AN UNUSUAL NEW BRACHYMYRMEX MAYR (HYMENOPTERA: FORMICIDAE) FROM COSTA RICA, WITH IMPLICATIONS FOR THE PHYLOGENY OF THE LASINE TRIBE GROUP

JOHN S. LAPOLLA AND JOHN T. LONGINO

(JSL) Department of Entomology, National Museum of Natural History, Smithsonian Institution, P.O. 37012, MRC 188, Washington, DC 20013-7012, U.S.A. (e-mail: lapollaj@si.edu); (JTL) The Evergreen State College, Olympia WA 98505, U.S.A. (e-mail: longinoj@evergreen.edu)

Abstract.—Brachymyrmex Mayr is an exclusively New World ant genus that currently contains 38 described species. In this study, we describe Brachymyrmex nebulosus, new species from Costa Rica. The new species exhibits morphological characters suggestive of both Brachymyrmex and Myrmelachista Roger. Notes on the morphological characters that separate these two genera from each other are provided. Analysis of male genitalia suggests that Brachymyrmex is most closely related to Myrmelachista and Cladomyrma Wheeler, W.M. Previously, the African genera Aphomomyrmex Emery and Petalomyrmex Snelling were thought to be close relatives of Brachymyrmex as well, but our analysis, based on evidence from male genitalia, suggests this is not the case. The monotypic genus Pseudaphomomyrmex Wheeler, W.M., originally placed in the Formicinae and long thought to be a relative of Brachymyrmex, is transferred to the Dolichoderinae. Pseudaphomomyrmex lacks the most obvious synapomorphy of the Formicinae, an acidopore. The species possesses a "dolichoderine habitus." Other morphological characteristics suggest placement within the Dolichoderinae. For instance, the juncture where the mandibular masticatory margin rounds into the basal margin bears many small denticles, a mandibular feature characteristic of many dolichoderines. The structure of the petiole also suggests placement within the subfamily.

Key Words: Pseudaphomomyrmex, Myrmelachista, new species, biogeography, Formicinae, Dolichoderinae

Brachymyrmex Mayr ants are among the smallest ants in the New World. The genus contains 38 described species with dozens of additional "subspecies", most from tropical America (Bolton 1995). One species, B. depilis Emery, is widespread in North America; a few are "tramp" species, widely distributed by human commerce, with the remainder found in the Neotropics.

In Neotropical forests, the common species of *Brachymyrmex* nest in a variety of small plant cavities, under epiphytes, or in the leaf litter. They seem quite generalized

in choice of nest site, and the nests can be in relatively fragile or ephemeral substrates, suggesting frequent nest movement. *Brachymyrmex* species seem to feed mainly at carbohydrate sources, being common at extrafloral nectaries and at sugar water baits. Some species are known to tend Coccoidea (Hemiptera) in underground chambers (Wheeler 1910; Santschi 1923). Very little is known about the natural history for the vast majority of *Brachymyrmex* species.

Taxonomic knowledge of *Brachymyrmex* is very limited and species boundaries are

not well established. The last taxonomic revision was by Santschi (1923). Perhaps further taxonomic work on Brachymyrmex has been discouraged by Creighton's (1950) remark about the "miserable little genus" prone to taxonomic difficulties, with seemingly impossible morphological complexes of species. Emery (1925) placed Brachymyrmex in the tribe Brachymyrmecini and there have since been several changes in the tribal classification. Hölldobler and Wilson (1990) considered Brachymyrmex part of an expanded Myrmelachistini that included Aphomomyrmex Emery, Brachymyrmex, Cladomyrma Wheeler, W.M., Myrmelachista Roger, Petalomyrmex Snelling, and Pseudaphomomyrmex Wheeler, W.M. Bolton (1995) considered a Brachymyrmecini that excluded Myrmelachista, returning Myrmelachista to is own tribe. More recently, however, Bolton (2003) synonymized both the Brachymyrmecini and the Myrmelachistini into a vastly expanded Plagiolepidini. The Plagiolepidini coupled with the Lasiini and Myrmoteratini form the lasiine tribe group (Bolton 2003).

Here we describe a new Brachymyrmex from Costa Rica. In the course of discovering this new species, its exact generic assignment came into question, for this peculiar species has morphological characteristics of both Brachymyrmex and Myrmelachista. The size and shape of the mesosoma is very similar to Myrmelachista zeledoni Emery, a common species found sympatrically with the new Brachymyrmex, and the visual similarity in the field to Crematogaster Lund is shared with several montane Myrmelachista species. Nonetheless, the antennae are 9-segmented and there is no antennal club, characters that suggested placement within Brachymyrmex. We therefore examine the generic definitions of both Brachymyrmex and Myrmelachista and provide notes on their phylogenetic relationship to each other and to other genera within the lasiine tribe group.

MATERIALS AND METHODS

Specimens were examined from a number of research collections and below follows the list of the institutions and individuals' collections that contributed to this study.

BMNH: The Natural History Museum, London, United Kingdom.

INBC: Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

JTLC: J.T. Longino Collection, Evergreen State College, Olympia, WA, USA.

LACM: Natural History Museum of Los Angeles County, Los Angeles, CA, USA.

MCZC: Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA.

NHMB: Naturhistorisches Museum Basel, Basel, Switzerland.

USNM: National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Examination and measurement of specimens were completed at various magnifications using a light microscope (Leica Wild M10) and were recorded to the nearest 0.001 mm. All measurements are given in millimeters. Specimens were photographed using a JVC KY-F70B video camera mounted on a Leica M420 microscope and attached to an IBM Intellistation M Pro computer, on which composite images were assembled using Auto-Montage Version 3.04 software (Synoptics Ltd. 2003). Morphological terminology employed throughout follows Bolton (1994), with modifications where noted. Anatomical abbreviations are elaborated here:

HW Total Length: HL+ML+GL.

HL Head length: the length of the head proper, excluding the mandibles; measured in full-face view from the midpoint of the anterior clypeal margin to a line drawn across the posterior mar-

- gin from its highest points (to accommodate species where the posterior margin is concave).
- HW Head Width: the maximum width of the head in full-face view (excluding the portion of the eyes that extend pass the lateral sides of the head).
- SL Scape Length: the maximum straight line of the antennal scape excluding the condylar bulb.
- ML Mesosoma Length: the length of the mesosoma (= alitrunk) in lateral view from the anteriormost point of the pronotum (including the "neck" of the pronotum) to the posteriormost point of the metapleuron.
- GL Gaster Length: the length of the gaster in lateral view from the anteriormost point of first gastral segment (third abdominal segment) to the posteriormost point of the acidopore.
- CI Cephalic Index: HW-100/HL.
- SI Scape Index: SL·100/HW.

Systematic Treatment

Brachymyrmex nebulosus LaPolla and Longino, new species

(Figs. 1A, B)

Type material.—Holotype worker, COSTA RICA: Puntarenas Prov.; 6 km south of Monteverde; 10°15′N, 84°49′W; 800 m; 22 June 1990 (J. Longino #4050) (LACM ENT 143546) (INBC); 1 paratype worker data same as holotype (INBC); 2 paratype workers COSTA RICA: Puntarenas Prov.; Ojo de Agua; 10°16′N, 84°50′W; 800 m; 5 July 1991 (J. Longino #2965) (INBI-OCRI001279916) (MCZC) (USNM); 2 paratype workers COSTA RICA: Puntarenas Prov.; Ojo de Agua; 10°16′N, 84°50′W; 800 m; 28 July 1984 (INBI-OCRI002281199) (BMNH) (LACM).

Diagnosis.—Face smooth, with abundant erect setae; scapes surpass posterior margin of head by about length of first funicular segment; metanotum deeply impressed, mesosoma hour-glass shaped; erect hairs on legs.

Description.—Head dark brown, with

scapes and mandibles lighter brown to dusty yellow; smooth and shiny; abundant suberect to erect hairs throughout, with longest along posterior margin and clypeus; posterior margin entire; antenna 9-segmented; scape with abundant, short subcrect to erect hairs; scapes surpass posterior margin by length of first funicular segment; 3 small ocelli present, though lateral ocelli often difficult to distinguish; clypeus broad with median portion extended from margin forming a "lip"; mandible with 5 teeth, apical and 4th (measured from apical) longest. Mesosoma dark brown; roughly hour-glass shaped; smooth and shiny, with erect hairs on pronotal dorsum; katepisternum and side of propodeum shagreened; declivity short and indistinct; legs dark brown with abundant suberect to erect hairs; tarsi lighter in color. Petiole short and inclined forward. Gaster dark brown, with appressed to erect hairs throughout. Measurements (from holotype worker): TL: 2.90 mm; HL: 0.767 mm; HW: 0.704 mm; SL: 0.736 mm; ML: 0.892 mm; GL: 1.24 mm; CI: 92; SI: 105.

Etymology.—The specific epithet, *nebulosus*, is Latin for misty or cloudy in reference to the type locality being near Monteverde Cloud Forest Reserve and to the fact the generic designation of this species was in doubt for a time.

Distribution and natural history.—This species has been collected only three times, from two nearby sites on the Pacific slope just below Monteverde Cloud Forest Reserve in Costa Rica. Both sites are about 800 m elevation and are in the moist forest transition zone between cloud forest and lowland dry forest climate zones. Both areas were mosaics of forest patches, pastures, scrubby vegetation, and road edges. All three collections have been of workers on vegetation in open scrubby vegetation. In the field, these ants look and behave remarkably like *Crematogaster*.

DISCUSSION

This species is easy to distinguish from other *Brachymyrmex* species in Costa Rica.

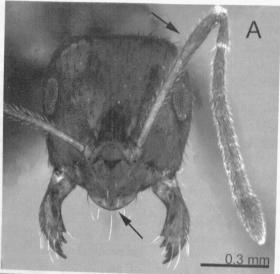




Fig. 1. Brachymyrmex nebulosus, holotype worker. A, Head in full frontal view. B, Lateral view. Arrows indicate diagnostic characters.

A distinctly large *Brachymyrmex*, *B. nebulosus* possesses the following diagnostic traits: blackish-brown and shiny, hourglassed shaped mesonoma, and legs and scapes with erect hairs. The hour-glass shaped mesonoma could only be confused with *B. santschii* Menozzi, which possesses

a similarly shaped mesonoma, but it is not as well-defined as in *B. nebulosus* and the ant overall is smaller, much lighter in color (brownish yellow), and the cuticle is not shiny. Finally, *B. santschii* does not have erect hairs on the legs or scapes. Erect hairs on the legs and scapes is what Santschi

(1923) used to define the subgenus Bryscha Santschi. The monophyly of Bryscha has been questioned (Brown 1973) and Bolton (2003) recently synonymized the subgenus under Brachymyrmex. While a phylogeny of Brachymyrmex is not within the scope of this study, it is worth noting that erect hairs on the legs and scapes are rarely observed in Brachymyrmex and may be of phylogenetic importance. Only four other species have been reported with erect hairs on the legs and scapes (this has only been confirmed by us for B. gaucho): B. antennatus Santschi, B. gaucho Santschi, B. micromegas Emery, and B. pilipes Mayr.

Based on worker morphology, the closest relative to B. nebulosus appears to be B. gaucho, which is known only from its type locality in Argentina. Like B. nebulosus, B. gaucho is a large, black, and shiny species. Unfortunately, the holotype of B. gaucho (and the only known specimen) has been badly damaged, with only the broken head and gaster remaining (holotype worker examined [JSL], ARGENTINA: Córdoba: Unquillo, in NHMB). Nonetheless, comparison of the holotype with B. nebulosus was possible. The main morphological difference between the two species appears to be that the erect hairs on B. gaucho are much shorter than those observed on B. nebulosus, especially on the gaster.

Brachymyrmex and Related Genera

The genus *Brachymyrmex* is most likely to be confused with *Myrmelachista*. The most obvious distinction between these two genera is the presence of a 3 to 4-segmented antennal club in *Myrmelachista*. Although *Brachymyrmex* usually possess incrassate antennae, they never form a distinct antennal club. Both genera include species with 9-segmented antennae, although *Myrmelachista* also includes some species with 10-segmented antennae (species in the synonymized subgenus *Hincksidris* [Snelling and Hunt 1975]). No *Brachymyrmex* have been recorded with 10-segmented antennae. Two other morpholog-

ical characteristics separate the two genera. The clypeus of *Myrmelachista* is typically subquadrate and compact, whereas *Brachymyrmex* possess a broadly rounded (along the anterior margin) and wide clypeus. The shape of the mandible also differs between the two genera. In *Myrmelachista*, the masticatory and basal margins form a right angle. Whereas in *Brachymyrmex* the masticatory and basal margins form an obtuse angle (compare Figs. 1A and 2A).

The uncertainty of the morphological boundaries of *Brachymyrmex* and *Myrmelachista* underscores even greater uncertainty regarding their relationship to each other and other formicine genera. In the most current classification, Bolton (2003) places *Brachymyrmex* and *Myrmelachista* into the Plagiolepidini. While we do not present a phylogenetic analysis of the lasiine tribe group in this study, we do present notes on male genitalia that may reveal phylogentic relationships within the tribe group and provide the basis for future morphological study.

Examination of the male genitalia, in particular the penis valves, reveals a potential synapomorphy for Brachymyrmex and Myrmelachista. Figs. 3A-D show that the apodemal ridge in both Brachymyrmex and Myrmelachista species is dorsally placed, running along the dorsal margin of the penis valve. Further investigation of other potentially related genera found that only Cladomyrma, a genus restricted to southeastern Asia, possesses a dorsal apodemal ridge. Contrary to Bolton's (2003) placement of Cladomyrma in the Lasiini, we hypothesize that Brachymyrmex, Cladomyrma, and Myrmelachista are closely related. Furthermore, molecular evidence from the D2 region of the 28S ribosomal RNA and EFI-alpha protein-coding genes place Brachymyrmex and Cladomyrma together (Myrmelachista was not included in the analysis) (LaPolla et al. in preparation). Bolton (2003) stated that the Plagiolepidini and Lasiini might need to be combined in the future.

Two other genera, Aphomomyrmex and Petalomyrmex, which are sister taxa (Snell-

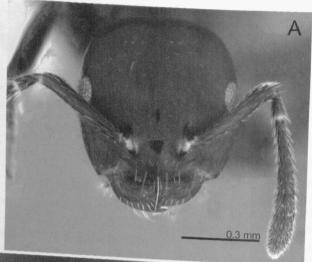




Fig. 2. Myrmelachista zeledoni, worker. A, Head in full frontal view. B, Lateral view.

ing 1979; Chenuil and McKey 1996), have at various times been thought closely related to *Brachymyrmex*. Bolton (2003) placed them in the Plagiolepidini. Based on the placement of the apodemal ridge (Figs. 3A–H), however, the genera are not closely related to *Brachymyrmex*, *Cladomyrma*, or *Myrmelachista*. This is interesting because earlier work based solely on worker morphology suggested that *Myrmelachista* at least was closely related to *Aphomomyrmex* and *Petalomyrmex*. For example, Snelling and Hunt (1975) stated, "There appears to be little difference between *Myrmelachista*

and Aphomomyrmex other than the presence of an antennal club." The more medial placement of the apodemal ridge is difficult to assess across all other formicine genera, but the penis valve structure of Aphomomyrmex and Petalomyrmex is very similar to that of Acropyga (Fig. 3H; LaPolla 2004), which Bolton (2003) placed in the Lasiini. In fact, molecular evidence from the D2 region of the 28S ribosomal RNA and EFI-alpha protein-coding genes place Acropyga as the sister to Petalomyrmex (Aphomomyrmex was not included in the analysis) (LaPolla et al. in preparation).

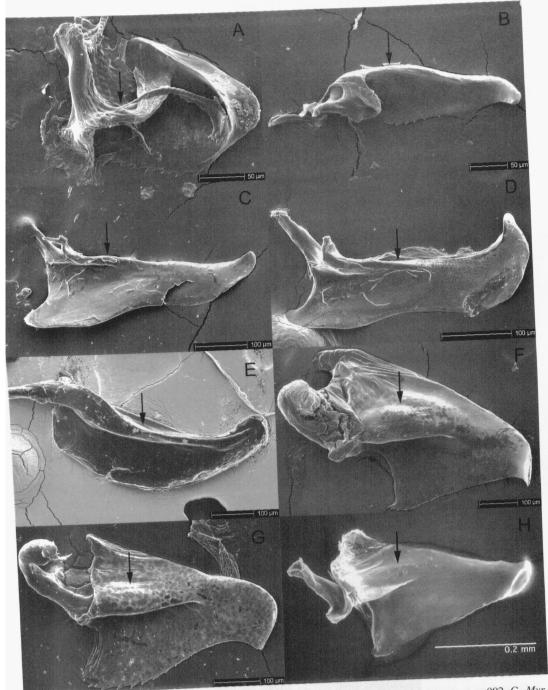


Fig. 3. Ectal (outer) view of penis valves. A, *Brachymyrmex* sp. 001. B, *Brachymyrmex* sp. 002. C, *Myrmelachista* sp. 001. D, *Myrmelachista skwarrae*. E, *Cladomyrma maryatiae*. F, *Aphomomymyrmex afer*. G, *Petalomyrmex phylax*. H, *Acropyga arnoldi*. Arrows indicate the apodemal ridge.



Fig. 4. Pseudaphomomyrmex emeryi, holotype queen. A, Head in full frontal view. B, Lateral view. C, SEM image of head in full frontal view.

Note on Pseudaphomomyrmex

The monotypic genus Pseudaphomomyrmex has been a source of confusion since its creation by Wheeler (1920). Its only species was originally described as Aphomomyrmex emeryi by Ashmead (1905). Pseudaphomomyrmex has been classified in various tribes with little reference to the holotype queen (holotype examined by JSL; label info: PHILIPPINES: Manila, coll. Robert Brown, in USNM), the only specimen known for this species (see Bolton 2003 for a summary of various tribal placements of the genus). The species does not possess an acidopore (we examined the disarticulated gaster with a scanning electron microscope) and in general the head has a "dolichoderine habitus" (Figs. 4A-B). The juncture where the mandibular masticatory margin rounds into the basal margin bears many small denticles, a mandibular feature characteristic of many dolichoderines. The structure of the petiole, which is similar to the petiolar structure found in Tapinoma Foerster, also suggests placement within the Dolichoderinae. Therefore, we propose the transfer of Pseudaphomomyrmex from the Formicinae to the Dolichoderinae, subfamily transfer. It is possible that Pseudaphomomyrmex is a synonym (junior or senior) of an already described genus within the Dolichoderinae; however, our preliminary assessment is that Pseudaphomomyrmex represents a distinct genus and therefore no other changes in classification are proposed at this time.

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