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

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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 Cladomyrmex 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 acicopore. 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. deplis 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 its own tribe. More recently, however, Bolton (2003) synonymized both the Brachymyrmecini and the Myrmelachistini into a vastly expanded Plagiolepini. The Plagiolepini coupled with the Lasini and Myrmotheratinia form the lasine 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 lasine 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 condyline 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 aciniform.

CI Cephalic Index: HW-100/HL.

SI Scape Index: SL-100/HW.

Systematic Treatment

Brachymyrmex nebulous 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) (INBIOCRI1001279916) (MCZC) (USNM); 2 paratype workers COSTA RICA: Puntarenas Prov.; Ojo de Agua; 10°16’N, 84°50’W; 800 m; 28 July 1984 (INBIOCRI0002281199) (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 suberect 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, nebulous, 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.
A distinctly large *Brachymyrmex*, *B. nebulosus* possesses the following diagnostic traits: blackish-brown and shiny, hour-glassed 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. micromeegas 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 Hincksidepis [Snelling and Hunt 1975]). No Brachymyrmex have been recorded with 10-segmented antennae. Two other morphological characteristics separate the two genera. The clypeus of Myrnelachista 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 Myrnelachista, 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 Myrnelachista underscores even greater uncertainty regarding their relationship to each other and other formicine genera. In the most current classification, Bolton (2003) places Brachymyrmex and Myrnelachista into the Plagiolepini. While we do not present a phylogenetic analysis of the lasiini tribe group in this study, we do present notes on male genitalia that may reveal phylogenetic 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 Myrnelachista. Figs. 3A–D show that the apodemal ridge in both Brachymyrmex and Myrnelachista 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 Lasini, we hypothesize that Brachymyrmex, Cladomyrma, and Myrnelachista are closely related. Furthermore, molecular evidence from the D2 region of the 28S ribosomal RNA and EF1-alpha protein-coding genes place Brachymyrmex and Cladomyrma together (Myrnelachista was not included in the analysis) (LaPolla et al. in preparation). Bolton (2003) stated that the Plagiolepini and Lasini might need to be combined in the future.

Two other genera, Aphomomyrmex and Petalomyrmex, which are sister taxa (Snell-
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 apodermal 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 *Aphonomyrnex* and *Petalomyrnex*. For example, Snelling and Hunt (1975) stated, “There appears to be little difference between *Myrmelachista* and *Aphonomyrnex* other than the presence of an antennal club.” The more medial placement of the apodernal ridge is difficult to assess across all other formicine genera, but the penis valve structure of *Aphonomyrnex* and *Petalomyrnex* 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 EF-1-alpha protein-coding genes place *Acropyga* as the sister to *Petalomyrnex* (*Aphonomyrnex* 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. Aphomomyrmex afer. G. Petalomyrmex phylax. H. Acropyga arnoldii. Arrows indicate the apodemal ridge.
Fig. 4. *Pseudophomomyrmex 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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