

A revision of the *phalangium* species complex of the ant genus *Aphaenogaster* (Hymenoptera: Formicidae: Myrmicinae)

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ABSTRACT

Discriminate analysis and canonical correlation analysis were used to separate the *Aphaenogaster phalangium* species complex into 5 species of tropical New World ants: *A. araneoides* Emery, *A. brevicollis* Forel, *A. inermis* Forel (= *Aphaenogaster araneoides* var. *nitidiventris* **new synonymy**), *Aphaenogaster* (*Deromyrma*) *araneoides* var. *canalis* **new synonymy**, *A. mexicana* (Pergande) and *A. phalangium* Emery. This complex is easily recognized as a long necked group of *Aphaenogaster* found primarily in tropical forests. *Aphaenogaster araneoides*, distributed from El Salvador to Panama, can be recognized by the relatively elongated neck, lack of erect hairs on the dorsum of the posterior femur, and in that the sculpture of the head is similar to that of the dorsum of the first tergum of the gaster. *Aphaenogaster brevicollis*, known only from northern Panamá, is a robust, relatively large species with a short neck. *Aphaenogaster inermis* is a smaller species found from Nicaragua south into Colombia, with numerous semierect hairs on the dorsum of the hind femur, the only species with this characteristic. *Aphaenogaster mexicana* is known only from central western México, and is a weakly sculptured species with a small eye and moderately developed propodeal spines. Finally, *A. phalangium* is similar to *A. araneoides*, except that the dorsum of the first gastral tergum is finely sculptured, much more weakly than the sculpture of the dorsum of the head, and is known from El Salvador to NW Colombia. The workers and males are separated by keys in English and Spanish, the characteristics and distributions of each species are discussed.

Key words: Neotropics, North America, New World, ants, Formicidae, *Aphaenogaster*, canonical correlation analysis, discriminant analysis

RESUMEN

Análisis discriminatorio y análisis canónico de correlación fueron usados para separar las cinco especies del complejo *phalangium* del género *Aphaenogaster*, hormigas tropicales de México al sur hasta Colombia, incluyendo: *A. araneoides* Emery, *A. brevicollis* Forel, *A. inermis* Forel, *A. mexicana* (Pergande) y *A. phalangium* Emery. Es un complejo fácil de reconocer por la forma del cuello, que es alargado y delgado. *Aphaenogaster araneoides*, conocida desde El Salvador hasta Panamá, puede identificarse por el cuello muy alargado, carencia de pelos rectos y subrectos en la superficie dorsal del fémur posterior y la escultura en la superficie del gáster, que es semejante a la escultura del dorso de la cabeza. *Aphaenogaster brevicollis* del norte de Panamá, es robusta y grande con un cuello relativamente corto. *Aphaenogaster inermis* es una especie pequeña de Nicaragua hasta NW de Colombia, que tiene muchos pelos rectos y subrectos en el dorso del fémur posterior, siendo la única especie con esta característica. *Aphaenogaster mexicana* es la única especie del complejo conocida de México (Nayarit y Jalisco) y tiene poca escultura en el cuerpo, ojos pequeños y espinas propodeales moderadamente desarrolladas. *Aphaenogaster phalangium* es similar a *A. araneoides*, con la excepción de que el dorso del primer tergo del gáster tiene poca escultura, mucho menos que la escultura del dorso de la cabeza; se conoce de El Salvador hasta Colombia. Incluimos claves para la identificación de las obreras y machos (en español), características de las especies y sus distribuciones.

Palabras claves: Neotrópicos, Norte América, Nuevo Mundo, hormigas, Formicidae, *Aphaenogaster*, análisis de correlación canónica, análisis discriminante

INTRODUCTION

The *phalangium* species complex of the genus *Aphaenogaster* consists of a group of Neotropical ants in which the neck is elongated. This complex contains some of the most spectacular ants in the genus, graceful elongate ants with long legs. These characters make them easily recognized, but unfortunately differentiating the species is difficult. They are tropical ants, occurring from México south to Colombia. Although this complex is considered to form a lineage (Longino and Cover, 2004), it may be related to several Old World species in which the neck is also elongated. The workers and males are most often collected, with generally a single ergatoid queen in each nest (Longino and Cover, 2004). Therefore we limit our diagnoses to workers and males.

Longino and Cover (2004) provided a well-developed hypothesis of species boundaries with a revision of the group, and reduced the 6 taxa to two: *A. araneoides* and *A. phalangium*. Unfortunately we do not agree with their synthesis, based on a number of points. First the lectotype of *A. phalangium* does not fit their (2004) characterization of the species. The lectotype lacks the erect hairs on all surfaces of the posterior femur and would therefore easily key to *A. araneoides* in their key. It actually has about 12 erect hairs on the left posterior femur, all restricted to the ventral surface. This is actually fewer than the number of similar hairs on the lectotype of *A. araneoides*, which has 13 hairs. The actual number of hairs is not important as they would be variable in number and could be broken. *Aphaenogaster phalangium* is apparently a valid species that they actually confused with *A. araneoides*. *Aphaenogaster phalangium* can be separated from the similar *A. araneoides* by the rougher sculpturing on the dorsum of the head, and in usually having the first gastral tergite at least partially smooth and glossy (usually completely punctate and dull in *A. araneoides*).

Second, their concept of *A. phalangium* actually corresponds to the lectotype of *A. inermis*, the only species that has abundant hairs on the entire surface of the femora.

Third, they did not include one of the species in the complex, *A. mexicana* in their analysis.

Finally, we consider *A. brevicollis* to be a valid species, differing from the other three species in being more robust and in having a shorter neck.

The males of the *phalangium* species complex are easy to recognize by the elongated neck and with the dorsal surface of the propodeum strongly depressed, making the propodeum very narrow as seen in side view (this latter character is found in all of the known males of the New World *Aphaenogaster*). These characteristics would allow them to be separated from all the other genera in the tropics.

Novomessor has recently been reestablished as a genus separate from *Aphaenogaster* (Demarco and Cognato, 2015). We include *Novomessor ensifera* in our comparisons as it has an elongated neck similar to the species of the *phalangium* species complex, is a Mexican species and could be confused with the species discussed in this paper. The minors of some species of *Pheidole* have elongated necks similar to ants of this group, thus the genus is included in the key to the workers for the sake of clarity and to avoid confusion.

We provide a new synthesis of the complex, and consider it to contain five valid species.

METHODS AND MATERIALS

Specimens of all of the species were collected in México, Central America and Colombia. Notes were made on the natural history and habitats of the species. Types of all five species were examined from the following museums, courtesy of the listed curators:

CWEM Collection of William and Emma Mackay,
University of Texas, El Paso
ICN Instituto de Ciencias Naturales, Universidad
Nacional de Colombia, Bogotá, F.
Fernández
MIFA Museo de Insectos, Facultad de Agronomía,
Universidad Nacional de Colombia, F. Serna
MCSN Museo Civico di Storia Naturale, Roberto
Poggi and Fabio Penati
MCZC Museum of Comparative Zoology, Harvard
University, Stefan Cover
MHNG Muséum d'Histoire naturelle, Genève,
Bernhard Merz

USNM United States National Museum, Ted
Schultz

The characteristics of the species were analyzed using discriminant analysis and canonical correlation analysis (SYSTAT version 12). Discriminant analysis allows the character states to be reduced to only those that have a significant effect in separating the taxa and canonical correlation analysis allows for visual separation of the taxa based on all of the useful character states. It also allows the plotting of 95% confidence intervals. Character states were limited in number by the few differences that exist in the species, were limited to continuously distributed variables and were based partially on characters which have been used in the past.

Triangle plots were used to show the relationships between the 5 species, based on the six characters used in the analysis.

Lectotypes and paralectotypes were designated in order to stabilize the identity of the species.

RESULTS

Five species are recognized in the New World; the workers and males can be separated with the following keys:

Key to the *phalangium* species complex, based on workers

- 1 Propodeal spines well developed, elongated, much longer than distance between bases; notopropodeal suture very poorly developed; México *Novomessor ensifera* (Forel)
 - Propodeal spines nearly always poorly developed or absent (Fig. 2); notopropodeal suture well developed. 2
- 2(1) Side and top of pronotum mostly smooth and glossy; propodeal tubercles or spines developed (Fig. 8); widely distributed. 3
 - Side and top of pronotum nearly completely sculptured; propodeal tubercles nearly always absent, but usually represented by swollen regions (Fig. 4); Central America south to Colombia 4
- 3(2) Relatively large (total length 6 mm); propodeal spines (Fig. 8) small (length about ½ or less distance between bases); mesonotum without transverse flange; central western México *mexicana* (Pergande)
 - Relatively small (total length 3.5 mm); propodeal spines slender and greatly elongated (length 3 X width at base); mesonotum with transverse flange; Neotropical minors of some species of *Pheidole*
- 4(2) All surfaces of posterior femur, including dorsal surface, covered with suberect and/or erect, bristly hairs (Fig. 6); Nicaragua to Colombia *inermis* Forel
 - Erect hairs on posterior femur, if present, restricted to ventral surface (Fig. 10) 5
- 5(4) Neck of posterior part of head relatively short, about twice as wide as long, head abruptly narrowing posteriorly (Fig. 3); head width greater than 1.4 mm (at posterior edge of eye); uncommon, northern Panamá. *brevicollis* Forel
 - Neck longer, at least as long as broad, head gradually narrowing posteriorly (Figs. 1, 5, 7 and 9); head width less than 1.2 mm (at posterior edge of eye); common. 6
- 6(5) Region of head posterior to eye level densely and relatively finely punctate, transverse striae, if present, mostly restricted to sides of neck, or pass over dorsum of neck near apex of neck, sculpture of head similar to sculpture on dorsum of first gastral tergite, nearly always densely punctate; El Salvador south to Panamá *araneoides* Emery
 - Region of head posterior to eye level granulated and roughly sculptured, dull, transversely and longitudinally reticulated, striae usually pass across dorsum of neck, neck may be polished near apex; first gastral tergite nearly always partially to completely smooth and glossy, sculpture on gaster much finer than that on head; Guatemala south Colombia. *phalangium* Emery

Key to the *phalangium* species complex, based on males (the male of *A. mexicana* is unknown)

- 1 Posterior femur with suberect hairs on dorsal surface, in addition to ventral surface (Fig. 16); Nicaragua to Colombia. ***inermis* Forel**
- Posterior femur without erect hairs or present only on ventral surface, dorsal surface usually with few appressed hairs (Fig. 14) **2**
- 2(1)** Roughly sculptured, specifically most of dorsum of head and scutum granulated; mesopleuron (episternum) with few erect or suberect hairs (Fig. 14); rarely collected, northern Panamá. ***brevicollis* Forel**
- Finely sculptured, head and scutum densely punctate; mesopleuron without erect or suberect hairs (Fig. 18); common. **3**
- 3(2)** Third antennal segment nearly twice length of fourth (Fig. 17); side of petiole and postpetiole partially smooth and shining; Guatemala to Colombia ***phalangium* Emery**
- Third antennal segment only slightly longer than fourth (Fig. 11); side of petiole and postpetiole finely punctate and dull; Guatemala to Panamá. ***araneoides* Emery**

Clave para la identificación de las obreras del complejo de *phalangium*

- 1** Espinas propodeales bien desarrolladas, mucho más largas que la distancia entre las bases; sutura notopropodeal poco desarrollada; México *Novomessor ensifera* (Forel)
- Espinas propodeales no desarrolladas o poco desarrolladas (Fig. 2); sutura notopropodeal bien desarrollada; México, América Central y Colombia **2**
- 2(1)** Lado y dorso del pronoto predominante liso y brillante; espinas propodeales presentes (Fig. 8); América Latina **3**
- Lado y dorso del pronoto casi complemente esculturados; espinas propodeales casi siempre ausentes, pero tubérculos pequeños pueden estar presentes (Fig. 4); América Central hasta

Colombia (no reportada para México) **4**

- 3(2)** Relativamente grande (largo total 6 mm); espinas propodeales (Fig. 8) pequeñas (largura ½ distancia que separa las bases); mesonoto sin repisa transversal; reportada solamente de centro-oeste de México (Nayarit y Jalisco) ***mexicana* (Pergande)**
- Relativamente pequeña (largo total 3.5 mm); espinas propodeales muy largas (largura tres veces la distancia que separa las bases); mesonoto con repisa transversal; América Latina algunas especies de *Pheidole*
- 4(2)** Toda la superficie del fémur posterior cubierta con pelos rectos (Fig. 6); Nicaragua hasta Colombia ***inermis* Forel**
- Pelos rectos, si presentes, restringidos a la superficie ventral del fémur posterior (Fig. 10) **5**
- 5(4)** Cuello en la parte posterior de la cabeza relativamente corto, aproximadamente dos veces más ancho que largo, cabeza abruptamente angosta posteriormente (Fig. 3); anchura de la cabeza (al extremo posterior del ojo) más de 1,4 mm; no común, norte de Panamá ***brevicollis* Forel**
- Cuello más largo, por lo menos más largo que ancho, cabeza gradualmente angosta posteriormente (Fig. 5); ancho de la cabeza menos que 1,2 mm; común. **6**
- 6(5)** Parte de la cabeza posterior del ojo punteada densamente pero finamente, estrias transversas, si presentes, restringidas casi siempre a los lados del cuello, o pasando por encima de la nuca cerca al ápice del cuello, escultura de la cabeza semejante a la escultura en el dorso del primer tergo del gáster, casi siempre punteado fuertemente; El Salvador al sur hasta Panamá ***araneoides* Emery**
- Parte posterior del ojo granulada y esculturada fuertemente, opaca, reticulada transversalmente y longitudinalmente, estrias usualmente pasan por encima del cuello, el cual puede ser liso cerca del ápice; primer tergo del gáster casi siempre parcialmente liso y brillante, escultura

del gáster mucha más fina que la escultura de la cabeza; Guatemala al sur hasta Colombia
 *phalangium* Emery

Clave para la identificación de los machos del complejo de *phalangium* (Se desconoce el macho de *A. mexicana*)

- 1 Fémur posterior muchas veces con pelos rectos en la superficie dorsal, y con pelos en la superficie ventral (Fig. 16); Nicaragua hasta Colombia *inermis* Forel
- Fémur posterior sin pelos rectos o con pelos rectos solamente en la superficie ventral (Fig. 14). 2
- 2(1) Escultura fuerte, específicamente en mucho del dorso de la cabeza y escudo granulado; mesopleura (epiesterno) con pocos pelos rectos y subrectos (Fig. 14); no común, del norte de Panamá *brevicollis* Forel
- Con escultura más fina, cabeza y escudo punteados densamente; mesopleura sin pelos rectos ni subrectos (Fig. 18); común 3
- 3(2) Tercer segmento de la antena casi dos veces más largo que el cuarto segmento (Fig. 17); lado del pecíolo y postpecíolo parcialmente lisos y brillantes, Guatemala hasta Colombia *phalangium* Emery
- Tercer segmento de la antena un poquito más largo que el cuarto segmento (Fig. 11); lado del pecíolo y postpecíolo opaco y esculturado; Guatemala hasta Panamá . . . *araneoides* Emery

LIST OF SPECIES

***Aphaenogaster araneoides* Emery**
 Figs. 1, 2, 11, 12; Plate 3; Plate 7 A

Aphaenogaster araneoides Emery, 1890:48, plate 5, Fig. f8, worker, Costa Rica: Alajuela [Longino and Cover, 2004 state true type locality Jiménez]; Borgmeier, 1949: 206 male; also described as new by Emery, 1894:54; *Aphaenogaster (Ischnomyrmex) araneoides*: Forel, 1899:60; *Stenammina araneoides*: Forel, 1907:4; *Aphaenogaster (Deromyrma) araneoides*: Emery, 1915:71

Worker Diagnosis — The worker of *Aphaenogaster araneoides* is easily recognized, as the posterior part of the head is narrowed into a slender, constricted neck. The head is mostly punctate, with a few scattered striae, with distinct striae on the anterior clypeal margin, the mesonotum is raised into a bump, and the metanotal suture is depressed below the level of the remainder of the mesosoma. The region between the two faces of the propodeum is completely rounded, without any evidence of tubercles or spines. The first tergum of the gaster is generally completely punctate, and is usually only weakly shining. The sculpturing of the gaster is variable (Longino and Cover, 2004).

Female Diagnosis — Longino and Cover (2004) briefly characterize the wingless ergatoid female. Winged “normal” females apparently do not exist (McGlynn et al., 2002).

Male Diagnosis — The mandible of *Aphaenogaster araneoides* has 11-12 well developed teeth, decreasing in size from the apex. The eyes are very large, occupying most of the sides of the head; the ocelli are also very large (0.18 mm maximum diameter) and are separated by less than one minimum diameter. The neck of the head is well narrowed, developed as in the worker. The mesosoma has the same shape as in the males of the other species in this complex, with a narrow propodeum and without propodeal angles or processes. All surfaces except for the gaster are dull and finely punctate, and the side of the mesosoma is also covered with poorly defined striae. The gaster is smooth and glossy. The entire ant is ferrugineous red.

Comparison — The worker of *A. araneoides* is very similar to that of *A. phalangium*, but can usually be separated as the first tergum of the gaster is punctate, not mostly smooth and glossy as in *A. phalangium*. Additionally, the punctate head would separate it from *A. phalangium*, in which the head is mostly covered with striae and granulated sculpture. The neck is more constricted and narrowed than that of *A. brevicollis*.

It can be separated from the Mexican *Novomessor ensifera*, in which the neck is also narrowed, by the well-marked notopropodeal suture, and the lack of propodeal spines (which are well-

developed in *N. ensifera*).

The male is nearly identical to that of *A. phalangium*, but can be separated by the form of the antenna: the third segment of the antenna is only slightly longer than the fourth segment. In *A. phalangium* the third segment is twice as long as the fourth segment. The male differs from that of *A. inermis* in that it lacks suberect hairs on the dorsal surface of the posterior femur (appressed hairs are present, which are present) in the male of *A. inermis*. The femur also seems to be somewhat more swollen than the femur of *A. inermis* males, at least based on the limited material available.

Material examined — **EL SALVADOR**: 2 - 4 k S Quezaltepeque. **HONDURAS**: **Cortes**, Lago Yojoa. **NICARAGUA**: **San Juan**, San Juan & Sarapiquí Rivers (10°42'N 58°W). **COSTA RICA** **Alajuela**: Río Peñas Blancas; **Cartago**: Turrialba, vicinity of Guápiles; **Heredia**: La Selva, 6 k W Puerto Viejo; **Limón**, Bataan; **Puntarenas**, Fila Cruces, Monteverde, 6 k S Monteverde, Corcovado National Park. **PANAMÁ**: **Panamá**: Canal Zone, Fort Sherman; **Bocas del Toro**.

Type series — Lectotype worker (seen, designated by Longino).

Habitat — Lowland rain forest, up into tropical wet, montane forest.

Biology — *Aphaenogaster araneoides* nests in and under logs in tropical rain forests. One nest was collected in a twig. Brood were present in nests in July and August. They are apparently carnivores, as foragers were collected in traps baited with Vienna sausages, fish, chicken parts, and feeding on a dead snake. Workers were collected loose on the soil surface and on tropical vegetation, and in leaf litter extraction samples.

***Aphaenogaster brevicollis* Forel, New status**
Figs. 3, 4, 13, 14; Plate 7 B

Aphaenogaster (Ischnomyrmex) phalangium var. *brevicollis* Forel, 1899:59 worker, male, Panamá, Volcán de Chiriquí; *Aphaenogaster (Deromyrma) brevicollis*: Emery, 1921:65 (synonymized with *Aphaenogaster araneoides* by Longino and Cover, 2004:9)

Worker Diagnosis — The worker is a robust

specimen as compared with other species in the complex. The entire dorsum of the head is covered with granulated sculpture, which forms poorly defined longitudinal striae; the sculpture of the mesosoma is similar, and the propodeal spines are not developed. The sculpture of the petiole is similar to that of the mesosoma, the postpetiole and most of the first tergum of the gaster are primarily punctate. Short (0.15 mm) erect blunt-tipped hairs cover most surfaces except for the tibiae and tarsi.

Male Diagnosis — The male is an intermediate sized (total length 6 mm) ferruginous red specimen with large eyes and the greatly elongated neck. The propodeum is very narrow and is armed only with a pair of swellings. The posterior femur has a few erect hairs on the ventral surface, but none on the sides nor on the dorsal surface (a few appressed hairs are present). The mesopleuron has a few erect hairs. All surfaces, except for the legs and gaster, are sculptured. The mandibles are finely striate and moderately shining, the head, propodeum, petiole and postpetiole are covered in fine granulated or punctate sculpture, with a few poorly defined striae between the eyes, on the side of the mesosoma and side of the propodeum.

Comparison — The workers of this species could be confused with those of *A. phalangium*. Both species are roughly sculptured and have short erect blunt-tipped hairs covering most surfaces. The two species can be separated, as *A. brevicollis* has a wider head (> 1.4 mm at posterior edge of the eye) as compared to *A. phalangium* (less than 1.2 mm at the same position). Additionally, *A. brevicollis* is known only from northern Panamá, whereas *A. phalangium* is widely distributed in Central America. The same characteristics would separate *A. brevicollis* from *A. araneoides*. *Aphaenogaster brevicollis* does not have the erect hairs on all surfaces of the posterior femur as does *A. inermis* and is not partially smooth and shiny as is *A. mexicana*.

Longino and Cover (2004) considered *A. brevicollis* to bridge the gap between *A. araneoides* and *A. phalangium* (as *A. inermis*). It actually appears to us to be distinct robust species with a wide head and a relatively short neck, not similar to either one of them.

Material examined — **PANAMÁ**: **Chiriquí**, La

Fortuna, Finca La Suisse, Palmira Arriba (Boquete), Cerro Enjalme (Los Planes Fortuna).

Type series — Lectotype worker, 1 paralectotype worker, 1 paralectotype male (here designated, MHNG).

Habitat — Oak and bamboo forest at 1200m.

Biology — Unknown except workers have been collected from the extraction of leaf litter in June.

***Aphaenogaster inermis* Forel, New status**

Figs. 5. 6. 15, 16; Plate 4; Plate 7 C

Aphaenogaster (Ischnomyrmex) araneoides var. *inermis* Forel, 1899:60, worker, male, Costa Rica, Panamá: Bugaba; *Aphaenogaster (Deromyrma) araneoides inermis*: Wheeler and Wheeler, 1953:64, larva; *Aphaenogaster (Deromyrma) araneoides* var. *inermis*: Kempf, 1972:23 (synonymized with *Aphaenogaster phalangium* by Longino and Cover, 2004:10)

Aphaenogaster araneoides var. *nitidiventris* Forel, 1912:15, worker, male Costa Rica?: Cañas Gordas (synonymized with *Aphaenogaster phalangium* by Longino and Cover, 2004:10) **new synonym**

Aphaenogaster (Deromyrma) araneoides var. *canalis* J. Enzmann, 1947:149, plate 8 worker, Panamá, (synonymized with *Aphaenogaster phalangium* by Longino and Cover, 2004:10) **new synonym**

Worker Diagnosis — *Aphaenogaster inermis* workers are elongate, delicate ants. Most surfaces are covered by short (0.1 mm in length) blunt-tipped hairs. The distinguishing characteristic is that all surfaces of the posterior femur are covered with similar suberect hairs (the other femora have similar hairs). The sculpture on the head is relatively fine and consists mostly of punctures, the mesosoma has punctures, together with mostly longitudinal poorly defined striae and the petiole, postpetiole, and gaster are entirely sculptured and dull (type series, most specimens from Costa Rica south) or the gaster may be smooth and glossy (especially specimens from Nicaragua). The specimens from Colombia are especially strongly sculptured. Most hairs on the scapes of the members of the type series are appressed, but other specimens may have semierect

hairs. Longino and Cover (2004:9) state that two workers in the MCZC labeled *A. phalangium* are thought to be part of the type series; they are mislabeled and are actually *A. inermis*, as they have pilose femora.

Female Diagnosis — Unknown.

Male Diagnosis — *Aphaenogaster inermis* specimens are moderate in size (total length 6 mm) and reddish brown specimens. The neck is greatly elongated and slender as in the worker. The eye is large and covers nearly ½ of the side of the head; the ocelli are large and closely spaced (maximum diameter 0.1 mm, distances between ocelli slightly less than 0.1 mm). The propodeum lacks spines or bumps, but is slightly swollen at the location of the normal position of spines.

The head is mostly finely, but densely punctate, the neck region has a few transverse striae. The scutum and scutellum are roughly sculptured and granulate, the side of the mesosoma has poorly defined, mostly horizontal striae. The petiole and postpetiole are mostly finely punctate and weakly shining, at least dorsally. The first tergum of the gaster is coriaceous and somewhat smooth and shining, less sculptured than the head.

Both the dorsal and ventral surfaces of the head have scattered, relatively long (up to 0.25 mm in length) erect hairs, as does the mesosoma, the petiole, postpetiole and gaster and all of the femora have a few erect hairs, those on the posterior femur are more abundant and about 0.1 mm in length, many of the hairs are suberect.

Comparison — The workers and males of this species could be confused with those of *A. araneoides*, but differ in that the posterior femur has erect and suberect hairs on all surfaces. This characteristic would separate *A. inermis* from all of the others in the *phalangium* species complex.

The male seems to have a narrower posterior femur than that of *A. araneoides*, based on the limited material available, and also has suberect hairs on the femur, which are lacking in *A. araneoides*.

Material examined — **NICARAGUA: Río San Juan**, 5.1 mi SE El Castillo. **COSTA RICA: Guanacaste**, Maritza Field Station (875m). **PANAMÁ: Panamá**, Barro Colorado Island, **Chiriquí**, Monte Verde, Gariché, Potrerillos

Arriba. **COLOMBIA:** Chocó, Quibdó, Tutunendo (5°41'16"N, 76°39'56"W), 48 m, 18-xi-2001, J. Neita (5 workers Facultad de Agronomía, Universidad Nacional de Colombia), Tadó, Corregimiento de Salero (5°16'10"N, 76°33'10"W), 90m, 9-v-2002, J. Neita.

Type series — Lectotype worker and 5 paralectotype workers, 2 paralectotype males (here designated, MHNG)

Habitat — *Aphaenogaster inermis* is found in tropical rain forests, dry tropical forests, open areas in rain forests, and in transitional dry montane forests.

Biology — *Aphaenogaster inermis* nests in and under logs, and are not aggressive and escape when the nest is disturbed. Brood were present in a nest in July (Nicaragua). Workers forage into the litter and can be collected from litter extractions and with pitfall traps. The often have the nest in the forest and forage out into open areas.

***Aphaenogaster mexicana* (Pergande)**

Figs. 7, 8; Plate 5; Plate 7 D

Ischnomyrmex mexicanus Pergande, 1896:893-894, MEXICO: Tepic

Worker Diagnosis — The worker is a small (total length 6 mm), ferruginous red specimen, with a slightly darker postpetiole and gaster. The antennal scape extends well past the posterior border of the head, which is developed into a slender neck, with a flanged posterior border. The head is finely granulated and partially smooth and glossy, the pronotum is mostly smooth and glossy, and the mesopleuron and the side of the propodeum are sculptured with punctures, which are located in rows, forming poorly developed striae. The propodeal spines are weakly developed.

Female and male — Unknown.

Comparison — The workers of *A. mexicana* can be separated with most of the other Mexican species in the genus by the slender elongated neck. It could be confused with the other Mexican species with an elongated neck: *Novomessor ensifera*, but is easily separated as it has short propodeal spines (elongated in *N. ensifera*). *Aphaenogaster araneoides* is similar and is the same size, but is

not found in México, and completely lacks angles on the propodeum. Additionally the sculpturing of the pronotum of these two species, as well as the remainder of the species in the *phalangium* species complex, is rough, not smooth and glossy as in *A. mexicana*. The petiolar node is higher and more developed than it is in the remainder of the species in the *phalangium* species complex, similar to most of the other North American species.

A specimen (# 985) collected by Margarita Villapalacio is nearly identical to the lectotype, and will be deposited in the MCZC. It differs in being slightly larger and darker.

A third specimen (# 673, CWEM) from Margarita is larger, darker, and more sculptured (pronotum is punctate and weakly shining) and the propodeal spines are simply angles. The head is finely granulated, and partially smooth and glossy, and the mesopleuron and side of the propodeum are sculptured with punctures, which are outlined in rows, forming poorly defined striae. It may not be conspecific.

Distribution — States of Nayarit and Jalisco, México. We were unable to find additional specimens at the type locality, despite considerable effort. We have not collected it in other localities, despite making more than 30 major expeditions to all of the Mexican states.

Material examined — **MEXICO:** Jalisco, Ayutla, Sierra de Cacoma, 19°52'22"N 104°29'01.59"W, 1782m, 16-xi-2008, M. Villapalacio # 673, Sierra de Quila, Rancho Viejo, 20°15'24"N, 104°06'10.8"W, 1468m, 11-vii-2009, M. Villapalacio # 985.

Type series — Lectotype worker (CASC) [seen as photograph, see Plate 5], paralectotype worker (USNM #'s 53997 & 55164) [here designated].

Habitat — The region around Tepic is extensively disturbed, but would have had vegetation in the 1890's.

Biology — Unknown. Worker 985 was under litter.

***Aphaenogaster phalangium* Emery**

Figs. 9, 10, 17, 18; Plate 6; Plate 7 E

Aphaenogaster phalangium Emery, 1890:47, plate 5, figs. 6 and 7, worker, male, Costa Rica:

Alajuela (Longino and Cover, 2004): Emery, 1894:54; *Aphaenogaster* (*Ischnomyrmex*) *phalangium*: Forel, 1899:59; *Aphaenogaster* (*Deromyrma*) *phalangium*: Emery, 1915:71 *Aphaenogaster araneoides* var. *inermis* Forel, 1899:60 (synonymized by Longino and Cover, 2004:10, here considered as valid species)

Worker Diagnosis — The worker of this species is easily recognized by the narrowed neck at the posterior margin of the head. The head is mostly covered with coarsely granulated striae, with the striae near the posterior border of the head being mostly transverse across the dorsum of the neck. The mesosoma is mostly covered with similar striae, and the mesonotum forms a bump (seen best in profile). The region between the two faces of the propodeum is formed into poorly defined bumps. The dorsum of the first tergum is nearly always completely smooth and glossy.

Female Diagnosis — Unknown.

Male Diagnosis — The male has the elongated neck and depressed propodeum, characteristics of the males of the *phalangium* species complex. The lack of erect hairs on the upper surface of the femur would separate it from the male of *A. inermis*, and the lack of erect hairs on the mesopleuron would separate it from *A. brevicollis*. It is difficult to separate the male from that of *A. araneoides*, but the funiculi of the specimens available suggest that the second segment (third antennal segment) of *A. phalangium* is approximately twice as long as the third segment, not only slightly longer than the third, as in males of *A. araneoides*.

Comparison — The entire dorsum of the head of the worker of *A. phalangium* is covered with striae (punctures in *A. araneoides*), and the first tergum is nearly always smooth and glossy, not normally punctate as in *A. araneoides*.

It can be easily separated from the Mexican *Novomessor ensifera*, in which the neck is also narrowed, as it lacks propodeal spines and with the notopropodeal suture well marked.

Material examined — **GUATEMALA:** Izabal, Parque Arqueológico Quiriguá). **HONDURAS** (Kempf, 1972). **COSTA RICA:** Puntarenas: San José (Cerrado Helado). **PANAMA:** Panamá, Barro Colorado, Darién (Longino and Cover, 2004).

COLOMBIA: Chocó, Quibdó (ICN).

Type series — Lectotype worker (seen, designated by Longino).

Habitat — Oak and bamboo forest, tropical rain forest.

Biology — Specimens were collected in leaf litter extractions.

DISCUSSION

Morphological characters (Tables 1 and 2) and discriminant analysis and canonical correlation analysis (Fig. 19) indicate there are five species in this complex. Only one of the characters used in the analysis did not significantly discriminate among the species: eye length (Table 2). When plots are done of the 4 factors generated by canonical correlation analysis (Fig. 19) it is clear that in most cases the species are separated and there is little or no overlap in the 95% confidence intervals, further supporting the conclusion that 5 species are involved. *Aphaenogaster brevicollis* and *A. mexicana* are well separated from all of the others (Fig. 19). *Aphaenogaster araneoides*, *A. inermis* and *A. phalangium* are usually separated from the others, although there is some overlap with some of the factors (Fig. 19). The canonical correlation analysis indicates there are 5 different species.

Aphaenogaster phalangium can be seen to have shorter scapes among the species (only *A. brevicollis* has shorter scapes) and *A. araneoides* the longest (Table 1, Figure 20). Head width also separates the species, with *A. brevicollis* having a wider head than the other species (Table 1, Fig. 20). The long erect hairs on the dorsum of the posterior femur separates *A. inermis* from all of the others (Table 1, Fig. 21). The relatively long propodeal spines separates *A. mexicana* from the remainder of the species (Table 1, Fig. 21).

Longino and Cover (2004) reduced six taxa to two species, and predicted that a “splitter” could generate at least ten taxa. So how did we arrive at five species? First we included *A. mexicana* in the complex, which is very similar to the other species and obviously belongs there. Second, we conclude that *A. brevicollis*, with robust workers, wide heads and short antennal scapes, is different from the others, based on its morphology and on the

statistical analysis. Third, we recognize *A. inermis* as a species, which Longino and Cover (2004) also considered to be a valid species (as *A. phalangium*). The fourth and fifth species are *A. araneoides* and *A. phalangium* which are nearly identical, but which can be separated by characters in the key and were separate species in the statistical analyses. Longino and Cover (2000) made it good argument that the *A. phalangium* (as *A. inermis*) is a synonym of *A. araneoides*, as the major difference between them is the sculpturing on the gaster, which they argue is not a reliable character. As they stated, molecular analysis will be needed to clarify the status of these two taxa.

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Table 1. Means, ranges and standard errors of the 6 variables for the 5 species of *Aphaenogaster*, using primarily type specimens.

Variable	Species				
	<i>araneoides</i>	<i>brevicollis</i>	<i>inermis</i>	<i>mexicana</i>	<i>phalangium</i>
	n=5	n=5	n=5	n=2	n=5
Scape length	2.84	2.68	2.48	2.45	2.40
Range	2.64-3.00	2.15-2.76	2.38-2.60	2.42-2.48	2.26-2.60
SE	0.067	0.035	0.038	0.030	0.056
Head length	1.91	2.11	1.76	1.78	1.74
Range	1.78-2.00	2.06-2.18	1.64-1.90	1.78	1.64-1.88
SE	0.036	0.021	0.054	0	0.042
Head width	1.05	1.46	1.06	0.99	1.05
Range	0.96-1.12	1.44-1.54	1.00-1.14	0.96-1.02	0.98-1.12
SE	0.027	0.019	0.028	0.030	0.024
Eye diameter	0.40	0.44	0.35	0.28	0.37
Range	0.35-0.44	0.41-0.48	0.34-0.38	0.28	0.31-0.50
SE	0.016	0.011	0.007	0	0.034
Spine length	0.20	0	0	0.09	0
Range	0-0.040			0.06-0.12	0-0.01
SE	0.007			0.030	0.002
Femur hairs	0	0	23.8	0	0
Range			10-40		
SE			5.161		

Table 2. F table for the 6 variables for the 5 species of *Aphaenogaster*. Eye diameter is the only variable that has no significant effect on discriminating among the species.

Variable	F-to-remove	Tolerance
Scape length	4.343	0.333
Head length	1.526	0.140
Head width	16.890	0.158
Eye diameter	0.359	0.951
Spine length	8.724	0.859
Femur hairs	11.959	0.620

Plate 1

Fig. 1. Head of a worker of *A. araneoides* (La Selva, Costa Rica).

Fig. 2. Mesosoma of a worker of *A. araneoides* (La Selva, Costa Rica).

Fig. 3. Head of the lectotype worker of *A. brevicollis*. The inset shows the neck as seen from above.

Fig. 4. Posterior part of the head, mesosoma, petiole and postpetiole of the lectotype worker of *A. brevicollis*.

Fig. 5. Head of the lectotype worker of *A. inermis*. The inset shows the base of the scape as seen from above (magnified 1.6 X scale of head).

Fig. 6. Posterior part of the head, mesosoma, petiole and postpetiole of the lectotype worker of *A. inermis*; posterior left femur of the lectotype worker of *A. inermis*.

Fig. 7. Head of the lectotype worker of *A. mexicana*. The inset shows a frontal view of the clypeus and mandible.

Fig. 8. Mesosoma, petiole and postpetiole of the lectotype worker of *A. mexicana*. Part of the mesosoma is hidden by the legs. The upper inset shows the propodeum, petiole and postpetiole as seen from above.

Fig. 9. Head of the lectotype worker of *A. phalangium*. The inset shows the base of the left scape as seen from above.

Fig. 10. Mesosoma and petiole of the lectotype worker of *A. phalangium*. The inset shows the posterior left femur of the lectotype worker of *A. phalangium*.

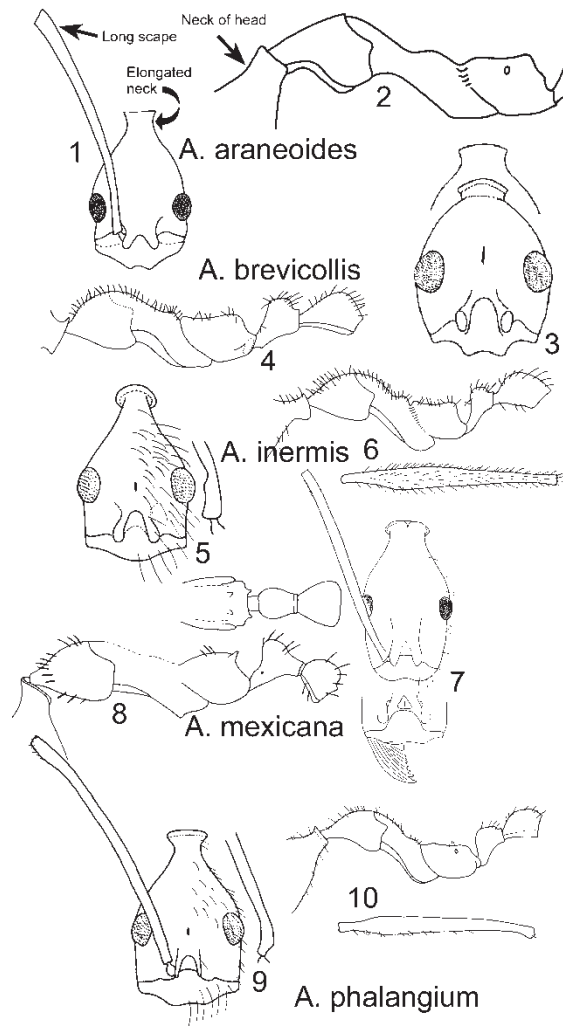


Plate 2 Males

Fig. 11. Head of a male of *A. araneoides* (Batan, Costa Rica, MCZC). The inset shows the end of the scape and the first 3 funicular segments.

Fig. 12. Posterior part of the head, mesosoma, petiole and postpetiole of a male of *A. araneoides* (Batan, Costa Rica, MCZC). The inset shows the left posterior femur as seen from the front.

Fig. 13. Head of a paralectotype male of *A. brevicollis*.

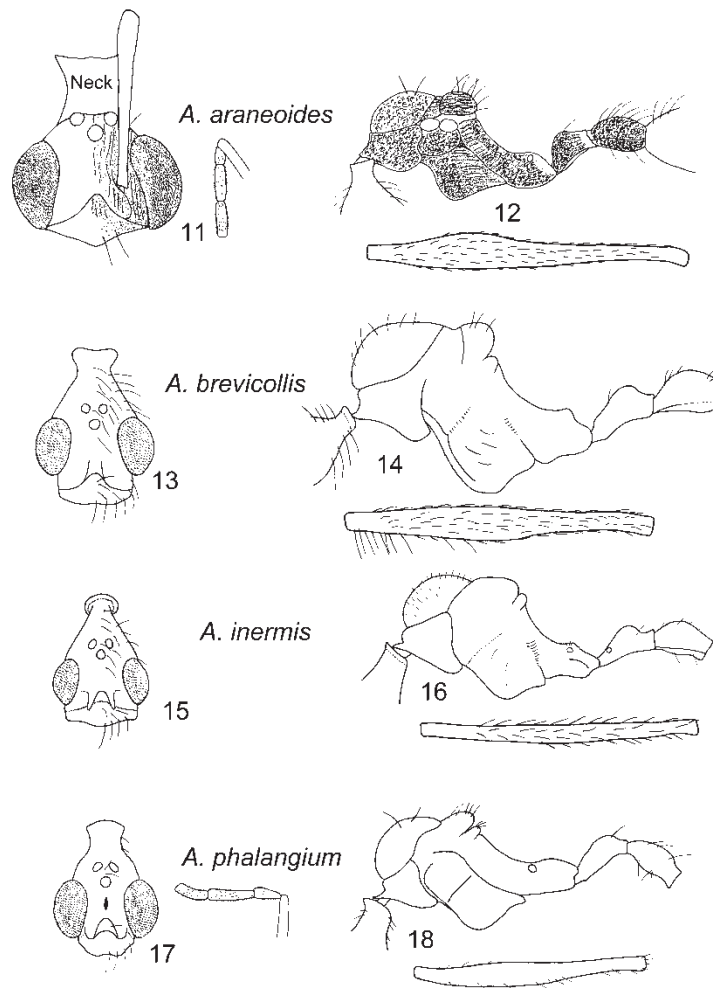
Fig. 14. Posterior part of the head, mesosoma, petiole and postpetiole of a paralectotype male of *A. brevicollis*. The inset shows the left posterior femur as seen from the front.

Fig. 15. Head of a male of *A. inermis* (paralectotype of *A. araneoides* var. *nitidiventris*).

Fig. 16. Posterior part of the head, mesosoma, petiole and postpetiole of a paralectotype male of *A. inermis* (paralectotype of *A. araneoides* var. *nitidiventris*). The inset shows the posterior left femur as seen from the front.

Fig. 17. Head of a male of *A. phalangium* (Izabal, Guatemala, CWEM). The inset shows the end of the scape and the first 3 funicular segments.

Fig. 18. Mesosoma and petiole of a male of *A. phalangium* (Izabal, Guatemala, CWEM). The inset shows the posterior left femur as seen from the front.



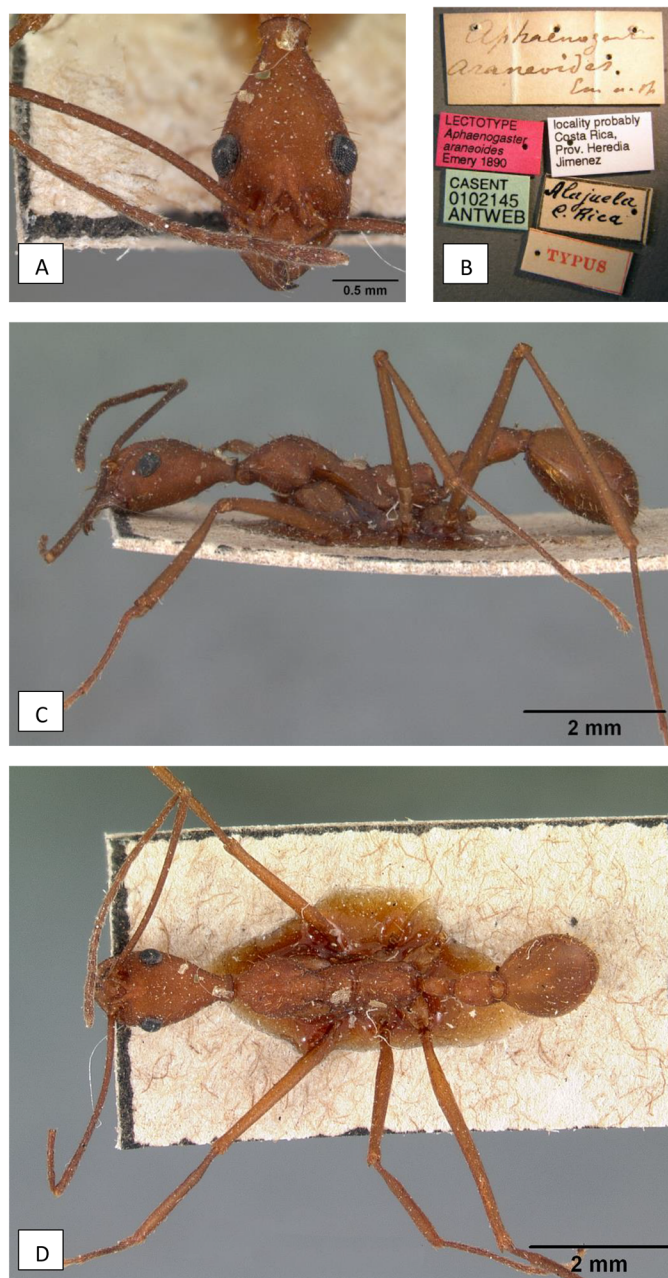


Plate 3. Lectotype worker of *A. araneoides*: A. Frontal view of head; B. Labels; C. Side view of ant; D. Top View of ant. Photo from Antweb.org, photo taken by April Nobile.



Plate 4. Worker of *A. inermis*: A. Frontal view of head; B. Labels; C. Side view of ant; D. Top View of ant. Photo from Antweb.org, photo taken by A. Westrich, ant image by Corrie Moreau.



Plate 5. Lectotype worker of *A. mexicana*: A. Frontal view of head; B. Labels; C. Side view of ant; D. Top View of ant. Photo from Antweb.org.

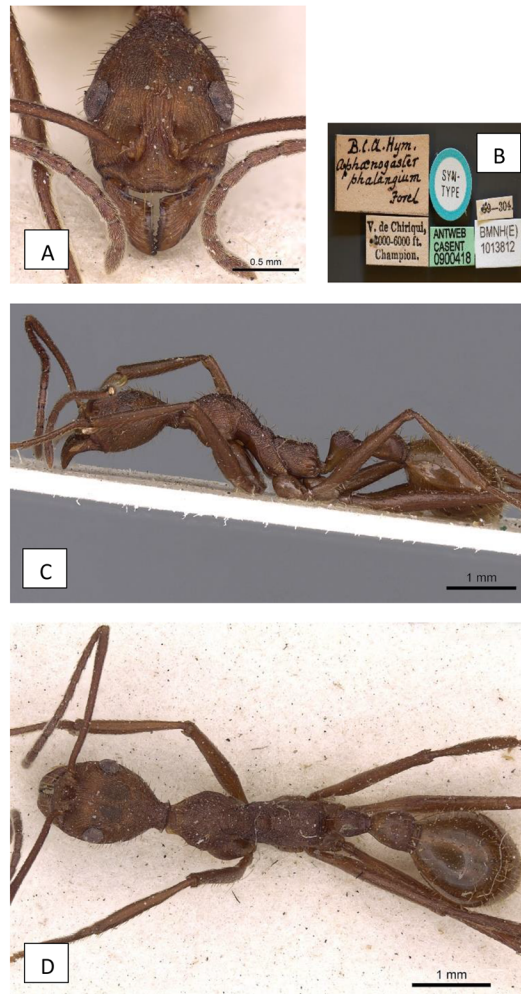


Plate 6. Syntype worker of *A. plalangium*: A. Frontal view of head; B. Labels; C. Side view of ant; D. Top View of ant. Photo from Antweb.org, photo taken by Ryan Perry.

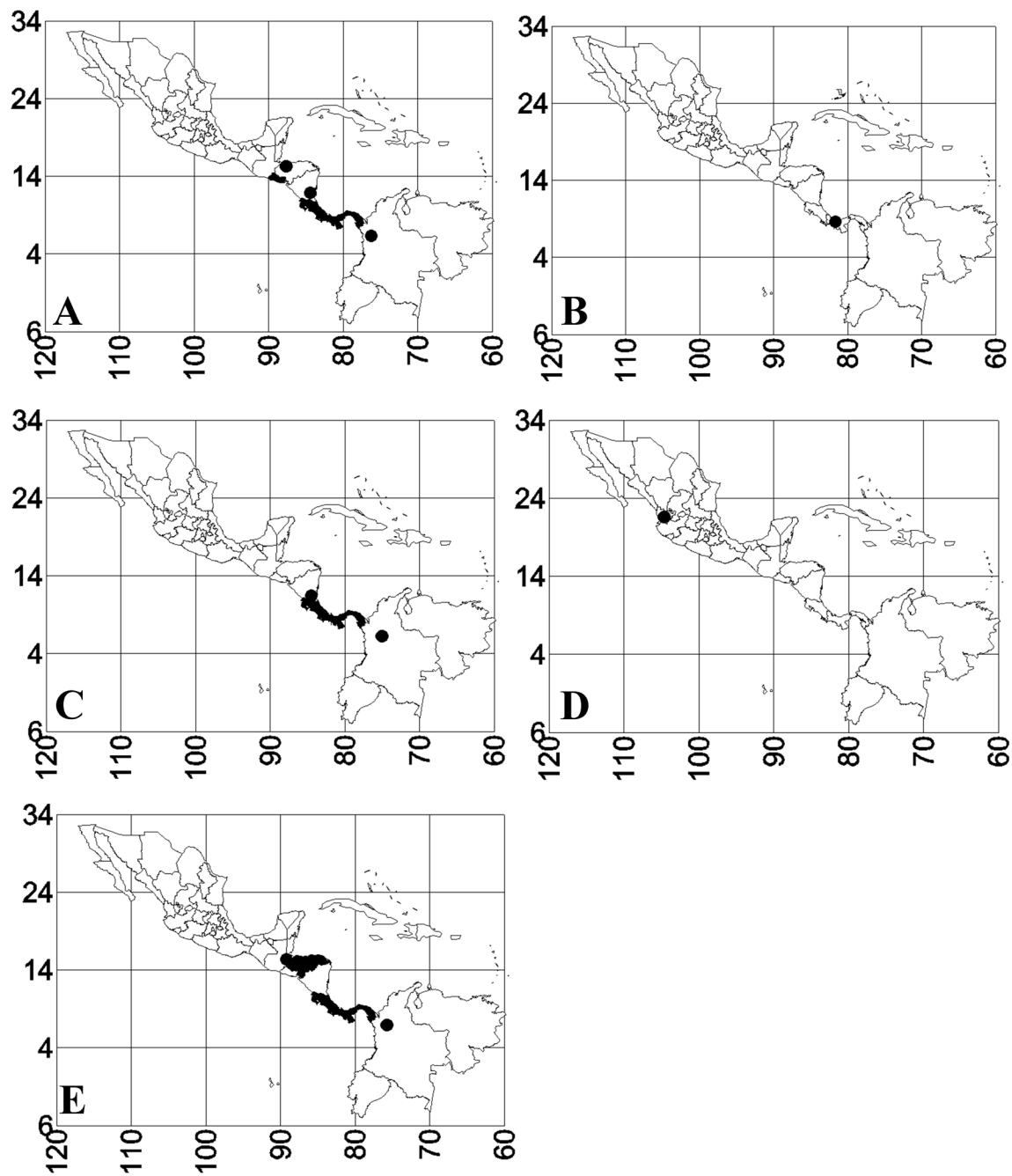


Plate 7. Distribution of *Aphaenogaster phalangium* species complex A. *Aphaenogaster araneoides*, B. *Aphaenogaster brevicollis*, C. *Aphaenogaster inermis*, D. *Aphaenogaster mexicana*, E. *Aphaenogaster phalangium*.

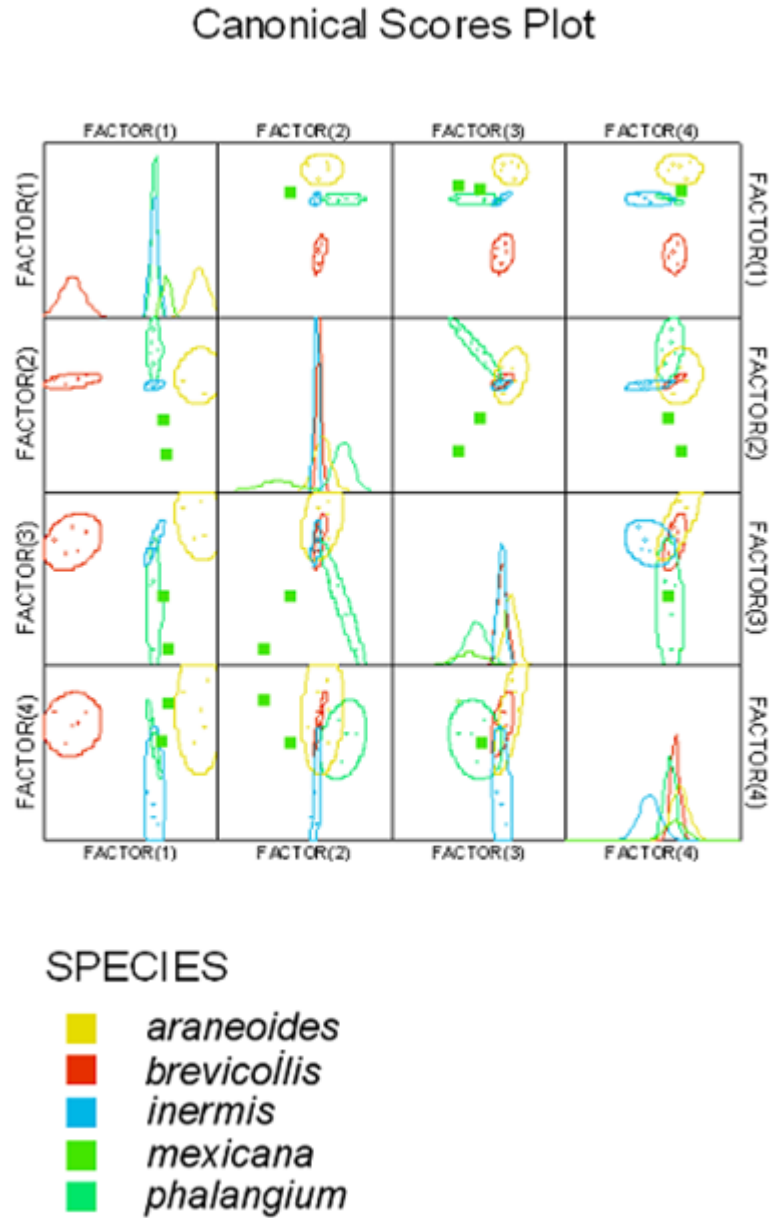


Fig. 19. Canonical correlation plots of the 5 species in the *phalangium* species complex. The ellipses indicate the 95% confidence intervals, using primarily type material. The green squares are the two specimens of *A. mexicana*.

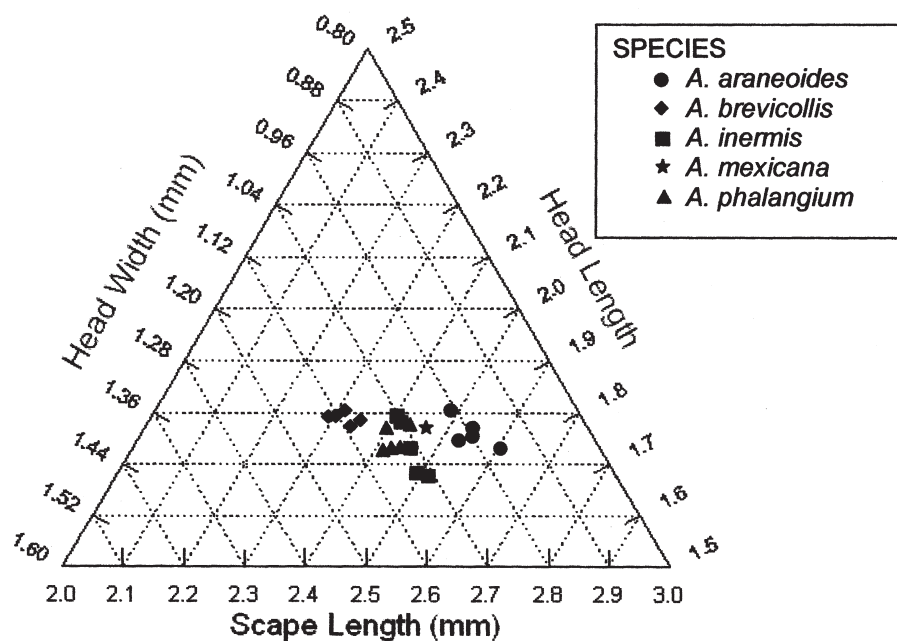


Fig. 20. Triangle plot showing the relationships between head width, head length and scape length of the 5 species of *Aphaenogaster*.

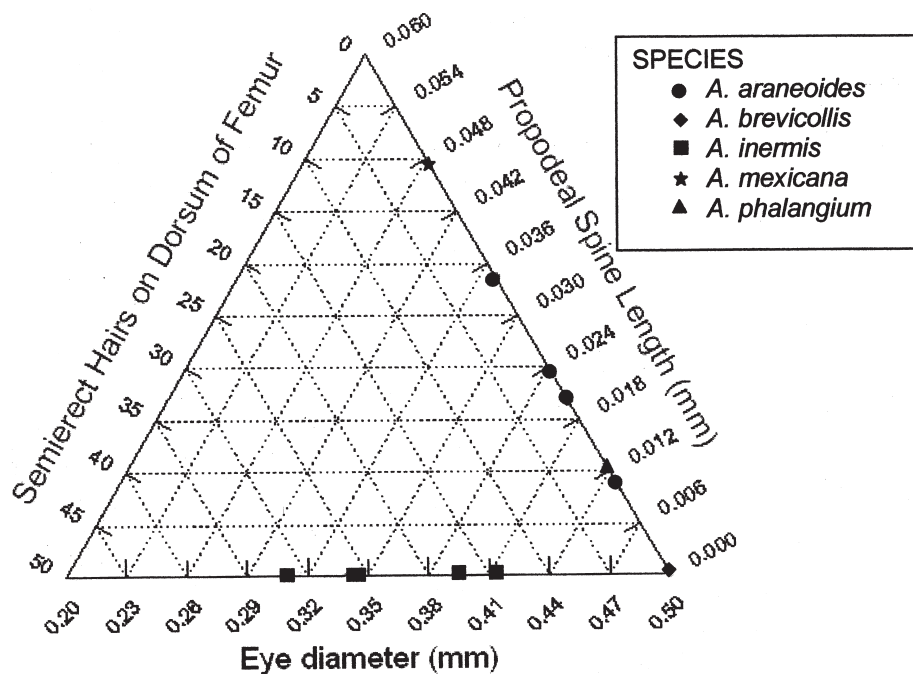


Fig. 21. Triangle plot showing the relationships between number of semierect hairs on the outline of the dorsal face of the femur (seen in profile), propodeal spine length and eye diameter of the 5 species of *Aphaenogaster*.