affinis* (see under *affinis*). We have examined abundant material from Puerto Rico, multiple collections from Costa Rica, and a collection from Guarico state in Venezuela. Thus the current known range of *sigmoidea* is circumcaribbean.

The few Costa Rican records are as follows. David Olson collected workers during his study of Winkler and pitfall trap sampling methods at La Selva Biological Station (Olson 1991, as *Wasmannia* sp.1). This was the only known collection from La Selva, in spite of intensive inventory effort there (Longino *et al*., 2002), until an August, 2004 collection of workers and alate queens from the rootball of a palm tree in the laboratory clearing. Workers occurred in four different samples from the Project ALAS expeditions to the 500m site on the Barva Transect: two Malaise trap samples, one flight-intercept sample, and one sweep net sample (Table 2). It is likely that *sigmoidea* prefers open and synanthropic habitats, hence its undersampling in Costa Rica, where sampling emphasis has been in forested habitats.

Wasmannia sulcaticeps Emery
Table 1

Wasmannia sulcaticeps Emery, 1894: 195. Holotype worker: **Argentina**, Buenos Aires. Description of queen, male: Forel, 1914: 280.

Wasmannia sulcaticeps var. *weiseri* Forel, 1914: 281. Syntype queen, male: **Argentina**, Cordoba, Canals (Weiser) [MHNG] (*examined*). **NEW SYNONYMY**.

Wasmannia bruchi Santschi, 1919: 43. Syntype worker: **Argentina**, La Plata (Bruch) [NHMB] (*examined*). Junior synonym of *sulcaticeps*: Kusnezov, 1952: 174.

Comments

Wasmannia sulcaticeps and *williamsoni* are two related species that occur at the far southern limit of the genus, in Argentina. They are both distinguished from other members of the genus by the heavy striate sculpture on the face and by the very small propodeal spiracle.

Kusnezov (1952) described the *Wasmannia* fauna of Argentina, and *sulcaticeps* and *williamsoni* were described as having an allopatric distribution. *Wasmannia sulcaticeps* occurred in more humid environments near Buenos Aires and in the northern provinces of Tucumán, Salta, and Jujuy. *Wasmannia williamsoni* occurred in the more arid habitats west of Buenos

Aires. Kusnezov did not mention var. *weiseri*, and its type locality is between the ranges of *sulcaticeps* and *williamsoni* shown on his distribution map. Forel's description of *weiseri* noted only minor differences from *sulcaticeps*.

Wasmannia villosa Emery

Wasmannia villosa Emery, 1894: 196. Holotype queen: **Brazil**, Rio Grande do Sul (v. Ihering).

Comments

Emery described this single queen from Rio Grande do Sul. He distinguished it from other species by the long, abundant, appressed pilosity; robust dentiform propodeal spine; and transverse petiolar node. We have not examined this specimen, but the description sets it apart from any *Wasmannia* queen with which we are familiar. However, its status as a species of *Wasmannia* is not assured. It would not surprise us if it were revealed to be an attine queen or a member of some other myrmicine genus.

Wasmannia williamsoni Kusnezov

Table 1

Wasmannia williamsoni Kusnezov, 1952: 181, figs. 1, 4–7. Syntype worker, queen: **Argentina**, La Pampa, Winifreda, Castex (Kusnezov). [MZSP] (worker examined).

Remarks

Wasmannia williamsoni has the largest workers in the genus, based on the one worker we have examined. It is far larger than any other *Wasmannia* worker we have seen (Table 1). See further information under *sulcaticeps*.

GENERAL DISCUSSION

Kusnezov (1952) observed that *Wasmannia auropunctata* was the dominant *Wasmannia* species in Argentina and that it had the greatest difference between worker size and queen size. The Argentinean species *sulcaticeps* and *williamsoni* were restricted to the subtropical and semiarid limits of the genus, and the queens were much smaller and closer to the workers in size. He suggested that the species such as *sulcaticeps* and *williamsoni* were the more primitive members of the genus, and *auropunctata* was more recent and more advanced. We examined the relationship between worker size and queen size for the eight species of *Wasmannia* for which we had data, and there is a negative relationship (Fig. 3). Species with the smallest workers have the largest queens. The species fall roughly into three groups. *Wasmannia sigmoidea*, *iheringi*, *sulcaticeps*, and *scrobifera* have very small queens, little larger than the workers. *Wasmannia rochai*, *affinis*, and *lutzi* are intermediate, with relatively smaller workers and larger queens. *Wasmannia auropunctata* is at the top, with the smallest workers and largest queens.

These results support Kusnezov's conclusions. A general trend in ant evolution is the development of increasing caste differences, and it follows that a greater difference in size between worker and queen is often apomorphic. If that is the case with *Wasmannia*, then *auropunctata*, *lutzi*, *affinis*, and *rochai* may form a clade within *Wasmannia* based on larger queen size. If increasing caste differentiation is associated with greater ecological success, the ecological dominance of *auropunctata* could be explained by it having the largest queens and smallest workers in the genus.

A case can also be made for *iheringi* being the sister taxon to all other *Wasmannia*. It has the most plesiomorphic mesosoma and petiole shape, resembling other generalized myrmicines. Other *Wasmannia* show a trend toward shorter, more compact mesosoma and shorter petiolar peduncle and/or more quadrate node. A biogeographic scenario would thus have *iheringi* as the oldest lineage in the genus, with disjunct populations at scattered localities over a large area, having been largely displaced from a formerly extensive range. Other rare or localized species in the genus — *sulcaticeps, williamsoni, sigmoidea, scrobifera, affinis, lutzi* — could also be relicts from an early radiation of the genus. *Wasmannia rochai* is the second most common and widespread species. Its small workers and large queens could have been an initial step in the direction of ecological dominance. *Wasmannia auropunctata*, with its even smaller workers and larger queens, is the most recent manifestation of this trend. It has swept the Neotropical field and is now conquering the world.

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Table 1. Measurement data for *Wasmannia* queens and workers. The additional set of measurements for *W. auropunctata* queen head sizes are shown in Fig. 2.

Species	specimen[1]	WL	HW	HL	EL	CI	OI
Queens							
affinis	Brazil (SC), MZSP2594	1.16	0.74	0.72	0.16	1.01	0.22
auropunctata	INBIOCRI002280087	1.13	0.77	0.69	0.22	1.13	0.33
auropunctata	INBIOCRI002280107	1.19	0.80	0.71	0.21	1.13	0.30
auropunctata	holotype *glabra*	-	0.84	0.74	0.26	1.13	0.35
iheringi	INBIOCRI001271987	0.86	0.60	0.61	0.18	0.99	0.29
iheringi	syntype	0.88	0.62	0.63	0.16	0.99	0.26
lutzi	syntype	1.15	0.76	0.69	0.19	1.10	0.27
rochai	LACM ENT 141402	1.08	0.68	0.64	0.22	1.06	0.34
rochai	INBIOCRI002280101	1.08	0.68	0.65	0.20	1.05	0.31
rochai	Brazil (SP), MZSP1843	1.20	0.75	0.70	0.24	1.07	0.34
scrobifera	INBIOCRI002280114	0.67	0.56	0.60	0.17	0.94	0.28
scrobifera	Brazil (BA), ICN	0.70	0.54	0.61	0.16	0.88	0.27
sigmoidea	St. Vincent	0.82	0.61	0.62	0.20	0.97	0.33
sigmoidea	Puerto Rico LACM	0.86	0.58	0.65	0.21	0.89	0.32
sulcaticeps	syntype *weiseri*	0.80	0.59	0.63	0.18	0.93	0.28
Workers							
affinis	holotype	0.58	0.51	0.55	0.11	0.93	0.20
affinis	Brazil (SC), MZSP2594	0.62	0.55	0.61	0.13	0.91	0.21
auropunctata	lectotype *obscura*	0.46	0.42	0.46	0.11	0.92	0.23
auropunctata	syntype *rugosa*	0.48	0.45	0.48	0.10	0.95	0.20
auropunctata	Colombia ICN	0.46	0.42	0.46	0.11	0.92	0.23
iheringi	syntype MHNG	0.65	0.57	0.53	0.11	1.06	0.21
iheringi	syntype MZSP	0.63	0.49	0.56	0.11	0.87	0.20
iheringi	INBIOCRI001271987	0.65	0.52	0.54	0.13	0.97	0.24
lutzi	syntype	0.56	0.49	0.55	0.10	0.89	0.19
rochai	LACM ENT 140078	0.46	0.43	0.45	0.11	0.97	0.24
rochai	LACM ENT 141402	0.45	0.44	0.46	0.10	0.96	0.21
rochai	lectotype	0.54	0.50	0.50	0.11	0.99	0.22
rochai	Brazil (SP), MZSP	0.50	0.47	0.48	0.11	0.97	0.23
scrobifera	INBIOCRI002280114	0.56	0.52	0.52	0.15	0.99	0.29
sigmoidea	LACM ENT 141401	0.56	0.49	0.55	0.14	0.89	0.26
sigmoidea	lectotype	0.58	0.51	0.56	0.14	0.91	0.26
sigmoidea	INB0003235900	0.60	0.52	0.57	0.15	0.90	0.26
sigmoidea	INB0003231652	0.61	0.52	0.58	0.15	0.90	0.26
sulcaticeps	syntype *bruchi*	0.57	0.48	0.55	0.12	0.88	0.22
sulcaticeps	syntype *bruchi*	0.58	0.49	0.57	0.12	0.85	0.21
williamsoni	syntype MSZP	0.71	0.59	0.69	0.15	0.85	0.22

1. Specimen barcodes or type data. Barcoded specimens are all from Costa Rica; additional specimen data available from senior author.

Table 2. Abundance of *Wasmannia* species along an elevational gradient on the Atlantic slope of Costa Rica. Table values are percent of samples in which a species occurred. Details of sampling methods are in Longino *et al*. (2002) and http://viceroy.eeb.uconn.edu/ALAS/ALAS.html.

	No. Samples	*Wasmannia auropunctata*	*Wasmannia iheringi*	*Wasmannia sigmoidea*	*Wasmannia scrobifera*
La Selva					
Baits	40	0%	0%	0%	0%
Berlese	217	11%	0%	0%	<1%
Fogging	52	40%	25%	0%	23%
Malaise	62	11%	15%	0%	3%
Litter nests	222	8%	0%	0%	0%
Winkler	41	83%	2%	0%	7%
500m					
Berlese	94	14%	0%	0%	0%
Fogging[1]	3	0%	0%	0%	0%
Malaise[2]	20	65%	5%	10%	0%
Sweepnet	58	33%	0%	2%	0%
Flt intercept[3]	10	70%	0%	10%	0%
MiniWinkler	250	20%	0%	0%	<1%
1070m					
Berlese	104	0%	0%	0%	0%
Malaise	20	5%	0%	0%	0%
Sweepnet	34	0%	0%	0%	0%
Flt intercept	10	0%	0%	0%	0%
MiniWinkler	150	0%	0%	0%	0%
2000m	Sampling effort similar to 1070m; *Wasmannia* absent				

1. Each fogging sample is one fogged tree with 40 1m^2 funnels.
2. Each sample is 10-week catch of one Malaise trap.
3. Each sample is 6-weeks catch of one flight-intercept trap.

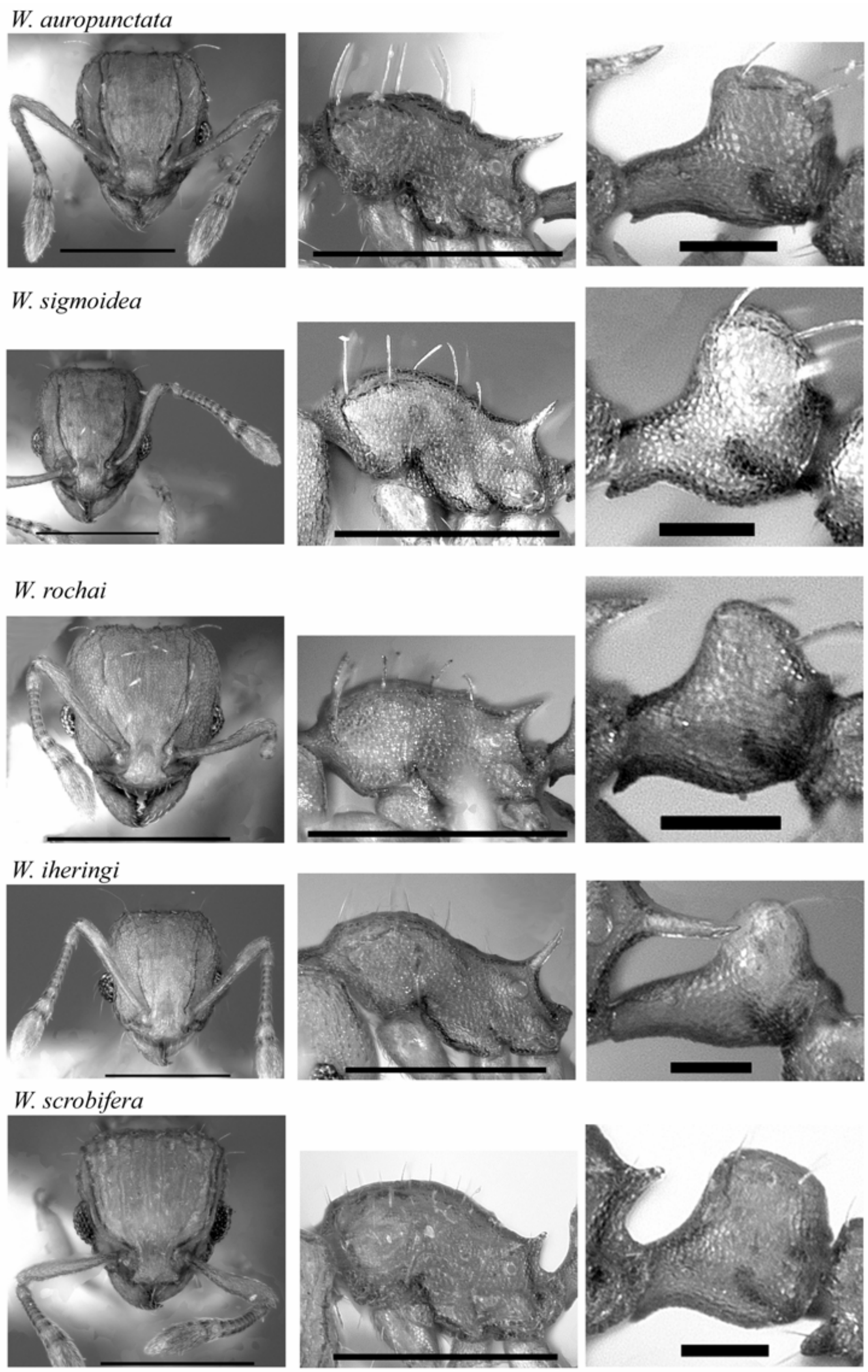

Figure 1. The five most widely distributed *Wasmannia* species. Views from left to right are face, lateral mesosoma, and lateral petiole. Scale bars in face and mesosoma views are 0.5 mm, in petiole views 0.1 mm.

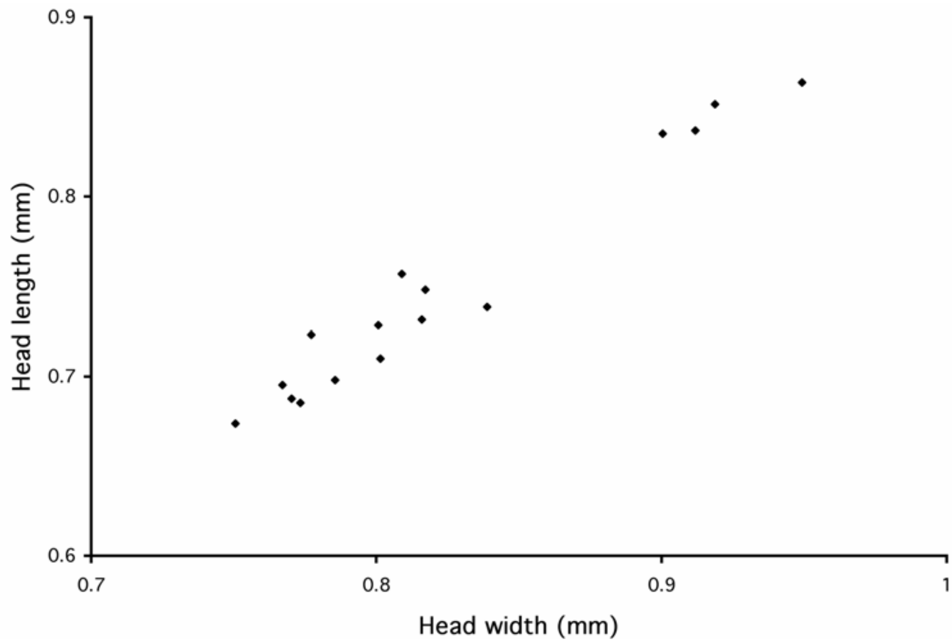

Figure 2. Queens of *Wasmannia auropunctata* occur in two size classes. In cluster of queens with smaller head size, one is from Jamaica and one from Venezuela. All others (n=14) are from Costa Rica.

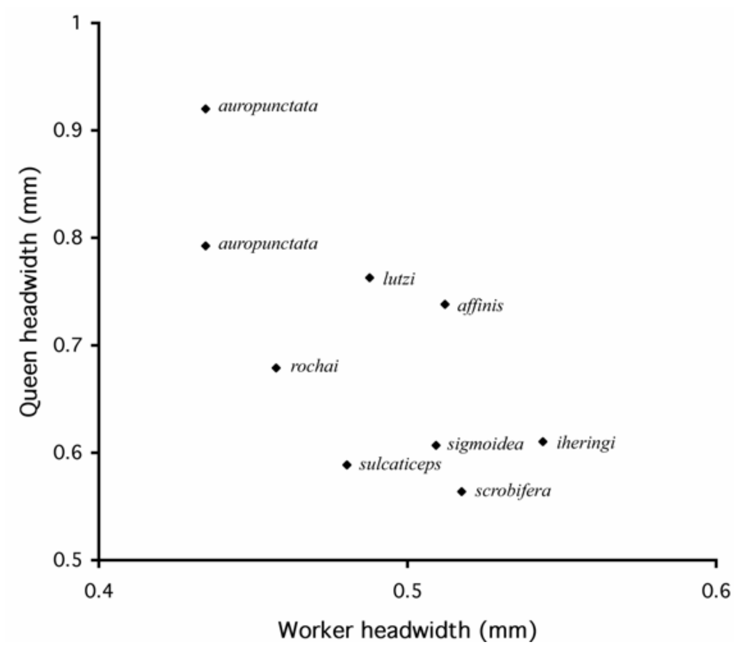

Figure 3. Relationship of queen head width to worker head width among *Wasmannia* species. Average values are shown, based on data in Table 1 and Figure 2. *Wasmannia auropunctata* is plotted twice, with different values for the dimorphic queens. A regression of queen head width on worker head width has a negative slope, r^2=0.50, p<0.05 (removing the large-headed *W. auropunctata* queens renders the regression nonsignificant).