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Ancient Trophophoresy: A Fossil *Acropyga* (Hymenoptera: Formicidae) from Dominican Amber

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ABSTRACT

The discovery of several pieces of Dominican amber with *Acropyga* inclusions provides evidence that the trophophoretic behavior of *Acropyga* queens is at least 15-20 million years old. A fossil species, *A. glaesaria*, is described and its relationship to extant *Acropyga* is discussed.

Keywords: *Acropyga*, Formicinae, trophobiosis, ant, fossil, amber.

INTRODUCTION

Extant *Acropyga* ants are perhaps best known for their trophophoretic habits, defined by LaPolla et al. (2002) as the behavior of queens emerging from their nests prior to their mating flight with a mealybug held in their mandibles. The mealybug that each queen carries presumably serves as a "seed individual" from which a new generation of mealybugs will be started in the newly founded ant colony (see LaPolla, 2004 for a thorough review of this behavior). It has been suggested that *Acropyga* are completely dependent on their mealybugs for food (LaPolla et al. 2002; LaPolla 2004).

Given their subterranean lifestyle, and the fact that reproductives only emerge for a short time for their mating flights, *Acropyga* specimens would not necessarily be expected in amber inclusions (DuBois and LaPolla, 1999). Remarkably, however, *Acropyga* reproductives have been found in at least 4 pieces of Dominican amber (Johnson et al. 2001, Anderson and Santiago-Blay 2003). Johnson et al. (2001) were the first to report on the presence of *Acropyga* in Dominican amber, and since queens were found either clutching mealybugs in their mandibles or with mealybugs nearby, the fossils represent the oldest definitive record of trophobiosis. Thus, the trophophoretic behavior of *Acropyga* queens is at least 15-20 million years old, the estimated age of Dominican amber (Grimaldi 1995). A recent taxonomic revision of the genus by LaPolla (2004) found a total of 37 extant species, and discussed the *Acropyga* found in Dominican amber, though no fossil species were formally described in that study. This paper presents the first description of a fossil *Acropyga* species. The relationship of the fossil species to extant species is discussed, and a review of associated mealybug species is provided.

MATERIALS AND METHODS

Three pieces of Dominican amber with *Acropyga* inclusions were examined. The exact origins of the amber cannot be known with certainty because the pieces are from mixed mines (D. Grimaldi, pers. comm.).

Examination and measurement of specimens were completed at various magnifications using a light microscope (Nikon SMU-Z) and were recorded to the nearest 0.001 mm. All measurements are given in millimeters, unless noted otherwise. Morphological terminology employed throughout follows Bolton (1994), with modifications where noted. Anatomical abbreviations are elaborated here:

TL—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 margin 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 past 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 anterior most 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.

FWL—Forewing Length: the length of the forewing from its mesosomal articulation point to the most distal portion of the wing tip.

MDL—Mandible Length: the length of the mandible in full-face view from the articulation point to the apex of the apical tooth.

CI—Cephalic Index: $HW \times 100/HL$

SI—Scape Index: $SL \times 100/HW$

SYSTEMATIC TREATMENT

Acropyga glaesaria, new species

figures 1-2 (queen), 3a-b (male)

Description of Queen.—Specimens appear to be entirely yellowish in color, as is typical for extant *Acropyga*. Head: distinctly longer than broad; covered in a layer of short appressed hairs; darker towards apex around 3 prominent ocelli; eyes large, taking up most of the lateral portions of the head; 9-segmented, incrassate antennae; apical segment slightly longer than preceding 3 segments combined; scape reaches to the posterior margin; clypeus with several erect hairs; mandibles with 8 teeth; dorsal surface of mandibles with hairs; palp formula 2:3. Mesosoma: pronotum small and collar-like, overarched by much higher rounded mesonotum; mesosomal dorsum flat, though sloping towards petiole; dorsum covered in a layer of short appressed hairs; propodeum low and indistinct. Gaster: petiole thick and erect; gaster with dense layer of short appressed hairs, with erect hairs throughout.

Queen measurements (n=3).—TL: 2.37-2.94; HW: 0.364-0.386; HL: 0.451-0.510; SL: 0.333-0.409; ML: 0.672-0.868; GL: 1.04-1.56; FWL: 3.05-3.06 (from only 2 queens); CI: 77.51-84.26; SI: 86.27-106.84. Measured queen specimens are the two queens from the AMNH collection (from two pieces of amber, one with the mealybug *E. reginae* and the other with *E. inclusus*), and a queen from the Senckenberg collection. The measured queen from the Senckenberg collection is the specimen closest to the males in the amber.

Description of Male.—Specimens appear slightly darker than queen, similar to the dusty yellow that extant *Acropyga* males often display. Head: about as broad as long; darker in color around 3 prominent ocelli; eyes large, taking up most of the lateral portions of the head; 10-segmented, incrassate antennae; apical segment about as long as preceding 3 segments combined; scape surpasses the posterior margin by about the length of the pedicel; mandible with 4 distinct teeth, the basal tooth separated by a short diastema; palp formula 2:3. Mesosoma: pronotum small and collar-like, overarched by higher, rounded mesonotum; mesosomal dorsum flat, with a layer of short appressed hairs; propodeum lower than mesonotum and scutellum; declivity short but steep. Gaster: petiole compressed in the amber; gaster with many short appressed hairs and scattered erect hairs throughout, especially along segmental margins. Genitalia: parameres in lateral view broad, reaching towards dorsal midline; parameres subrectangular in shape, ventrally with a rounded apex that bears many long hairs. Cuspi could not be examined due to obstructions in the amber. A digitus was visible, though very difficult to examine. It appears to be a large structure around 0.13 mm long, and the apex may simply be rounded as seen in members of the extant *panamensis* species-group or hooked as observed in the extant *A. donisthorpei*. Penis valves appear to be rounded ventrally with many small teeth; apex of penis valves with slight lateral expansions as they pass length of parameres.

Male measurements (n=1).—TL: 1.63; HL: 0.328; SL: 0.291; ML: 0.613; GL: 0.692; FWL: 2.43; MDL: 0.164. Measured male is with *E. abductus* holotype and is the male specimen closest to the queen.

Type material examined.—Holotype queen, from a piece of amber containing the alate queen, with a mealybug specimen nearby (*Electromyrmoccus inclusus* holotype), deposited in the American Museum of Natural History (= AMNH) (New York, NY, USA) (code no. DR-16-603 in box with amber); 1 paratype queen (wings broken off at the base and not found anyway in the amber) holding mealybug *E. reginae* holotype, in amber (AMNH); 2 paratype queens (both alate), 2 paratype males in amber piece with mealybug *E. abductus* holotype deposited in the Natur-Museum Senckenberg (Germany) (code: SMF VII 169 in box with amber).

Etymology.—The specific epithet, *glaesaria*, is Latin for “of amber.”

Discussion.—There has been uncertainty as to whether or not the fossils discussed here even belong in *Acropyga*. For instance, Poinar and Poinar (1999) misidentified an *Acropyga* fossil as *Brachymyrmex*. In part, this reflects confusion regarding the taxonomic status, and morphological limits of the genus. A recent world revision of *Acropyga* revealed seven morphological synapomorphies for the genus (LaPolla, 2004), and these characters were examined on the fossil specimens. Based on those, the fossil is shown to definitively belong to *Acropyga*, possessing 6 of 7 morphological synapomorphies: incrassate antennae (9-segmented), tubular torulae, 2:3 palpal formula, large and round propodeal spiracles

placed dorsolaterally, and the male with 10-segmented antennae (reduced from the primitive 13 segments). The last synapomorphy, a long hair placed medially on the anterior clypeal margin, cannot be scored because workers are needed to properly analyze the character.

Johnson et al. (2001) speculated that the AMNH and Senckenberg (listed as the Frankfurt specimens in their paper) specimens represented different species based on differences in head shape. However, the differences in the posterior margin and posterior corners are not as distinct as Johnson et al. (2001) implied, and some of the observed morphological differences are undoubtedly the result of the amber preservation process. Given that all fossil queens share the same number of antennal segments (9 segments) and have similar morphometric measurements, I feel unjustified in describing more than one species. The number of mandibular teeth is an important diagnostic character that can only be reliably counted on the holotype queen, but the shape of the mandible of all the queens implies that the specimens are conspecific.

RELATIONSHIP TO EXTANT *ACROPYGA*

The relationship of *A. glaesaria* to extant species is difficult to ascertain. *A. glaesaria* queens possess 8 mandibular teeth, with the apical, 4th, and 7th teeth (from apical to basal) being the longest. Only two extant species have such a high mandibular tooth count: the southern African *A. arnoldi* (6-9 teeth) and the Mediterranean *A. palearctica* (6-8 teeth). Two other extant species, *A. hystrix* and *A. pallida* (both from the Australian and Indo-Australian regions), are observed with up to 7 mandibular teeth. In the New World, no extant species possess over 5 mandibular teeth, making *A. glaesaria* unique among New World species. Likewise, the 4-toothed male mandible is highly unusual. Only *A. ayanganna* males have been observed among extant New World species with 4 mandibular teeth.

Two aspects of the torulae are noteworthy. 1) The torulae are widely separated from each other, a characteristic observed among several members of the Old World *myops* species-group. Among extant *Acropyga*, the separation of the torulae reaches its greatest extreme in *A. kinomurai*, a species known only from Yaeyama Island in extreme southern Japan. *A. glaesaria* torulae most resemble those of *A. kinomurai* with regards to the extent of their separation from each other. 2) The tubular torulae are extremely short compared to extant species.

The male genitalia are curious in that the parameres are roughly rectangular in shape, but rounded caudoventrally. This is a unique combination of characters, which loosely resembles the genitalia of *A. yaeyamensis*, a species found in southern China and Nepal that LaPolla (2004) speculated was the most closely related Old World species to the New World fauna. The roughly rectangular-shaped parameres also suggest a relationship with the New World *decedens* species-group, though the mandible of the queen contradicts such a placement (extant *decedens* species-group members possess only 3-5 mandibular teeth). Because characters such as the penis valves cannot be examined properly, phylogenetic placement of the species is difficult. LaPolla (2004) found that the most informative phylogenetic characters were from the male genitalia, and examination of those often required dissection.

What can be presently said about *A. glaesaria* is that most of the examined characters suggest it more closely related to the Old World fauna than to the New

World fauna, which is consistent with the hypothesis of LaPolla (2004) that the genus evolved in the Old World. An Asian/Australian link among ants in Dominican amber is not unusual. In the genus *Pheidole*, a species from Dominican amber belongs to a species-group now restricted to the Indo-Australian region (Wilson, 2003). The dolichoderine genus *Leptomyrmex*, also found in Dominican amber, is now extinct in the New World, and is presently found only in Sulawesi, New Guinea and the Australasian region (Bolton, 1995).

ASSOCIATED MEALYBUG SPECIES

Williams (2001) described 3 species of mealybugs associated with *A. glaesaria*: *Electromyrmococcus inclusus*, *E. reginae*, and *E. abductus*. The genus *Electomyrmococcus* was created to accommodate those species, which combine a number of morphological characters that are unique among rhizoecine mealybugs. Williams (2001) states that the genus appears to be most closely related to the extant genera *Eumyrmococcus* (Old World) and *Neochavesia* (New World) and may provide a link between the *Eumyrmococcus* group and the *Rhizoecus* group of *Acropyga* associated mealybugs. Unfortunately, the phylogeny of rhizoecine mealybugs remains to be elucidated. Once phylogenetic studies are completed, however, such a phylogeny may offer insight into the evolution and origin of *Acropyga*, including whether or not ant and mealybug have coevolved.

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Figure 1. *A. glaesaria* queen (paratype), with mealybug *Electromyrmoccus reginae* (holotype), in amber.

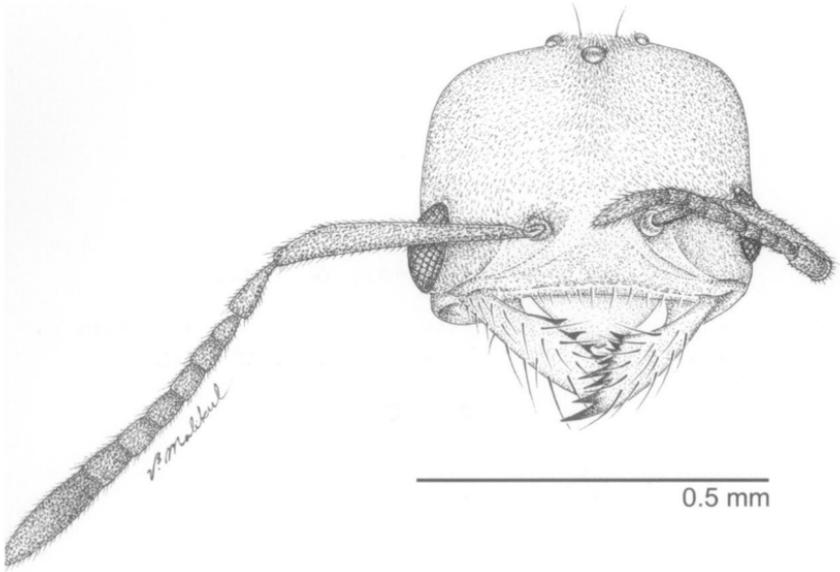


Figure 2. *A. glaesaria* queen (holotype) in full-face view. Note that the head is drawn slightly shorter (lengthwise) due to distortion of the specimen within the amber.

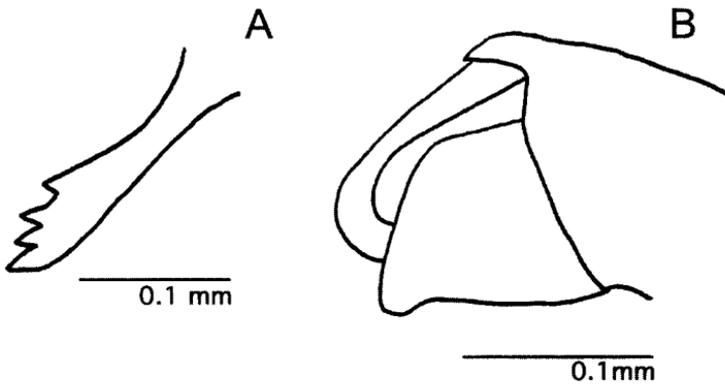


Figure 3. *A. glaesaria* male. A) mandible; B) lateral view of paramere drawn without hairs.