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Acropyga and *Azteca* Ants (Hymenoptera: Formicidae) with Scale Insects (Sternorrhyncha: Coccoidea): 20 Million Years of Intimate Symbiosis

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ABSTRACT

Species of the genus *Acropyga* are rarely encountered subterranean ants that rely on mealybugs or aphids to provide their nutritional needs. Female *Acropyga* (Formicinae) alates of pantropical and Mediterranean species carry mealybugs with their mandibles while swarming and probably inoculate their new nests with these mealybugs. The natural history of *Acropyga* and other mealybug-tending ant species, a summary of the various reports of *Acropyga* females toting mealybugs, and a new record from French Guiana are presented here. Also provided are a first report and description of *Acropyga* alates with mealybugs in Dominican amber dated to the Miocene, a discovery indicating that this intimate association and relatively uncommon behavior has existed for at least 15–20 million years. The mealybugs found with the *Acropyga* females in amber are related to the hypogaeic genera *Eumyrmococcus* Silvestri and *Neochavesia* Williams & Granara de Willink (Pseudococcidae, Rhizoecinae) and represent three new species of a new genus. The genus *Electromyrmococcus* and the species *Electromyrmococcus abductus* Williams, *Electromyrmococcus inclusus* Williams and Agosti, and *Electromyrmococcus reginae* Williams are described. A piece of Dominican amber containing workers of *Azteca alpha* Wilson (Dolichoderinae) and 23 scale insects is also presented and the significance of these specimens in Dominican amber is discussed.

INTRODUCTION

Of the numerous symbiotic relationships known from animals, few are as impressively intimate as those that occur between ants and a variety of arthropods (reviewed in Hölldobler and Wilson, 1990). The trophobiotic associations, which involve the trophobiont providing nutrient-rich excretions or secre-

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TABLE 1
Species of *Dolichoderus* Herder Ants and of Allomyrmococcini Mealybugs Herded, and Region

Dolichoderus spp.	*Allomyrmococcini* spp.	Region
D. coniger	*Malaicoccus sp. E*[a]	Borneo (Sabah: Poring)
D. coniger	*M.* sp. L	Borneo (West Sarawak)
D. cuspidatus	*M. formicarii*	W. Malaysia (various areas)
D. cuspidatus	*M. moundi*	W. Malaysia (Genting Highl.)
D. cuspidatus	*M. riouwensis*	North Sumatra
D. cuspidatus	*M. takahashii*	W. Malaysia (South)
D. cuspidatus	*M.* sp. B	W. Malaysia (Bukit Larut)
D. cuspidatus	*M.* sp. D	Borneo (East Sarawak)
D. cuspidatus	Genus 1 sp. A	Borneo (Sabah: Poring)
D. cuspidatus	Genus 6 sp. A	Borneo (West Sarawak)
D. cuspidatus	Genus 6 sp. B	Borneo (West Sarawak)
D. erectilobus	*Paramyrmococcus chiengraiensis*	Thailand
D. feae	*Allomyrmococcus acariformis*	Thailand
D. furcifer	Genus 5 sp. A	West Sumatra
D. gibberifer	*Hippeococcus wegneri*	West Java
D. tuberifer	*Malaicoccus khooi*	W. Malaysia (Genting Highl.)
D. tuberifer	*M.* sp. F	Sumatra (West Sumatra)
D. tuberifer	*M.* sp. G	W. Malaysia (Southeast coast)
D. tuberifer	*M.* sp. H	W. Malaysia (Cameron Highl.)
D. tuberifer	*M.* sp. I	W. Malaysia (Pahang)
D. sp. A	Genus 2 sp. A	Borneo (Sabah: Poring)
D. sp. B	Genus 4 sp. A	Borneo (Sabah: Poring)
D. sp. C	Genus 2 sp. B	Borneo (Sabah: Kinabalu HQ)
D. sp. D	Genus 3 sp. A	Borneo (Sabah: Poring)
D. sp. E	Genus 6 sp. C	Borneo (West Sarawak)

[a]Provisional numbers and letters refer to genera or species to be scientifically described and named (from Dill and Maschwitz, 1998).

tions in exchange for protection from natural enemies by the ants (e.g., Pierce and Easteal, 1986; DeVries, 1991), appear to be particularly successful, with numerous Lepidoptera (e.g., lycaenids, riodinids, and tortricids [Maschwitz et al., 1986, 1987; Fiedler and Maschwitz, 1989; Hölldobler and Wilson, 1990]), Heteroptera (Maschwitz and Klinger, 1974, Maschwitz et al., 1987), as well as Sternorrhyncha and Auchenorrhyncha (Maschwitz, 1990) serving as the trophobiont. Trophobiotic interactions may involve merely the harvesting of honeydew excretions from some Coccoidea, or ants may actually stimulate the trophobiont to exude honeydew by stroking them.

The many thousands of species of scales (Coccoidea), greenflies (Aphidoidea), whiteflies (Aleyrodoidea), plant lice (Psylloidea), and various membracids or fulgorids that live in trophobiosis with ants exhibiting different stages of symbiotic evolution suggest that these associations have evolved independently numerous times. In the most advanced stages of trophobiosis, the relationship between participants is obligatory. Among those obligatory relationships that involve homopterans, ants establish new nests or colonies with their trophobiont, transferring one or more directly from the parent colony. At least 12 *Dolichoderus* (Dolichoderinae) ant species from Southeast Asia were discovered recently to herd more than 24 species of mealybugs in 10 genera (see table 1). These *Dolichoderus* herdsmen establish new colonies by fission and the workers bring with them a self-contained colony of mealybugs (Maschwitz and Hänel, 1985; Dill and Maschwitz, 1998, Maschwitz and Dill, 1998).

In other genera, the trophobiont is brought to the new nest site by young gynes. Gynes of the myrmecophytic ant, *Aphomomyrmex*

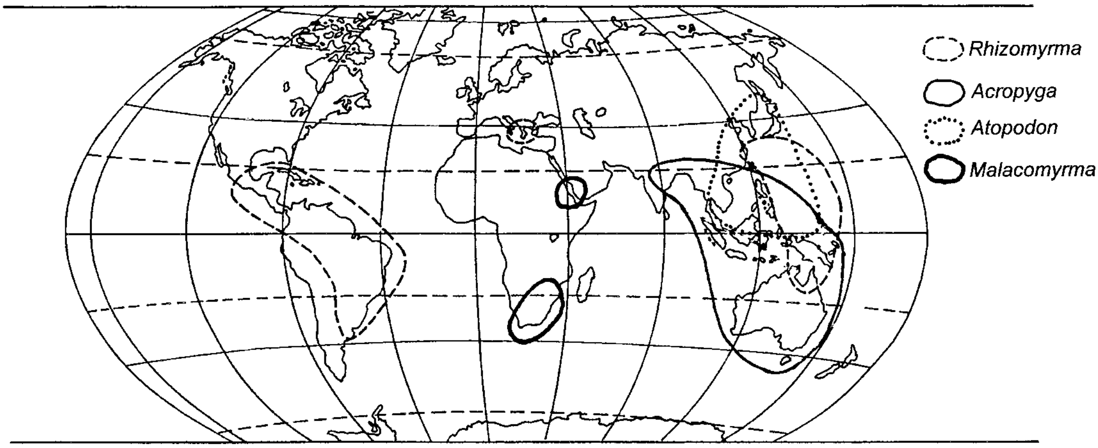

Fig. 1. World distribution of *Acropyga* subgenera (from Emery, 1925; Menozzi, 1936; Weber, 1944; Prins, 1982; Terayama, 1985; Williams, 1998).

afer (Formicinae), passively transfer the trophobiont to a new host plant via phoresis (Gaume et al., 2000). Young gynes of the Southeast Asian ant *Tetraponera* sp. near *attenuata* F. Smith (Pseudomyrmecinae) and of *Acropyga* (Formicinae), on the other hand, carry a trophobiont in their mandibles while swarming and bring it to the new nest site, a behavior that appears cognate to the transfer of symbiotic fungus by young gynes establishing colonies in the fungus-growing Attini of the New World (Weber, 1972). The gynes of *Tetraponera* sp. near *attenuata* F. Smith, which lives within the large hollow internodes of certain giant bamboo species (Klein et al., 1994), transport their trophobionts to empty bamboo internodes that had been excavated previously by stem-feeding pyralid caterpillars. *Tetraponera* gynes have been observed holding a mealybug for as long as 32 hours (Klein et al., 1992)!

Although rare in the species-rich, arboricolous pseudomyrmecine genus *Tetraponera,* the carrying of mealybugs by swarming gynes is widespread among the ground-dwelling, formicine genus *Acropyga* Roger. Colonies of *Acropyga* species that tend pseudococcids in South and Central America are found in mature tropical forests (Weber, 1944); in cacao, coffee, and banana plantations (Bünzli, 1935; Weber, 1944); and in grassy pastures (Weber, 1944; Eberhard, 1978). The colonies tend to be large and often surround the roots of many of these cultivated plants as well as some of the native plants on which the pseudococcids feed (Bünzli, 1935). There are two kinds of galleries, or chambers, in *Acropyga* ant nests (Bünzli, 1935; Weber, 1944; Delabie et al., 1991). The ‘‘blind’’ alley, where the mealybugs feed and are tended or ‘‘milked’’ by the ants, is a chamber that extends along the roots of the plants; the other chamber is used for rearing both ant and mealybug broods. The mealybugs rely on the workers to carry them through the galleries, and the ants appear to regulate honeydew production by adding or removing the mealybugs from the roots (Flanders, 1957). This network of underground tunnels may also be used to transport the mealybugs from nest site to nest site. *Acropyga* workers rarely, if ever, emerge from underground and, not surprisingly, have minute eyes and little cuticular sclerotization and coloration.

Currently, four subgenera of *Acropyga* are recognized (*Acropyga* sensu stricto, *Atopodon* Forel, *Malacomyrma* Emery, and *Rhizomyrma* Forel [Emery, 1925]) and each has a relatively well-defined geographic distribution (see fig. 1 for world distribution). *Acropyga* (*Rhizomyrma*) *paramaribensis* Borgmeier and *A. (R.) rutgersi* Bünzli are obligatory coccoidophiles that tend Pseudococcidae from a total of four genera. *Acropyga paramaribensis* tends five species of pseudococcids, one of which has also been found in nests of *A. rutgersi,* in the genera *Rhizoe-*

cus, Geococcus, and *Pseudorhizoecus.* Whereas four of these pseudococcid species have been found living independently, *Pseudorhizoecus proximus* Green and three other species have only been found living with *Acropyga,* evidence supporting their obligatory relationship. *Acropyga (R.) decedens* in Brazil was reported tending *Geococcus* and *Rhizoecus* mealybugs (Delabie et al., 1991). Table 2 lists all the mealybugs species known to associate with Neotropical *Acropyga.*

Although three of the four subgenera are known to have alate gynes that tote coccoids during nuptial flights, observations are relatively rare and little is known about the age of this behavior. Here we report a new record of *Acropyga* gynes carrying mealybugs from French Guiana and the discovery of several pieces of Dominican amber from the Miocene that contain *Acropyga* gynes with mealybugs, an indication that ants have had some type of symbiotic association with mealybugs for at least 15–20 m.y. The mealybugs in each of the three amber pieces represent three new species of a new genus and are described (see appendix 1). A piece of Dominican amber containing workers of *Azteca alpha* Wilson and 23 scale insects is also presented and the significance of finding scale insects together with ants in amber is discussed.

NEW RECORD OF EXTANT *ACROPYGA* TOTING MEALYBUGS

Observations and samples were taken by C. Johnson in central French Guiana (3°38′N, 53°13′W, approx. 300 m elevation) on December 26, 1996, near the town of Saül, approximately 6 weeks into the rainy season. A small swarm of male and female *Acropyga* was found during the early afternoon of a sunny day marked by only brief periods of light morning rain in a clearing of several acres that had several cabins and small plantations of fruits and vegetables. The surrounding area was intact, mature lowland Amazonian rainforest, which received an average annual rainfall of 240 cm/yr. Specimens from the swarm were collected and placed into small petri dishes (fig. 2). Several gynes were in copula and, after decoupling, promptly removed their wings without releasing the mealybug. None of the specimens survived in the dishes more than three hours. The swarm was approximately 2.5 m high, making it difficult to determine conclusively whether all the gynes were carrying mealybugs. Nonetheless, each gyne collected was holding a mealybug, suggesting that all had taken flight with mealybugs. That each gyne appeared to be carrying a mealybug is similar to observations made by Eberhard (1978) of swarming *Acropyga* in Colombia. No males were observed toting mealybugs and have never been reported doing so. Table 3 lists all the records of alate female *Acropyga* carrying pseudococcids; a representative alate female *Acropyga* from South Africa carrying a mealybug is illustrated in figure 3.

Some of the alate and dealate gynes carrying coccoids were preserved in ethanol. Several were critical point dried and examined with a scanning electron microscope. The habitus of the female mealybug is typically oval, and mandibles of the *Acropyga* gyne are distinctly scapulate, perhaps related to fossorial life but probably also for gentle transport of the tender coccids (fig. 4a, b). The species of *Acropyga* was not determined since the genus is in need of revision, despite the treatment by Weber (1944). lt is quite possible that this ant is one of the two species of *Acropyga* reported by Bünzli (1935) from nearby Surinam.

Whether the mealybugs carried by the gynes had mated was not determined. Reportedly, many coccoids taken on nuptial flights are mated females; however, others may be unmated females or even immature males that resemble females (Bünzli, 1935). In either case, this is unlikely to be problematic (1) since females of many mealybug species are parthenogenetic and thus could produce offspring in the new nest, and (2) if *Acropyga* is largely pleometrotic, as is *Acropyga paramaribensis* (Bünzli, 1935), and some cofoundresses transport female coccoids in addition to others transporting male coccoids to the new nest site.

AMBER FOSSILS OF *ACROPYGA*

Three pieces of Dominican amber, each containing an *Acropyga* gyne with a pseudococcid, were recovered from approximate-

TABLE 2

Mealybugs Associated with Neotropical *Acropyga* (corrections made by D. J. Williams)

Mealybug Species	Rhizoecini	*Acropyga* (*Rhizomyrma*) sp.	Country	Reference
Neochavesia[a] sp.	X	*A. berwicki*	Trinidad	Wheeler, 1935; Weber, 1944
Neochavesia sp.	X	*A. decedens*	Brazil	Delabie, unpublished
Neochavesia[a] sp.	X	*A. donisthorpei*	Guyana	Weber, 1944
Neochavesia[a] sp., possibly *eversi*[b]	X	*A. fuhrmanni*	Colombia	Roba, 1936; Weber, 1944; Flanders, 1957
Neochavesia[a] sp.	X	*A. goeldi*	Brazil	Weber, 1944
Neochavesia[a] sp.	X	*A.* near *paramaribensis*	Brazil	Delabie et al., 1989
Neochavesia caldasiae	X	*A. robae*	Colombia	Balachowsky, 1957
Neochavesia eversi	X	*A. kathrynae*	Panama	Beardsley, 1970
Neochavesia weberi	X	*A. paludis*	Guyana	Weber, 1944; Beardsley, 1970
Geococcus coffeae	X	*A. decedens*	Brazil	Delabie et al., 1989 Encarnacao et al., 1993
Geococcus coffeae	X	*A. urichi*	Brazil	Encarnacao et al., 1993
Geococcus coffeae	X	*A. paramaribensis*	Surinam	Bünzli, 1935
Rhizoecus coffeae	X	*A. decedens*	Brazil	Goeldi, in Wheeler, 1935
		A. paramaribensis	Surinam	Bünzli, 1935; Weber, 1944
			Colombia	Roba, 1936
		A. pickeli	Brazil	Borgmeier, 1927; Weber, 1944
Dysmicoccus radicis	—	*A. rutgersi*	Surinam	Bünzli, 1935
Pseudorhizoecus sp.	X	*A. wheeleri*	Costa Rica	Weber, 1957
Capitisetella migrans	X	*A. rutgersi*	Guyana	Bünzli, 1935
			Surinam	Bünzli, 1935
Pseudorhizoecus proximus	X	*A. paramaribensis*	Surinam	Bünzli, 1935
		A. rutgersi	Surinam	Bünzli, 1935
Rhizoecus sp.	X	*A. decedens*	Brazil	Delabie et al., 1989
Rhizoecus caladii	X	*A. paramaribensis*	Surinam	Bünzli, 1935
Rhizoecus falcifer Künckel d'Herculais	X	*A. paramaribensis*	Surinam	Bünzli, 1935
Unidentified	?	*Acropyga* sp.	Colombia	Eberhard, 1978
Unidentified	?	*Acropyga* sp.	Brazil	Campos and Morais, 1986
Unidentified	?	*A. bruchi*	Argentina	Weber, 1944
Unidentified	?	*A. guianensis*	Guyana	Weber, 1944
Unidentified	?	*A. mesonotalis*	Haiti	Weber, 1944
Unidentified	?	*A. quadriceps*	Trinidad	Weber, 1944
Unidentified	?	*A. trinitatis*	Trinidad	Weber, 1944
Unidentified	?	*A. urichi*	Trinidad	Weber, 1944

[a] Identified in the literature as *Eumyrmococcus* prior to the Balachowsky (1957) and Beardsley (1970) papers.

[b] See Beardsley (1970).

ly 30,000 small pieces of Dominican amber screened by D. Grimaldi. Two pieces, which contain complete gynes, are in the amber fossil collection of the Division of Invertebrate Zoology, AMNH. The third piece, in which only a portion of the gyne is preserved, is in the private collection of Roy Larimer. Virtually all Dominican amber pieces that are sold through dealers from Santiago and Santo Domingo come from various mines but are mixed together. Hence, exact provenance of these pieces cannot be stated with certainty. However, recent stratigraphic and other evidence presented by Iturralde and MacPhee (1996) and Grimaldi (1995) indicate that all pieces are approximately contemporaneous and were formed in the mid- to lower-middle Miocene (15–20 Ma). The fourth piece of Dominican amber was provided by M. v. Tschirnhaus (Frankfurt collection) and con-

Fig. 2. *Acropyga* from Saül, French Guiana. An alate gyne carrying a mealybug while in copula.

tains two *Acropyga* gynes with mealybugs and a male ant. This piece is approximately contemporaneous with the other Dominican amber pieces. Roy Larimer provided the fifth amber piece, which contains workers of *Azteca alpha* Wilson and mealybugs.

One amber piece from the Dominican Republic (Frankfurt collection) contains a single alate *Acropyga* gyne holding a mealybug between her mandibles and one *Acropyga* male (figs. 5a [detail] and 5b). The genus of the specimen was determined using the original description of Roger (1862). Of the four subgenera of *Acropyga*, only *Rhizomyrma* is recorded from the New World. Forel (1893) established *Rhizomyrma* as a subgenus of *Acropyga*, the characteristics of which are clavate antennae with 7–11 segments, 2-segmented maxillary and 3-segmented labial palpi, long, narrow mandibles with 3–4 teeth on an extremely oblique border, extremely small eyes, no ocelli, and triangular and distinct frontal area. The single female that Forel examined lacked wings and was described merely as workerlike. The male caste was not described.

Specimen Descriptions

Frankfurt collection (fig. 5a, b): **Female**: Length nearly 3 mm. Color light, no darker than light brownish-yellow. Eyes normal size, situated very close to base of mandibles. Ocelli close together, situated in small indentation. Clypeus bearing long hairs (especially on anterior margin); antennae 9-segmented. Pronotum very short; mesonotum much higher than pronotum, nearly flat on top, as long as wide, with rounded corners. Gaster more than 1 mm in length, tapered posteriorad. Wings translucent, with single cubital cell; veins brownish-yellow. **Male**: Length approximately 1.5 mm. Color distinctly darker than that of females, especially head and alitrunk. Head nearly as long as broad; eyes more than half head length, reaching from anterior clypeal margin to occiput. Mandibles long and narrow; antennae 10-segmented; scapes projecting beyond occipital margin. Ocelli protruding considerably. Alitrunk only slightly broader than head width; mesonotum slightly convex, much higher than propodeum; propodeum rounded on top with short part descending perpendicularly. Petiole base in profile broad, tapering to transverse ridge. Wings with single closed cubital cell.

Harvard collection: Specimen AMNH DR-10-228 is a dealate gyne (fig. 5c); her cuticle and that of the scale insect are slightly distorted by compression. Specimen AMNH DR-14-403 (fig. 5d) has an inner droplet of amber at the core, bearing a complete alate gyne that has been perfectly preserved and a mealybug (fig. 6 [detail]) fortuitously dislodged from her mandibles. See appendix 1 for descriptions of mealybugs.

The queens from specimens AMNH DR-10-228 and AMNH DR-14-403 resemble each other strongly with respect to head shape (fig. 5c, d). The head shape, however, is distinctly different from the Frankfurt collection specimen (fig. 5a, b). Whereas the occipital corners of the Frankfurt specimen are rounded and the occiput is nearly straight, the Harvard queens have distinctly pronounced occipital corners and an impressed occiput. Thus, the Frankfurt and Harvard queens represent different species.

AMBER FOSSILS OF *AZTECA*

Dominican amber piece AMNH DR-14-955 (2.4 × 2.8 × 1.1 cm) contains 9 workers of *Azteca alpha* Wilson and 20 female/nymphal and 3 male pseudococcids, plus debris and a female cecidomyiid midge (fig. 7). The mealybugs are not the same taxon as those discussed above; in fact, their mor-

TABLE 3

Observations of *Acropyga* Gynes Carrying Coccids (corrections made by D. J. Williams)

Acropyga species	Coccid species	Source of coccid: Mating flight	Source of coccid: In the nest	Country	Reference
Acropyga sp.[a] possibly *A. (Rhizomyrma)* sp.[b] *paleartica*	*Eumyrmococcus corinthiacus* Williams	X		Greece	Buschinger et al., 1987
A. (Acropyga) acutiventris	unidentified	X		China	Brown in Eberhard, 1978
A. (Acropyga) acutiventris	*Xenococcus annandalei*	X		India	Silvestri, 1924 Williams, 1998
A. (Acropyga) acutiventris	*Xenococcus acropygae* Williams	X	X	Austral-asia	Williams, 1998
A. (Atopodon) ambigua	*Eumyrmococcus kusiacus* Williams	X	X	Papua New Guinea	Williams, 1998
A. (Acropyga) ambigua	*Xenococcus acropygae* Williams	X	X	Papua New Guinea	Williams, 1998
A. (Malacomyrma) arnoldi	*Eumyrmococcus scorpioides*		X	South Africa	Prins, 1982
A. (Rhizomyrma) sp.	unidentified	X		Colombia	Eberhard, 1978
A. (Rhizomyrma) sp.	unidentified	X		Brazil	Campos and Morais, 1986
A. (Rhizomyrma) fuhrmanni	*Neochavesia*[c] sp.	X		Colombia	Roba, 1936
A. (Rhizomyrma) fuhrmanni	*Neochavesia*[c] sp.	X		Colombia	Flanders, 1957
A. (Rhizomyrma) kinomurai	*Eumyrmococcus* sp.	X	X	Japan	Williams & Terayama, 2000
A. (Rhizomyrma) lauta	*Eumyrmococcus kolombangarae* Williams	X	X	Solomon Is.	Williams, 1998
A. (Rhizomyrma) lauta	*Eumyrmococcus kusiacus* Williams	X	X	Solomon Is.	Williams, 1998
A. (Rhizomyrma) lauta	*Xenococcus acropyga* Williams	X	X	Solomon Is.	Williams, 1998
A. (Rhizomyrma) nipponensis	*Eumyrmococcus nipponensis* Terayama		X	Japan	Terayama, 1986
A. (Rhizomyrma) paramaribensis	*Rhizoecus coffeae*	X		Surinam	Bünzli, 1935
A. (Rhizomyrma) paramaribensis	*Rhizoecus coffeae*	X[d]		Colombia	Roba, 1936
A. (Rhizomyrma) near *paramaribensis*	*Neochavesia* sp.		X	Brazil	Delabie et al., 1991
A. (Rhizomyrma) rutgersi	*Capitisetella migrans*	X	X	Guyana	Weber, 1957
A. (Rhizomyrma) sauteri	*Eumyrmococcus smithii* Silvestri	X	X	Japan	Terayama, 1988 Williams, 1998
A. (Rhizomyrma) wheeleri	*Pseudorhizoecus* sp.	X		Costa Rica	Weber, 1957
Cladomyrma (misidentification)	unidentified			Indonesia	Agosti, 1991 Agosti & Collingwood, 1987
A. (Rhizomyrma) decedens	*Geococcus coffea*		X	Brazil	Encarnacao et al., 1993
A. (Rhizomyrma) decedens	Ortheziidae		X	Brazil	Encarnacao et al., 1993
A. (Rhizomyrma) urichi	*Geococcus coffea*		X	Brazil	Encarnacao et al., 1993
A. (Rhizomyrma) urichi	Ortheziidae		X	Brazil	Encarnacao et al., 1993

[a] Incorrectly identified as *Plagiolepis* sp. according to Agosti and Collingwood (1987).
[b] See Menozzi (1936).
[c] Identified as *Eumyrmococcus* in the literature prior to the Balachowsky (1957) and Beardsley (1970) papers.
[d] Observations were insufficient to determine whether the observed mating flights belong to one or two of the referred ant species.

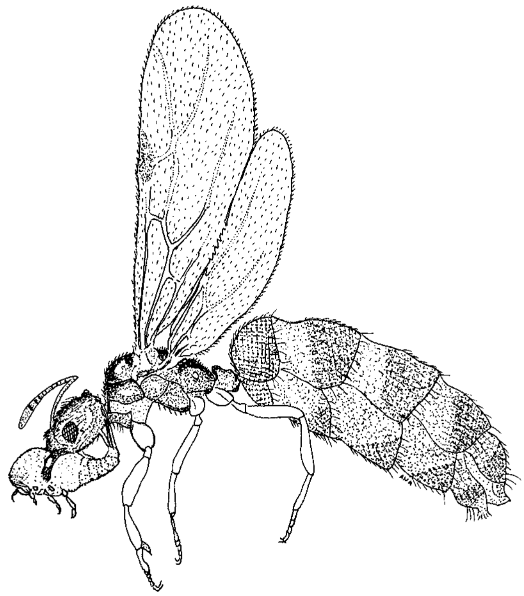

Fig. 3. Alate female of a South African *Acropyga* carrying a *Eumyrmococcus* mealybug (redrawn from Prins [1982] by Williams [1993]).

phology is much more generalized than the morphology of mealybugs that are obligate trophobionts. For example, the body shape is oval, not elongate-pyriform, and the antennae are relatively short. Furthermore, the small to fairly large cloud of milky substance around the center of the dorsal surface of each mealybug, including various instars, suggests that the mealybugs in this amber piece have exuded wax, possibly from between abdominal segments 3 and 4. Thus, it has been hypothesized that these mealybugs were not as intimately symbiotic with *Azteca* as are the mealybugs with *Acropyga* (J. Koteja, personal commun.).

It is, however, almost certain that these coccoids were tended by the ants, even though none of the workers is actually carrying a mealybug. *Azteca* species, like most dolichoderines, are renowned for tending homopteran insects. And while *Azteca alpha* is probably the most common insect species in Dominican amber, comprising at least 30%, and perhaps as much as 50%, of all ant inclusions, coccoids, particularly nymphs, are extremely rare. The chance of finding a cluster of coccoids in a piece of Dominican amber is infinitesimally small, as is the chance of finding a fortuitous cluster of coccoids and *Azteca alpha* ants. The presence of males and females coccoids at several developmental stages indicates that the amber captured them virtually in situ. Although the transport of mealybugs by *Acropyga* gynes implies a symbiotic relationship, this amber piece with *Azteca* ants and mealybugs is probably the

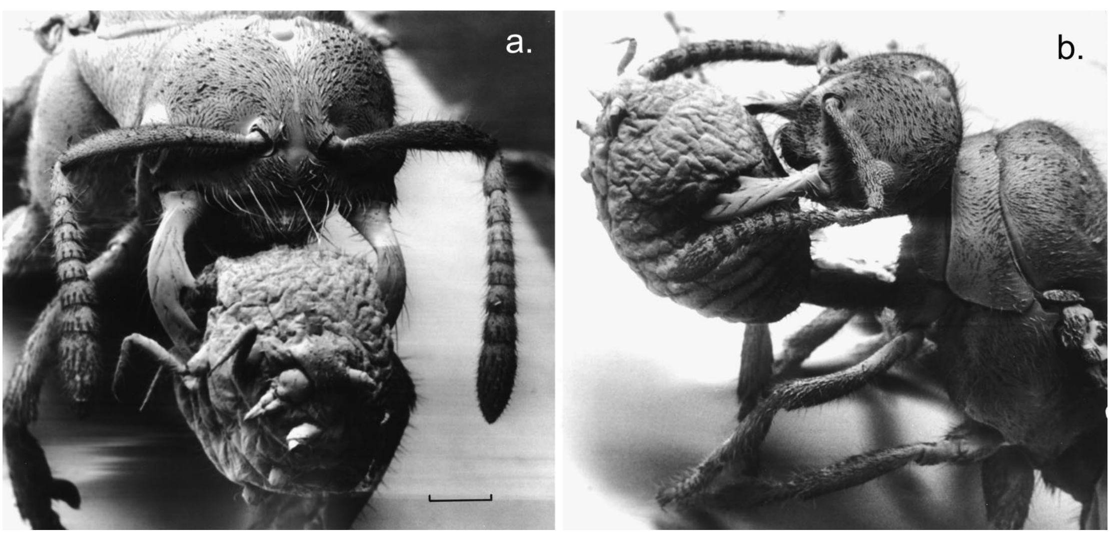

Fig. 4. Scanning electron micrographs (40–50×) of an *Acropyga* gyne from Saül, French Guiana, carrying a mealybug (collected by C. Johnson). **a.** Frontal view. **b.** Oblique lateral view.

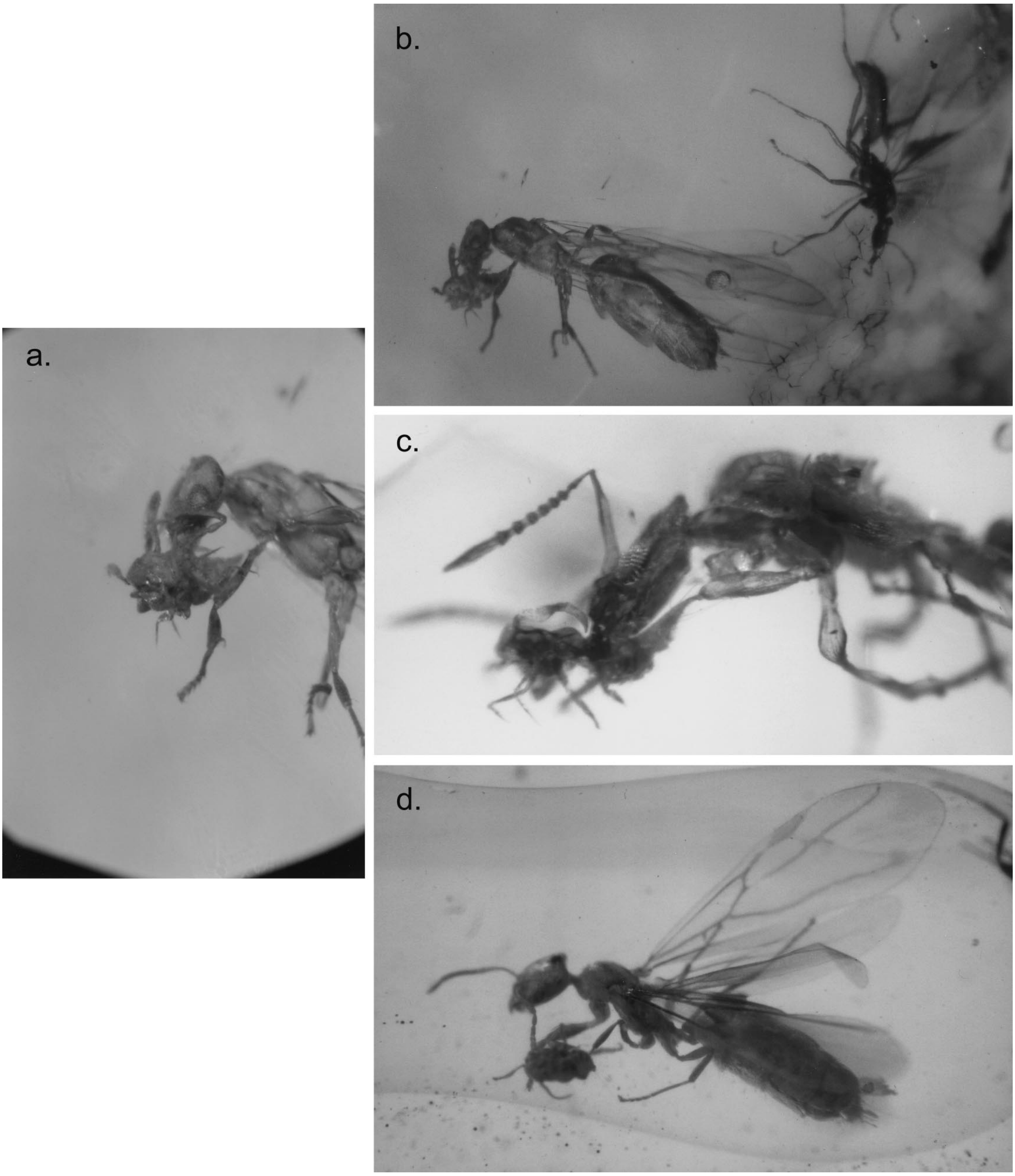

Fig. 5. **a.** *Acropyga* sp. 1, gyne with mealybug between mandibles in amber from the Dominican Republic (Frankfurt collection piece, detail). **b.** *Acropyga* sp. 1, alate gyne and male in Dominican amber (Frankfurt collection piece). **c.** *Acropyga* sp. 2, dealate gyne and mealybug in Miocene amber from the Dominican Republic (Harvard collection piece, AMNH DR-10-228). **d.** *Acropyga* sp. 2, alate gyne and mealybug in Miocene amber from the Dominican Republic (Harvard collection piece, AMNH DR-14-403).

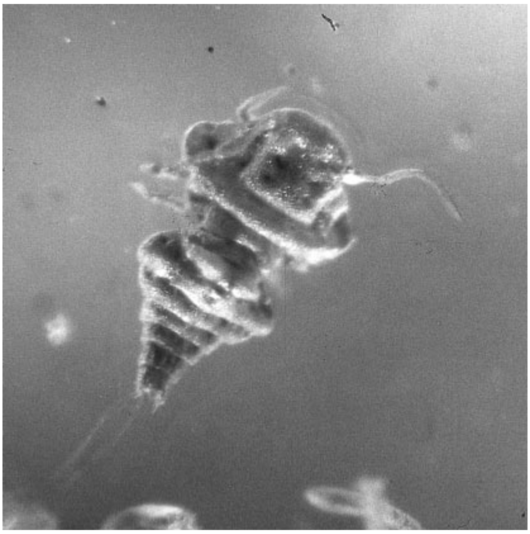

Fig. 6. Mealybug (detail) in amber (Harvard collection piece, AMNH DR-14-403).

earliest documentation of actual homopteran-tending behavior.

DISCUSSION

Considering the disparate geological records of ants and pertinent groups of homopterans, particularly Sternorrhyncha, the discovery of current symbiotic relationships in Miocene amber has profound implications for understanding ant and homopteran coevolution.

Fossil Record of the Ants

Knowledge of Cretaceous ants began merely 30 years ago, with the discovery of two workers (*Sphecomyrma freyi* Wilson and Brown) in a piece of Turonian (90–94 Ma) amber from central New Jersey (Wilson et al., 1967a, 1967b). In the last 15 years, however, many new species and genera of Cretaceous ants have been described, primarily from mid to upper Cretaceous rocks and amber of Russia and Kazakhstan (Dlussky, 1975, 1983, 1987); from Aptian limestone (ca. 110 Ma) of Brazil (Brandão et al., 1990); and from upper Cretaceous amber of Canada (Wilson, 1985a and unpub. data). Wilson (1987) revised the taxonomy of Dlussky's Cretaceous ants, synonymizing several genera. Recently, Grimaldi et al. (1997) reported another worker and a possible male of *Sphecomyrma* from new collections of New Jersey amber, as well as several other genera of primitive ants based on males, and even a new genus of a very primitive ponerine. Grimaldi et al. (1997) reviewed and evaluated all of the Cretaceous records of ants, and concluded that the specimens in amber are the only definitive Cretaceous Formicidae; the specimens compressed in rock lacked critical features and were deemed ambiguous. Thus far, all ants in Cretaceous amber are among the most primitive morphologically and it is likely the origin of the true ants dates approximately 100–120 Ma.

The fossil record for ants is exceedingly poor in the lowest Tertiary (Paleocene). Only a few taxa are described from the amber of Sakhalin Island, Far East Russia (Dlussky, 1988), apparently Paleocene in age, whereas several taxa are described from Eocene Arkansas amber (Wilson, 1987) and more than 50 genera and hundreds of species are reported from early Eocene Baltic amber (Wheeler, 1915). The lower Tertiary ants indicate a global fauna that was entirely transformed from the Cretaceous fauna, mostly with the emergence of modern subfamilies in the Paleocene (although the Ponerinae actually appear in the Cretaceous) and many modern genera in the early Oligocene (Lutz, 1986).

Fossil Record of the Sternorrhyncha

The evolutionary history of Sternorrhyncha greatly exceeds the evolutionary history of ants. Heie (1987) reviewed the fossil record of aphids (superfamily Aphidoidea), and determined the oldest record thus far to be *Triassoaphis cubitus* Evans from the Triassic of Australia. From the Cretaceous amber of Canada, Richards (1966) reported six genera in three families; from Siberian amber, Konova (1976, 1977) reported eight families, two of them extant. Aphid nymphs are common in both of these ambers and are, in fact, the most abundant inclusions in Canadian amber. This strongly contrasts with the slightly older New Jersey amber, in which aphids are extremely rare (only two specimens out of 1000 insects have been found thus far) and coccoids are the most abundant kind of inclusion (20% of all inclusions) (Grimaldi, 1997). Coccoids are very

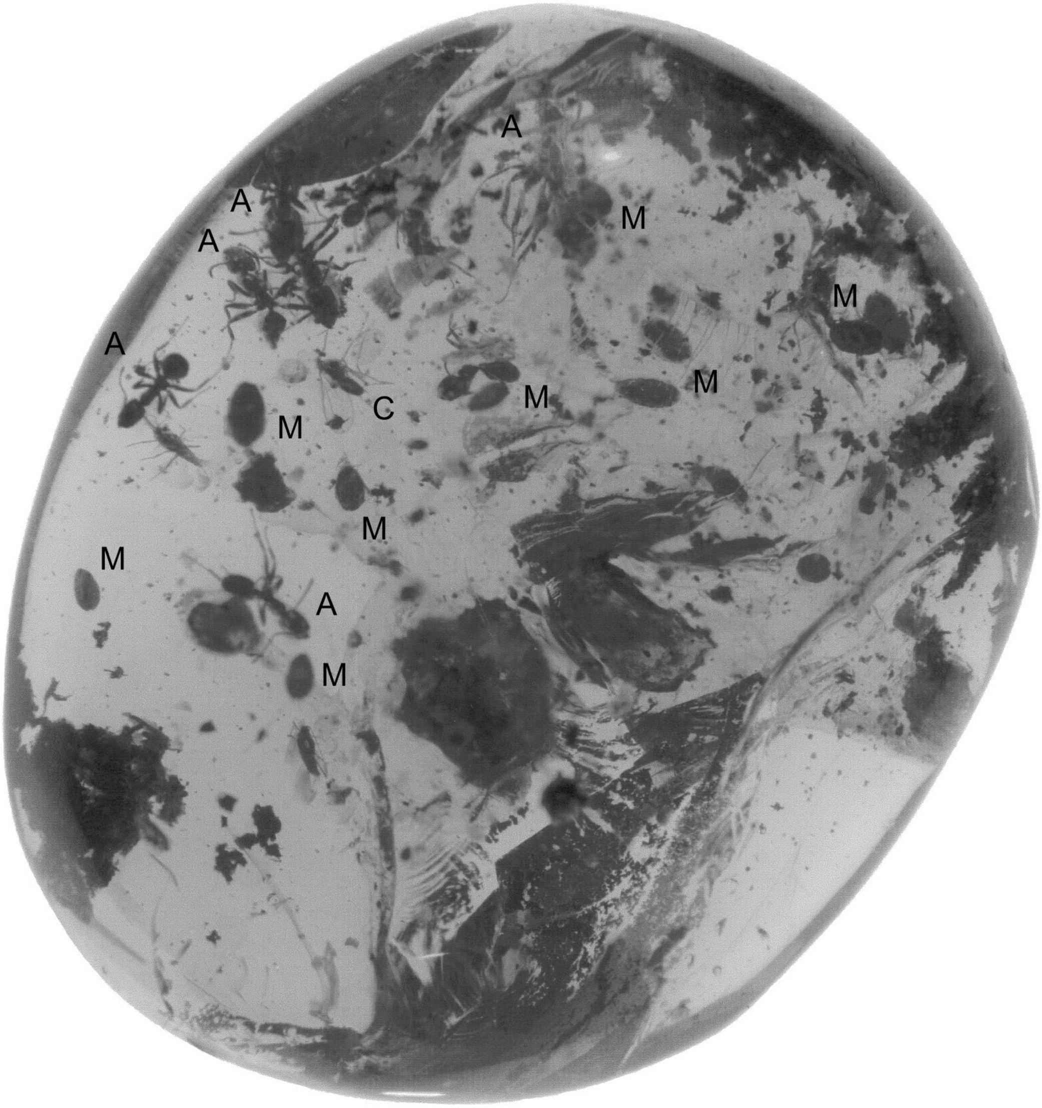

Fig. 7. *Azteca alpha* Wilson workers with mealybugs in Dominican amber (Larimer piece, AMNH DR-14–955). A = *Azteca alpha* Wilson; M = mealybug; C = Cecidomyiidae.

rare in Canadian amber, and it is unknown whether the difference between Canadian and New Jersey amber is due to ecological replacement of one sternorrhynchan group for the other, or to taxonomic circumstance. Coccoids have a sparser fossil record, one that is restricted primarily to the Cretaceous, and virtually all of the specimens are in amber, a probable result of their frail, minute bodies. The oldest coccoids are in lower Cretaceous amber of Lebanon, whereas younger ones [*Electrococcus canadiensis* Beardsley (1969)] are in Canadian amber, and undescribed forms are in Siberian and New Jersey ambers. The specimens we found in Miocene amber belong to an extinct coccoid genus that had already radiated into three different species (see appendix 1). Koteja (1989) has listed the Mesozoic scale insect fossils. In the Oligocene, seven families were preserved in Baltic amber, all of which are still in existence (Koteja, 1985, 1987).

Age and Trends of Ant–Homopteran Symbioses

The Dominican amber specimens of *Acropyga* captured with coccoids in their mandibles reported here represent the oldest *definitive* record of ant-homopteran symbiosis, although an earlier origination of such associations is likely (Grimaldi and Agosti, 2000). Little is known about Cretaceous formicines; however, the widespread use of homopterans by almost all formicine genera suggests that the relationship originated as early as the Cretaceous (Grimaldi and Agosti, 2000). Nonetheless, the primitive nature of the Cretaceous ants and the tendency of most primitive living subfamilies of ants to be largely predatory and/or scavenging suggest that the relationship between Cretaceous ants and coccoids was not yet mutualistic, if even obligatorily commensalistic, *despite* the probable widespread availability of honeydew in the Cretaceous.

The oldest report of ant-homopteran symbiosis was based on a piece of amber containing a group of *Germaraphis* aphids and 15 workers of *Iridomyrmex* (Wheeler, 1915). However, because *Germaraphis* aphids and *Iridomyrmex* ants are common in Baltic amber and are sometimes found grouped together, Heie (1987) considered the assemblage of *Germaraphis* with *Iridomyrmex* in that piece to be merely coincidental. Heie, furthermore, doubted that aphids with strong wax production, e.g., *Germaraphis* spp., had associations with ants (personal commun. in Boucot, 1990: 477). Nonetheless, Hölldobler and Wilson (1990) agreed with Wheeler's original conclusion that the two organisms were symbiotic. Although Wheeler's specimen is equivocal, an Eocene/Paleocene age of ant-homopteran symbioses is certainly expected, given the Miocene evidence of intimate relationships between extant ants and mealybugs.

Today, the genus *Acropyga* is distributed in Central and South America, Europe, Africa, Southeast Asia, and Australia. Inclusions of this genus in amber, however, are known only from Dominican amber, represented by two clearly distinguishable species. No *Acropyga* species have been found in Baltic amber. From this, one might conclude that *Acropyga* did not yet exist in the Oligocene and that the genus probably originated in the New World where the earliest findings are preserved in Miocene amber. The restricted distribution of the *Tetraponera* mealybug-carriers to the paleotropics and the fact that this genus is monotypic suggest that *Tetraponera* is substantially younger than *Acropyga*. Likewise, the regional restriction of *Dolichoderus* herdsmen ants to Southeast Asia indicates that they, too, are younger than *Acropyga*, albeit very successful. At least a dozen species of *Dolichoderus* tend more than two dozen species of mealybugs (table 1).

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APPENDIX 1

Descriptions of a New Genus and Three New Species of Rhizoecinae (Hemiptera: Coccoidea) Associated with Ants of the Genus *Acropyga* Roger in Dominican Amber

D. J. WILLIAMS

The three mealybug species discussed here, found in Dominican amber, belong to the subfamily Rhizoecinae and show a combination of characters that have not been observed so far. Within this subfamily, discussed recently by Williams (1998), most of the genera have the body elongate-oval, rotund, or only weakly pyriform. Three genera, *Neochavesia* Williams and Granara de Willink, *Eumyrmococcus* Silvestri, and *Xenococcus* Silvestri, differ in possessing a strongly dilated cephalothorax and a long tapered abdomen. Furthermore, these three genera, *Neochavesia* in the New World, and *Eumyrmococcus* and *Xenococcus* in the Old World, are associated with the ant genus *Acropyga*. *Neochavesia* differs from the two Old World genera in having protruding and rounded anal lobes and each antenna with 4 or 5 segments. In *Eumyrmococcus* and *Xenococcus,* each antenna has 2–4 segments and the anal lobes do not protrude. *Xenococcus* possesses antennae that are stout and about as long as the body but in *Eumyrmococcus* they are slender and short.

To separate the genera of the Rhizoecinae, there are other minute characters that can only be observed under high power in slide-mounted specimens. In the species under discussion, many of these characters cannot be observed when viewed under a stereoscopic microscope, and only some major characters can be discussed. Each of the three species found in Dominican amber, associated with ants of the genus *Acropyga,* possess a strongly dilated cephalothorax. The abdomen tapers gradually to a very narrow posterior end. Although the anal lobes are undeveloped or weakly developed, each anal lobe area possesses 4 long setae. The antennae are slender and 6-segmented. These are characters not found in *Eumyrmococcus, Neochavesia,* or *Xenococcus* but the new genus is most closely related to *Eumyrmococcus* and *Neochavesia.*

In *Rhizoecus* Künckel d'Herculais and most related genera, the antennae when developed, are short, usually with the segments as wide as or wider than long. The antennae never have more than 6 segments and this number may be basic to the whole subfamily. The new genus, therefore, with slender antennae having 6 segments that are mostly longer than wide, may be a link between the *Rhizoecus* group of genera and the *Eumyrmococcus* group.

As with many specimens examined in amber, it is sometimes difficult to measure certain structures exactly. Furthermore, it may be impossible to view the insect or structures in the correct plane to examine them critically.

Apart from the piece of amber from Dominican Republic containing a mealybug held in the mandibles of an ant, presently deposited in Germany, three other pieces have been kindly made available for study by David Grimaldi, Division of Invertebrate Zoology, AMNH. Two of these contain mealybugs that are described here, but the third mealybug (Miocene, Dominican Republic, DR-10-228 AMNH), held in the mandibles of a species of *Acropyga,* is too distorted to examine and describe adequately.

Abbreviations of the depositories are: **AMNH,** American Museum of Natural History, New York, NY, USA; **SMF,** Senckenberg Museum, Frankfurt am Main, Germany.

Electromyrmococcus Williams, new genus

TYPE SPECIES: ***Electromyrmococcus abductus,*** new species.

DESCRIPTION: Body with cephalothorax dilated, abdomen gently tapering to narrow posterior segment. Posterior end straight with anal lobes not developed, or with slightly developed anal lobes, last segment with 2 groups of 4 long flagellate setae, these either spaced on ventral margins or grouped on anal lobes. Legs normal, slender; trochanter + femur about as long as tibia + tarsus; tibia and tarsus subequal in length; claw long and slender. Antennae about as long as legs, slender, 6-segmented, segments mostly longer than wide.

COMMENTS: With a dilated cephalothorax and a long tapering abdomen, this genus appears to be related to the extant genera *Eumyrmococcus* and *Neochavesia.* It differs from the tropical New World genus *Neochavesia* in lacking rounded protruding anal lobes and from *Eumyrmococcus,* known from the tropical and temperate areas of the Old World, in possessing a group of 4 long setae in the position of each anal lobe. In *Eumyrmococcus,* the long setae on each anal lobe form a group of 3 except in species with the long setae not differentiated from others on the lobes. The antennal segments in *Eumyrmococcus* number 2–4 and in *Neochavesia* 4 or 5. In *Electromyrmococcus,* the antennae are long and slender, 6-segmented, 300–365 μm long, longer than in many species of *Eumyrmococcus* and *Neochavesia.* A new species of *Eumyrmococcus,* however, is currently being described with antennae as long as 620 μm (Williams and Terayama, in press).

ETYMOLOGY: The name *Electromyrmococcus* is based on the Greek word *elektron,* as used for amber, *myrmo-* from *myrmex,* the Greek word for ant, and the generic name *Coccus,* referring to the ant-attended genus found in amber.

Electromyrmococcus abductus Williams, new species

Figure 8

DESCRIPTION: Adult female about 0.7 mm long, elongate-pyriform, cephalothorax dilated, abdomen tapering gradually, segmentation distinct but segments not lobed laterally, segment VIII very narrow with anal opening slightly dorsal in position, situated between barely perceptible anal lobes; each lobe with 4 setae, each about 230 μm long, equispaced laterally from tip of each lobe to about half length of segment. Shorter abdominal setae present anterior to anal lobe setae on abdominal segment VIII, and in pairs arising laterally on venter of preceding abdominal segments. Antennae each about 300 μm long, with 6 segments each longer than wide. Legs well developed, slender, about as long as antennae; tibia and tarsus subequal in length; claw long and slender.

Holotype, adult female, Hispaniola: Dominican Republic (Provincia de Puerto Plata), mine: La Toca (near La Cumbre), in mandibles of *Acropyga* sp. (M. von Tschirnhaus) (SMF).

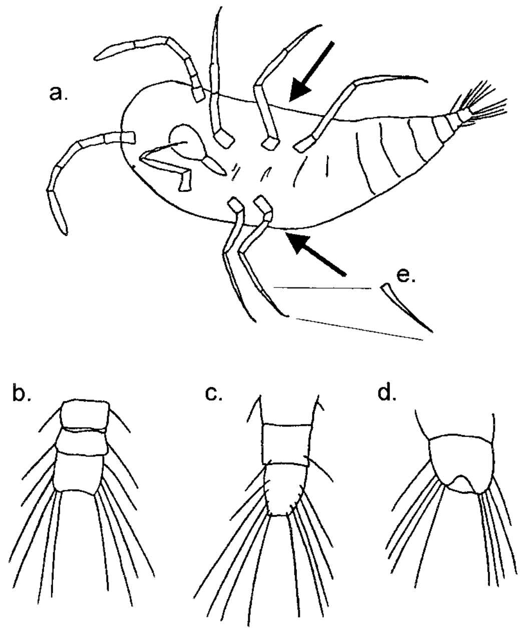

Fig. 8. *Electromyrmococcus abductus* Williams, new species **a.** Adult female, ventral aspect. Arrows point to area held by ant with mandibles. **b.** Posterior segments, dorsal aspect. **c.** Posterior segments, ventral aspect. **d.** Anal area. **e.** Claw.

DESCRIPTION: This species differs from the other two described here in having the long anal lobe setae spaced instead of grouped on each anal lobe.

ETYMOLOGY: The epithet *abductus* is Latin for ‘‘carried off’’ in allusion to being held in the mandibles of the ant.

Electromyrmococcus inclusus Williams and Agosti, new species

Figure 9

DESCRIPTION: Adult female 0.76 mm long; cephalothorax strongly dilated, about 0.46 mm wide; abdomen tapering, abdominal segmentation well defined, each segment stepped to narrow segment VIII, 83 μm wide at base; anal opening dorsal at apex. Abdominal segment II with a pair of dorsal submedian projections. Anal lobes slightly developed, each with 4 long flagellate setae about 265 μm long. Shorter setae present on lateral margins of anterior segments. Antennae slender, each about 365 μm long, with 6 segments. Legs well developed; hind trochanter + femur about 165 μm long.

Holotype adult female, Dominican Republic, Miocene, Dominican amber, No. DR-14–403 (AMNH).

DESCRIPTION: The specimen on which the description is based is distorted and has a deep constriction between the thorax and abdomen. This constriction may have been caused by the ant holding the mealybug in the mandibles. Although the mealybug is detached, it is only about 650 μm from the mandibles, and the ant probably released it immediately when being trapped. After a mealybug is held in the mandibles in life and then released, the body of the mealybug resumes its normal shape, but the body in the specimen described, apparently had no such time. Furthermore, it would be unlikely for any female mealybug to have a deep constriction between the thorax and abdomen because the ovaries in mealybugs are paired structures occupying almost the whole body cavity (Ali, 1959; Yadava, 1966). In gravid females, the eggs or embryos completely fill the insect as far forward as the head and there is never a constriction between the thorax and abdomen to impede oviposition. The lateral lobes on the thorax were also probably caused by pressure of the ant's mandibles, resulting in distortion.

Electromyrmococcus inclusus possesses small anal lobes that are more developed than in *E. abductus* and *E. reginae* described here.

ETYMOLOGY: The epithet *inclusus* is a Latin participle meaning ''enclosed'' or ''imprisoned,'' referring to the specimen being trapped in the amber.

Electromyrmococcus reginae Williams, new species

Figure 10

DESCRIPTION: Body of adult female 0.80 mm long, cephalothorax dilated, abdomen gently tapering, abdominal segment VIII narrow, anal lobes very slightly developed, each with 4 long flagellate setae, mostly about 265 μm long; segmentation of abdomen well defined, segments protruding postero-laterally to form lateral lobes so that segments appear to be stepped. Antennae slender, each about 333 μm long, with 6 segments. Legs well developed and clothed in some setae, those on trochanters longest; hind tibia + tarsus about 200 μm long; claw long and slender. Labium about 100 μm long, with long setae at apex.

Holotype, adult female, Dominican Republic, in mandibles of a queen *Acropyga* sp. RL No. 6 (AMNH).

DESCRIPTION: This species is closely related to *E. inclusus* in possessing long setae at the apex of each anal lobe. The anal lobes of *E. reginae*, however, are scarcely developed, whereas in *E. inclusus* they are more conspicuous.

ETYMOLOGY: The epithet *reginae* is based on the Latin word *regina* in the sense of belonging to a queen; in this case a queen ant.

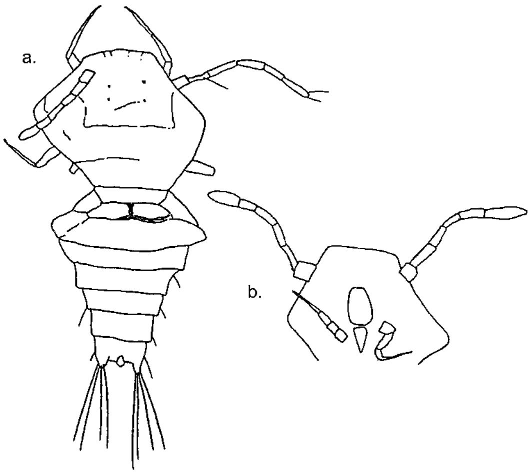

Fig. 9. *Electromyrmococcus inclusus* Williams and Agosti, new species **a.** Adult female, dorsal aspect. **b.** Cephalothorax, ventral aspect.

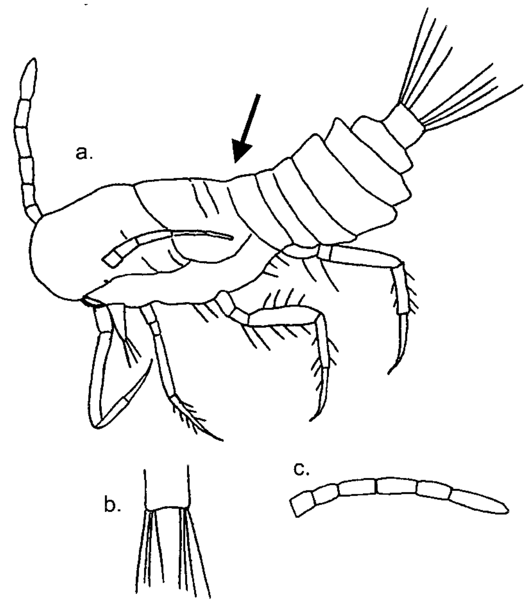

Fig. 10. *Electromyrmococcus reginae* Williams, new species **a.** Adult female, dorsolateral aspect. Arrow points to area held by ant with mandibles. **b.** Posterior segment, dorsal aspect. **c.** Antenna.

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