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Research article

Acromyrmex insinuator new species: an incipient social parasite of fungus-growing ants

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Summary

The two known social parasites of fungus-growing ants (tribe Attini) occupy an advanced grade of social parasitism characterized by absence of a worker caste and highly derived morphology and behavior. In contrast, the Panamanian *Acromyrmex insinuator* new species, described here, appears to occupy an early grade of social parasitism in which males, females, and minor workers are nearly indistinguishable from those of the host species. Based on allozyme and morphological evidence, the host, *A. octospinosus* ssp. *echinatior*, is clearly different and reproductively isolated from the sympatric *A. octospinosus* ssp. *octospinosus*, and is therefore elevated to species status.

Introduction

The 203 species of fungus-growing ants (subfamily Myrmicinae, tribe Attini) cultivate fungus gardens upon which they obligately depend for nourishment. Two social parasite species are exceptions to this rule, consuming but presumably not cultivating the fungus of their hosts. Males and females of these species are so morphologically aberrant that Gallardo (1916) erected the monotypic genus *Pseudoatta* to receive the northern Argentinean species *Pseudoatta argentina*. Because one of the first specimens was received along with two workers of *Acromyrmex balzani*, the latter species was initially suspected to serve as the host (Gallardo, 1916; Santschi, 1926); however, subsequent work established that both the typical form of *P. argentina* and the dubious subspecies *P. argentina platensis* parasitize *Acromyrmex lundi*

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(Santschi, 1926; Bruch, 1928; Gallardo, 1929). Recently, Delabie et al. (1993) reported (but did not formally describe) a second *Pseudoatta* species, a social parasite of *Acromyrmex rugosus* in Bahia, Brazil.

Both species, the only known attine social parasites, occupy extreme grades of social parasitism in which the worker caste has been lost and morphology has become highly specialized (Hölldobler and Wilson, 1990: 467–469). Here we describe an attine ant that occupies an apparently early grade of social parasitism in which a worker caste is produced and morphology closely resembles that of the host. We also examine the taxonomic status of the sympatric free-living forms of *Acromyrmex octospinosus sensu lato* as only a subset of these colonies appeared to be susceptible to the social parasite.

Methods

Fifty colonies of what originally were presumed to be *Acromyrmex octospinosus* subspecies *echinatior* were collected in Gamboa, Panama Canal Zone, Panama, during three time periods: 26 April to 9 May 1993, 17 April to 30 April 1994, and 18 January to 4 February 1996 (Appendix 1). This material was screened for variable allozyme loci to study relatedness and queen mating frequency (to be reported elsewhere). During these screenings it became clear that some allozyme loci were fixed for specific alleles without any detected heterozygosity. Data of this kind are evidence for the existence of several reproductively isolated gene pools, representing separate species when occurring sympatrically (Boomsma et al., 1990). Both allozymatic evidence for reproductive isolation of sympatric *Acromyrmex* species in Gamboa and morphological descriptions and analyses of this material are presented in this study.

Allozyme analyses of selected individuals from a subset of the 50 nests were carried out with 12% horizontal starch gel electrophoresis. Malate dehydrogenase (MDH) was run in a Tris (27 g/l) – Citric acid (18.07 g/l) tray buffer (pH 6.3) and a Tris (0.97 g/l) – Citric acid (0.63 g/l) gel buffer (pH 6.7). Aconitase (ACON) was run in a Tris (83.2 g/l) – Citric acid (30 g/l) tray buffer (pH 8.0) and a Tris (2.77 g/l) – Citric acid (1.1 g/l) gel buffer (pH 8.0). Mannosephosphate isomerase (MPI) was run in a Tris (18.17 g/l) – Boric Acid (5.15 g/l) – NaEDTH (1.24 g/l) tray buffer (pH 8.7) and a Tris (5.45 g/l) – Boric Acid (1.55 g/l) – NaEDTH (0.37 g/l) gel buffer (pH 8.7). For internal lab procedures in Aarhus these buffers are normally referred to as S4, S5 and F2, respectively. The S4 and F2 gels were run for 4 hours at 60 mA, whereas the S5 gel was run for 4.5 hours at 90 mA.

Morphological examination of individuals from these nests (males, females, the largest caste of major workers, and the smallest caste of minor workers) was undertaken in order to determine whether any morphological characters could be discovered that correlated with the pattern discovered by the allozyme analyses. Specimens from the Panamanian nests were compared with specimens of *A. octospinosus sensu lato* from throughout its geographic range, as well as with type material of *A. volcanus* and of the subspecies *A. octospinosus cubanus*, *echinatior*, *ekchuah*, and *inti*. This material included specimens from the following collections: American Museum of Natural History (AMNH), Museum of Comparative Zoology, Harvard (MCZ); National Museum of Natural History (NMNH); Los Angeles County

Museum (LACM): Muséum d'Histoire naturelle, Geneva, Switzerland (A. Forel Collection). Measurements follow Brown (1953); terminology follows Bolton (1994) and Gonçalves (1961).

Results and taxonomy

Protein gel electrophoresis revealed that the Panamanian nest collections actually included three distinct species: (1) A "non-parasitized" species, represented by all castes and always occurring alone, (2) a "host" species, represented by all castes and sometimes occurring alone and sometimes occurring in mixed nests with a third species, (3) a "parasite" species, represented only by males, females, and the smallest caste of minor workers, and always occurring in mixed nests with the "host" species. More detailed DNA microsatellite analysis of the nests containing mixtures of the host and parasite species (Bekkevold, Frydenberg, and Boomsma, in prep.) identified two categories of nests: those that contained alates of both species, and those that contained alates only of the parasite.

The allozyme loci analyzed were monomorphic within these species but consistently segregated for different alleles among species. The observed migration distances (mm) in the gels are given in Table 1, with a minus sign when the enzyme products migrated cathodally. Total sample sizes in Table 1 were 6 gynes and 4 males for *A. octospinosus*, 6 gynes and 4 males for *A. echinatior* new status, and 3 gynes and 3 males for *A. insinuator* new species. Earlier gels run in other, less clearly separating buffers showed similar differences as those given in Table 1 between workers and males of *A. octospinosus* and *A. echinatior* for ACON (sample sizes: 50 workers and 4 males and 75 workers and 6 males, respectively) and MPI (workers: sample sizes 4 and 16, respectively) and for ACON between 5 gynes and 5 males of *A. insinuator* new species and 25 workers and 5 males of *A. echinatior*.

Because specimens were destructively sampled for protein electrophoresis, it was not possible to study the same individuals for both allozyme complement and morphology. However, morphological study took advantage of the protein electrophoretic results by drawing on workers and alates of known identity from nests of the non-parasitized species, unparasitized nests of the host species, and nests in which the alate complement very probably consisted entirely of the parasite species. Alates from these "pure" nests of host and parasites were then compared with alates from mixed nests to confirm the presence of separate host and parasite morphotypes.

Table 1. Allozyme loci used for separating the three species of the *Acromyrmex octospinosus* complex from the Panamanian nest series (see text for details)

Species	*A. octospinosus*	*A. echinatior*	*A. insinuator*
Colony #	19 and 25	33 and 47	22 and 39
Allozyme locus (buffer)			
MDH (S4)	−9	−13	−13
MPI (F2)	11	13	13
ACON (S5)	20	23	26

All three species are members of *A. octospinosus* sensu lato, which is recognized by the following combination of characters in the major worker: (1) the inferior pronotal spine is rounded, blunt and usually flattened rather than sharp and spinelike; (2) an anterior pair of tubercles or carinae is present on the propodeum; (3) pilosity is moderately sparse; (4) the median pronotal tubercles are absent, reduced to a pair of setae (Santschi, 1925; Wheeler, 1937; Gonçalves, 1961). The last character is actually contradicted in specimens from various localities, in which a pair of small tubercles is present.

A. octospinosus sensu lato is one of the most widespread of attine species. The "typical" form has been reported from Brasil in the south to Mexico in the north; *A. octospinosus echinatior* has been reported from Ecuador, Columbia, and Central America north to Mexico; *A. octospinosus inti* was described from Peru; *A. octospinosus cubanus* from Cuba, and *A. octospinosus ekchuah* from Mexico (Wheeler, 1937; Kempf, 1972). Recently, the subspecies *volcanus* has been elevated to species status (Wetterer, 1993). The systematics of the *Acromyrmex octospinosus* complex of species, subspecies, and varieties is exceedingly confused (Brown, 1957). Resolution of this important problem is quite beyond the scope of this paper, which sets as its modest goal the identification of the three Panamanian species revealed by electrophoretic and morphological study.

Of these Panamanian species, the consistently non-parasitized species corresponds to the "typical" form of *A. octospinosus*. The host species, in which nests were sometimes free-living and sometimes parasitized, corresponds to *A. octospinosus echinatior*. The social parasite is new to science.

Acromyrmex echinatior, new status

Acromyrmex octospinosus var. *echinatior* was described by Forel (1900) and elevated to subspecies status by Wheeler (1937). These authors, as well as Santschi (1925), recognized *A. octospinosus echinatior* principally by the sculpture of the head and gaster of the major worker: "the tubercles on the posterior corners of the head, the pedicel, and the gaster are more developed and subspiniform, and some of those on the sides of the head are distinctly curved forward" (Wheeler, 1937).

The Panamanian host species corresponds to *A. octospinosus echinatior*, based on an examination of the type series and on other material from the geographic range of this form and allowing for reasonable within-species variation in size and sculpture. Given the electrophoretic evidence presented in Table 1, the Panamanian host is a distinct species, thus necessitating an elevation to species status of *A. echinatior*.

The list of specimens published in Forel's (1899) description includes two workers, one from Guatemala and one from Costa Rica, the latter now apparently lost. Forel (1899) did not designate a holotype; five pins (seven specimens) in the syntype series bear the designation "type" written in Forel's hand. Affixed to two of Forel's syntype pins, one bearing a single major worker, the other bearing two females, are red "Typus" labels, but these may have been added subsequently and at any rate have no formal standing. Wheeler (1937) designated the type locality of

A. octospinosus echinatior as Volcan de Chiriquí, Panama, the collection locality of two of Forel's syntype females, but did not designate a lectotype. We have chosen to ignore this action and to designate the only remaining major worker in Forel's syntype series as the lectotype for two important reasons: (1) species concepts in *Acromyrmex* are based entirely upon the characters of major workers and (2) Forel's syntype females vary in size and collection locality, raising the possibility that they represent multiple species.

LECTOTYPE: Major worker. Guatemala: Senahuen Vera Paz, El Reposo, Zapote, 800 ft. (Champion). A. Forel Collection, Muséum d'Histoire naturelle, Geneva, Switzerland. Measurements, in mm: HL = 2.16; HW = 2.64; WL = 3.72; SL = 2.64; maximum diameter of eye = 0.43.

WORKERS: In the fifty nests excavated in Panama, the largest major workers of *A. echinatior* are the same size as those of *A. octospinosus* (Table 2; two-tailed t-test on average values: HL: t = 0.380, d.f. = 18, n.s.; HW: t = 0.422, d.f. = 18, n.s.; WL: t = 0.563, d.f. = 18, n.s.). However, a previous study by Bot and Boomsma (1997) found that pronotum width in *A. echinatior* (species 1 in that study) was significantly smaller than pronotum width in *A. octospinosus* (species 2 in that study). Qualitatively, major workers of the two species differ in the following ways: In *A. echinatior* the lateral pronotal spines are nearly vertical and parallel in frontal view, the vertical angle noticeably different from the angle of the anterior mesonotal spines, which diverge (Fig. 1). In *A. octospinosus*, the anterior spines are not verti-

Table 2. Average values, standard deviations, and ranges (in parentheses) of head length (HL), head width (HW), and Weber's length (WL), in millimeters, for the three species from the Panamanian nest series. Eyes were included in the measurement of head width in males

	HL (mm)	HW (mm)	WL (mm)
Major workers			
A. octospinosus major workers N = 10 (9 nests)	1.98 ± 0.14 (1.66 – 2.22)	2.28 ± 0.19 (1.90 – 2.55)	3.25 ± 0.19 (2.85 – 3.42)
A. echinatior major workers N = 10 (10 nests)	1.96 ± 0.09 (1.78 – 2.10)	2.31 ± 0.12 (2.16 – 2.49)	3.29 ± 0.12 (3.08 – 3.46)
Females			
A. octospinosus females N = 10 (4 nests)	2.42 ± 0.04 (2.34 – 2.47)	2.86 ± 0.07 (2.76 – 2.96)	4.15 ± 0.11 (3.90 – 4.28)
A. echinatior females N = 11 (9 nests)	2.15 ± 0.08 (1.95 – 2.25)	2.58 ± 0.15 (2.25 – 2.70)	3.78 ± 0.13 (3.52 – 3.99)
A. insinuator females N = 25 (5 nests)	1.88 ± 0.09 (1.66 – 2.02)	2.27 ± 0.08 (2.04 – 2.38)	3.34 ± 0.17 (2.93 – 3.72)
Males			
A. octospinosus males N = 6 (4 nests)	1.53 ± 0.05 (1.46 – 1.62)	1.81 ± 0.07 (1.71 – 1.88)	3.53 ± 0.21 (3.23 – 3.90)
A. echinatior males N = 12 (11 nests)	1.44 ± 0.10 (1.25 – 1.66)	1.76 ± 0.09 (1.63 – 1.97)	3.50 ± 0.29 (2.96 – 4.13)
A. insinuator males N = 18 (5 nests)	1.36 ± 0.07 (1.16 – 1.48)	1.62 ± 0.07 (1.48 – 1.71)	3.02 ± 0.23 (2.34 – 3.42)

cal and both pairs of spines diverge at approximately the same angle (Fig. 2). Major workers of *A. echinatior* are hairier than those of *A. octospinosus*; e.g., at least some setae are present on the face of the propodeal dorsum in addition to those associated with the propodeal spines and with the anterior tubercles, whereas in *A. octospinosus* such setae are absent. In general, tubercles on the gaster of *A. echinatior* workers are sharp and dentiform to subspiniform (Fig. 3), whereas those in *A. octospinosus* are low and blunted (Fig. 4). Likewise, tubercles on the head of *A. echinatior* are sharp and spiniform, whereas those of *A. octospinosus* are shorter and blunter. We caution, however, that there is overlap between the two species in the form of the spines of the gaster and head and that these commonly cited characters are therefore not entirely reliable. Worker color is quite variable, ranging from yellow in callows to yellowish-ferrugineous to ferrugineous, with, as noted by Wheeler (1937) some workers acquiring a "bluish bloom."

When workers from the entire range of both species are taken into account, the most constant distinguishing characters are the form of the spines on the head and gaster and to a lesser extent the differing angles of the lateral pronotal vs. anterior mesonotal spines. Major workers of *A. echinatior* from Costa Rica, Nicaragua, Guatemala, and Mexico, including the lectotype, frequently lack setae on the propodeal dorsum and are often much larger than those from the Panamanian nests.

FEMALES: In the Panamanian nests, *A. echinatior* females are smaller than *A. octospinosus* females (Table 2; two-tailed t-test on average values: HL: $t = 9.477$, $d.f. = 19$, $P < 0.0001$; HW: $t = 5.385$, $d.f. = 19$, $P < 0.0001$; WL: $t = 7.002$, $d.f. = 19$, $P < 0.0001$), and differ from them in the presence of a pigment spot entirely surrounding the ocelli (absent in the Panamanian *A. octospinosus*), the presence of setae on the propodeal dorsum (absent in *A. octospinosus*) (Fig. 7), and the presence of a broadly convex median anteroventral postpetiolar extension (variable in *A. octospinosus*) (Fig. 9). The occipital tubercle is thin and sharp and the tubercles on the first gastric tergite are sharp and dentiform; in *A. octospinosus* the occipital tubercle is thick and blunt, and the gastric tubercles are blunt and rounded. Color variation in females corresponds to that in workers. Over the whole of the species' Central American range, *A. echinatior* females are more variable in size than in the Panamanian sample, tending to be larger, and variable in the presence/absence of the ocellar pigment spot.

MALES: In the Panamanian nests, *A. echinatior* males are the same size as *A. octospinosus* males (Table 2; two-tailed t-test on average values: HL: $t = 2.057$, $d.f. = 16$, n.s.; HW: $t = 1.187$, $d.f. = 16$, n.s.; WL: $t = 0.224$, $d.f. = 16$, n.s.), but differ from them by the presence of a pigmented frontal triangle that is entirely delineated by rugae (Fig. 11) (unpigmented and ill-defined in *A. octospinosus*), the presence of setae on the propodeal dorsum (Fig. 13) (absent in *A. octospinosus*), and the presence of a broadly convex median anteroventral postpetiolar extension (Fig. 15) (variable in *A. octospinosus*). Color is yellow-ferrugineous. *A. echinatior* males over the rest of the species' range are variable in the characters of the frontal triangle.

Assigning the Panamanian specimens to *A. echinatior* is not without problems. The largest Panamanian workers are smaller than the lectotype and smaller than other worker specimens from Costa Rica, Nicaragua, Guatemala, and Mexico. Differences also exist in the characters of the propodeal setae (all castes), the ocellar

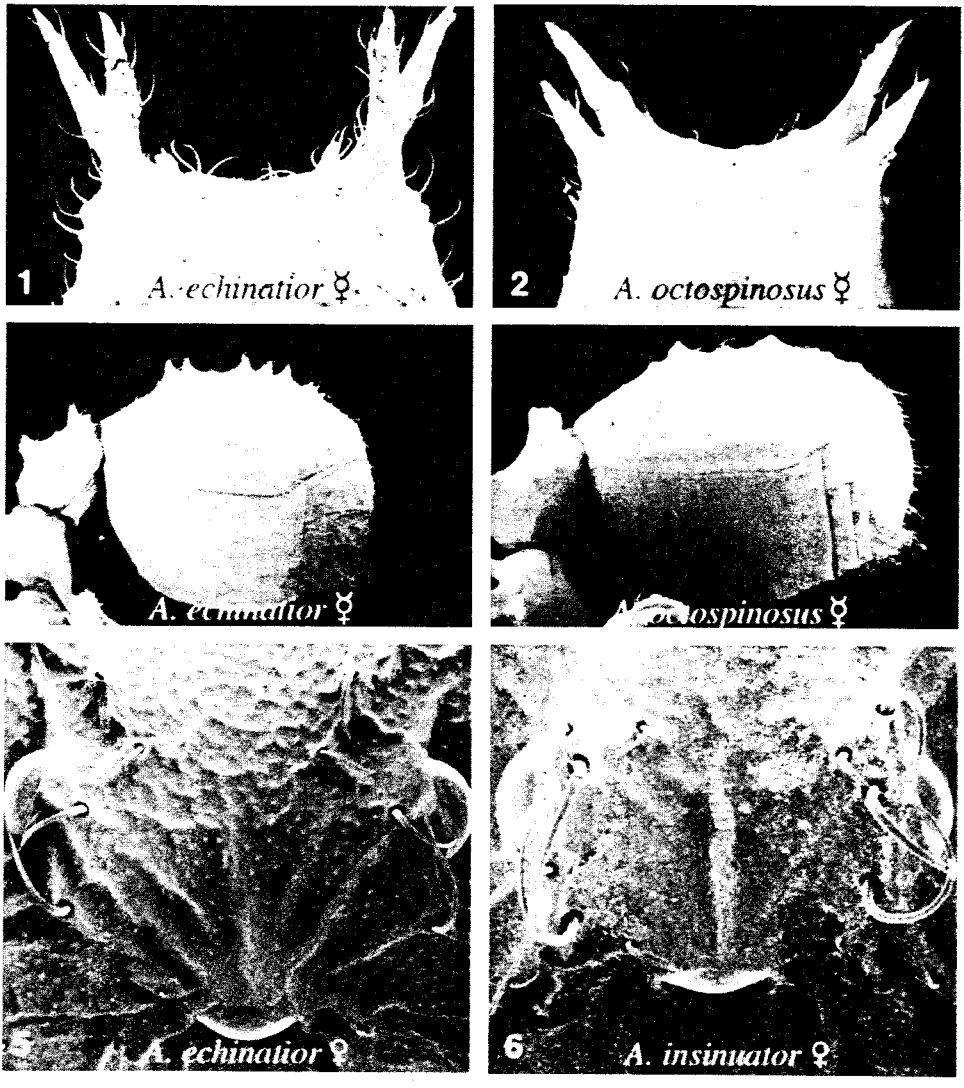

Figure 1. *Acromyrmex echinatior*, major worker (Panamanian nest series): frontal view of lateral propodeal and anterior mesonotal spines

Figure 2. *Acromyrmex octospinosus*, major worker (Panamanian nest series): frontal view of lateral propodeal and anterior mesonotal spines

Figure 3. *Acromyrmex echinatior*, major worker (Panamanian nest series): lateral view of gaster

Figure 4. *Acromyrmex octospinosus*, major worker (Panamanian nest series): lateral view of gaster

Figure 5. *Acromyrmex echinatior*, female (Panamanian nest series): median ocellus, posterodorsal view

Figure 6. *Acromyrmex insinuator*, female (Panamanian nest series): median ocellus

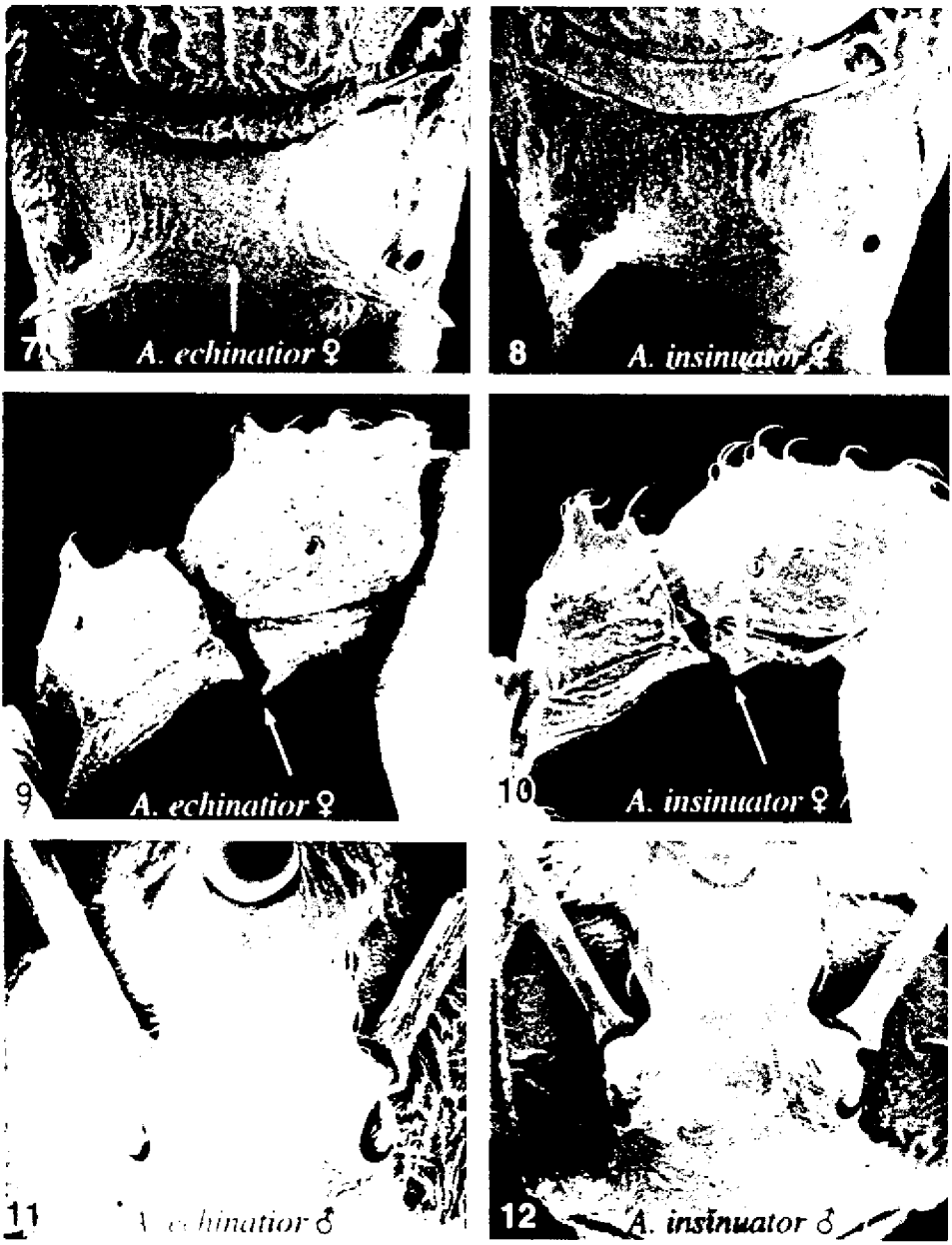

Figure 7. *Acromyrmex echinatior*, female (Panamanian nest series): propodeum, dorsal view.

Figure 8. *Acromyrmex insinuator*, female (Panamanian nest series): propodeum, dorsal view.

Figure 9. *Acromyrmex echinatior*, female (Panamanian nest series): petiole and postpetiole, lateral view.

Figure 10. *Acromyrmex insinuator*, female (Panamanian nest series): petiole and postpetiole, lateral view.

Figure 11. *Acromyrmex echinatior*, male (Panamanian nest series): frontal triangle.

Figure 12. *Acromyrmex insinuator*, male (Panamanian nest series): frontal triangle.

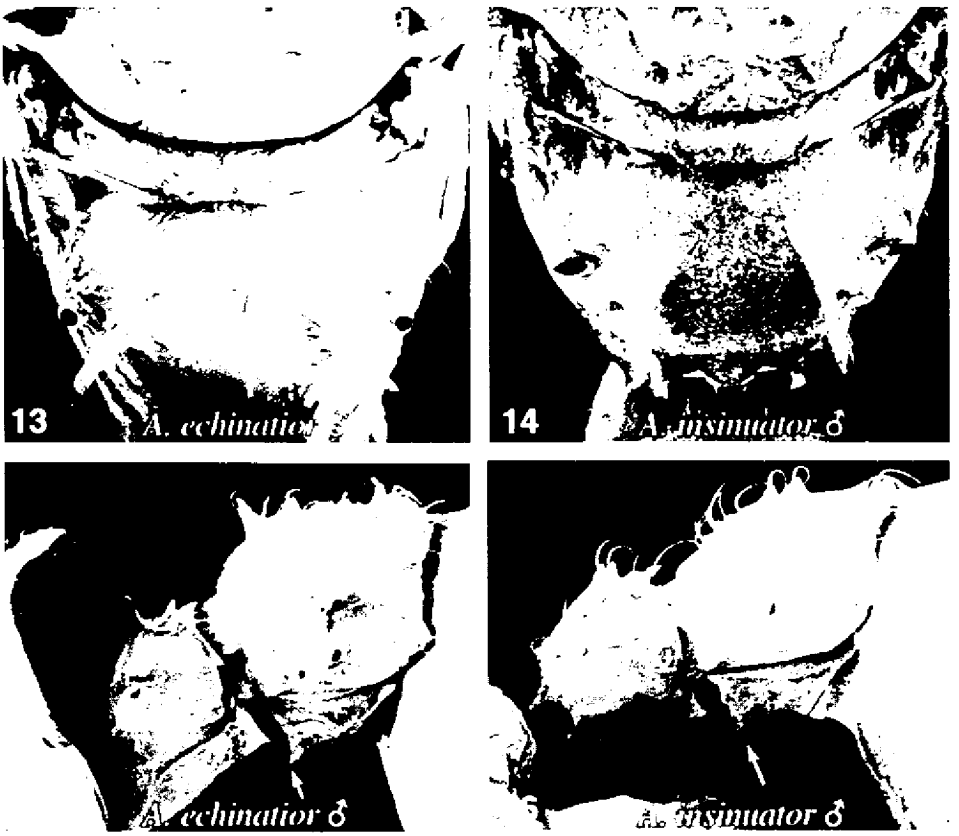

Figure 13. *Acromyrmex echinatior*, male (Panamanian nest series): propodeum, dorsal view

Figure 14. *Acromyrmex insinuator*, male (Panamanian nest series): propodeum, dorsal view

Figure 15. *Acromyrmex echinatior*, male (Panamanian nest series): petiole and postpetiole, lateral view

Figure 16. *Acromyrmex insinuator*, male (Panamanian nest series): petiole and postpetiole, lateral view

pigment spot in females, and the form of the frontal triangle in males. Although the conservative position taken here is that these differences fall within the normal range of variation expected from a species distributed over a wide area, we would not be at all surprised to find that both *Acromyrmex octospinosus sensu lato* and *Acromyrmex echinatior* are composed of a number of cryptic species. If this is established by future research, then the Panamanian host of *Acromyrmex insinuator* may require species status separate from *A. echinatior*. For this reason and because of the variability in character states discussed above, we consider it premature and inappropriate to draw up keys to species at this time, and none are provided here.

Paratypes examined: 2 minor workers: Guatemala: Senahuen Vera Paz, El Reposo, 800 ft. (Champion). 1 alate and 1 dealate female: Panama: Volcan de Chiriquí, 25–1000 ft. (Champion). 2 alate females: Panama: Bugaba (Champion).

Additional specimens examined: See Appendix.

Acromyrmex insinuator new species

Holotype female: Measurements (in mm): HL = 1.69; HW = 2.14; WL = 3.15; SL = 1.81; greatest diameter of eye = 0.43.

FEMALES (diagnosis): Measurements as in Table 2. Possessing the typical attine number of eleven antennal segments and typical palpal formula of 4, 2. Strongly resembling the female caste of the Panamanian form of the host species, *A. echinatior*, to which it is clearly closely related, but on average slightly smaller (Table 2; two-tailed t-test on average values: HL: $t = 8.56$, d.f. = 34, $P<0.0001$; HW: $t = 8.119$, d.f. = 34, $P<0.0001$; WL: $t = 7.635$, d.f. = 34, $P<0.0001$). Mandible with 8–10 (usually 10) teeth, the apical two larger than the rest. As in both *A. octospinosus* and *A. echinatior* from the Panamanian nests, the lateral pronotal spines (also called the "superior" pronotal spines) are short and spiniform and the inferior pronotal spines flattened with the tips rounded and blunt. Tubercles on the head are uniformly low and dentiform, agreeing in form and number with those of the host species, except that in both *A. echinatior* and *A. octospinosus* the occipital corners are drawn out into a distinct spine; in *A. insinuator* this tubercle is indistinguishable from the other tubercles on the head. A single strong median ruga extending posteriorly from the central ocellus to the level of the posterior borders of the lateral ocelli (Fig. 6); some specimens with an additional one or two weaker rugae. In the Panamanian *A. echinatior* three to five (typically five) strong rugae are present (Fig. 5). There is little or no dark pigmentation of the integument associated with the ocelli; when it is present, such pigmentation is isolated to the immediate areas of individual ocelli and never forms a single, continuous patch. In the Panamanian *A. echinatior* a single contiguous pigment spot surrounds all three ocelli. Setae are entirely absent from the propodeal dorsum of *A. insinuator* (Fig. 8), whereas they are present in Panamanian *A. echinatior* females (Fig. 7). The propodeal spines are laterally compressed, a condition found in neither *A. echinatior* or *A. octospinosus* from any region. In *A. insinuator* the anteroventral edge of the postpetiole is broadly and evenly concave and without a broad median anteroventral extension (Fig. 10); such an extension is consistently present in the Panamanian *A. echinatior* (Fig. 9) and variably present in *A. octospinosus*. Tubercles of the first gastric tergite are of medium height, dentiform and sharp, thus resembling the condition in the host species. Color is yellowish orange.

Allotype male: Measurements (in mm): HL = 1.41; HW = 1.70 (eyes included in measurement); WL = 3.04; SL = 1.81; greatest diameter of eye = 0.52.

MALES (diagnosis): Measurements as in Table 2. Possessing the typical attine number of 13 antennal segments (though in 4 individuals from 3 nests funicular segments 4 and 5 are partly fused), and the typical palpal formula of 4, 2. Strongly resembling the male caste of the Panamanian form of the host species, *A. echinatior*, though on average slightly smaller (Table 2; two-tailed t-test on average values: HL: $t = 2.584$, d.f. = 28, $P = 0.0153$; HW: $t = 4.787$, d.f. = 28, $P<0.0001$; WL: $t = 5.046$, d.f. = 28, $P<0.0001$). Mandible with 6–8 variably spaced teeth, the apical two larger than the rest. As in both *A. octospinosus* and *A. echinatior* from the Panamanian nests, the lateral pronotal spines are reduced to setigerous tubercles, and the inferior pronotal spines are short, flattened, and triangular. The frontal triangle of *A. insinuator* males is not delineated by rugae and lacks pigmentation (Fig. 12),

whereas the frontal triangle in the Panamanian *A. echinatior* males is darkly pigmented and clearly delimited on all three sides by rugae (Fig. 11). The propodeal spines in *A. insinuator* are extremely laterally compressed and virtually linear in cross section (Fig. 14), whereas those of *A. echinatior* (Fig. 13) and *A. octospinosus* males are not compressed and are cylindrical or quadrilateral in cross-section. Setae are absent from the propodeal dorsum in *A. insinuator* (Fig. 14) and the postpetiole lacks a broad, convex median anteroventral extension (Fig. 16). In Panamanian *A. echinatior* males both the propodeal setae (Fig. 13) and the postpetiolar anteroventral median extension are present (Fig. 15). Based on a single dissection from each species, there are no obvious differences between *A. insinuator* and *A. echinatior* in male genitalic morphology, which was found to conform to the plesiomorphic form for *Acromyrmex*. Color yellowish-ferrugineous.

WORKERS: Based on protein electrophoretic data, the smallest caste of minor workers is present in *A. insinuator*. However, no obvious morphological differences were detected in a comparison of minor workers from unparasitized nests with those from parasitized nests, including nests in which the alate population was entirely composed of *A. insinuator* sexuals and in which the complement of *A. insinuator* minor workers was presumably large. This suggests that workers of *A. insinuator* may be indistinguishable from workers of the host species, *A. echinatior*. Obviously, no minor workers of *A. insinuator* were included in the type series.

Biology: *Acromyrmex insinuator* is a social parasite of *A. echinatior*, and is so far known only from nests of the host species in Panama. Observations of laboratory nests (Bekkevold and Boomsma, in prep.) suggest that mating flights may occur either slightly prior to or slightly following the mating flights of the host species. If we are correct in assuming that *A. insinuator* is in the early stages of social parasite evolution, mating flights may be fairly "normal" and it is possible that specimens of both sexes could be collected outside of their symbiotic association, e.g., at light traps. It is not known how inseminated females enter new host nests. It is possible that they may enter established nests; however, the timing of the mating flight does not preclude the alternative possibility that inseminated *A. insinuator* females may join with *A. echinatior* queens in pleometrotic nest cofounding (Bekkevold and Boomsma, in prep.).

Paratypes: 28 females, 18 males.

Collection data: Panama, Canal Zone, Gamboa (J.J. Boomsma): holotype, 3 females, 8 males: Nest 22, 20 April 1994; allotype, 7 females, 3 males: Nest 23, 21 April 1994; 8 females, 5 males: Nest 1, 26 April 1993; 4 females, 1 male: Nest 7, 29 April 1993; 6 females, 1 male: Nest 39, 21 January 1996.

Specimen deposition: Holotype, allotype, paratypes: USNM; paratypes: MCZ; LACM; Natural History Museum (London); collection of Philip Ward, University of California, Davis; Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil.

Discussion

Acromyrmex insinuator differs remarkably from the only other known attine social parasites, two species that together entirely comprise the genus *Pseudoatta*. Mor-

phologically. *Pseudoatta argentina* and *P.* new species (Delabie et al., 1993) conform to a fairly advanced grade within the "social parasite syndrome" (Hölldobler and Wilson, 1990: 467–469): Males and females are nearly hairless and have remarkably smooth, shining integuments unique for attine ants. In *P. argentina*, palpal segment number is reduced from the plesiomorphic attine formula of 4, 2 to 3, 2 in both sexes (female: Kusnezov, 1951, 1954; male: TRS, personal observation), and male antennal segment number is reduced from the typical attine 13 to 11. The Bahian *Pseudoatta* new species retains plesiomorphic palpal formulae and antennal segment numbers in males and females (J. Delabie, pers. comm.). Males of *P. argentina* are degenerate fliers, mating with their sisters near the host nest entrance (Gallardo, 1929), whereas *P.* new species apparently conducts normal mating flights (Delabie et al., 1993). Both species are reportedly workerless (Bruch, 1928; Gallardo, 1929; Delabie et al., 1993; J. Delabie, pers. comm.).

In contrast, males and females of *A. insinuator* very closely resemble their hosts, with typically attine dull matte integuments and typically *Acromyrmex*-like sculpture, tubercles, and setae. Both sexes retain the plesiomorphic attine palpal formula of 4,2 and antennal segment numbers of 11/13 segments in females/males. A worker caste is still produced, but caste representation is limited to minor workers. The subtle morphological differences between *A. insinuator* and its host are all interpretable as transitional to a more derived grade of the social parasite syndrome (Hölldobler and Wilson, 1990: 467–469), including: reduction in size (both sexes), pigmentation (frontal triangle in males, ocellar margins in females), sculpture (posteromedian ocellar rugae in females, frontal triangle in males, and anteroventral postpetiole in both sexes), and setation (propodeal dorsum in both sexes). Perhaps significantly, some males have the fourth and fifth funicular segments of the antennae partly fused.

The preceding characters imply both that *A. insinuator* is an incipient social parasite and that it is closely related to its host. These conclusions, if confirmed, would lend support to "Emery's rule" in its strictest sense (Emery, 1909; e.g., supported by Baur et al., 1996, but contradicted by Carpenter et al., 1993). They would also suggest that further study of *A. insinuator*, combined with study of *Pseudoatta* species, will illuminate mechanisms of social parasite evolution possibly unique to fungus-growing ants. For instance, it has been suggested that mated *Pseudoatta* females enter mature nests of their hosts, but laboratory experiments and field observations described in the same sources resulted in the detection and repulsion of *Pseudoatta* queens (Bruch, 1928; Gallardo, 1929; Delabie et al., 1993). Since cofounding (pleometrosis) is known to occur in some *Acromyrmex* and closely related *Atta* species (Rissing et al., 1986; Rissing et al., 1989; Mintzer and Vinson, 1985), and since *A. insinuator* mating flights appear to be timed to precede or follow closely the mating flights of their hosts, it remains possible that *A. insinuator* queens join recently inseminated *A. echinatior* queens to cofound new nests. This scenario is at least consistent with a two-step route to social parasitism (Buschinger, 1970, 1986, 1990; Elmes, 1973) in which (1) initially, a proportion of conspecific cofoundresses employs a parasitic strategy in which they contribute little to the gardening worker force and focus on rapid production of reproductives, followed by (2) sympatric speciation, e.g., as a result of assortative mating due to divergence in reproductive emergence times. The obvious question prompted by this scenario is whether

foundress queens of *A. insinuator*, like those of other attines, contribute to the new garden with a mycelial pellet carried from the natal nest within the infrabuccal pocket.

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Appendix

Specimens examined

Panamanian nest series, *A. echinatior*:

Panama, Canal Zone, Gamboa (J.J. Boomsma): 6 major, 11 minor workers: Nest 1, 26 April 1993 (partial LACM); 3 major workers, 8 minor workers, 1 male, 1 female: Nest 3, 28 April 1993; 1 major worker, 1 male, 1 female: Nest 6, 29 April 1993; 1 major worker: Nest 8, 30 April 1993; 1 major worker, 1 female, Nest 9: 30 April 1993; 2 major workers, 1 male: Nest 10, 1 May 1993; 2 major workers, 1 minor worker: Nest 11, 1 May 1993; 1 major worker, Nest 12, 1 May 1993; 1 major worker, 1 male, Nest 13, 2 May 1993; 1 major worker, Nest 15, 9 May 1993; 2 major workers, 8 minor workers, 2 females: Nest 16, 9 May 1993; 1 major worker, 1 female, 1 male, Nest 20, 19 April 1993; 5 major workers, 6 minor workers, Nest 22: 20 April 1994; 3 major workers, 8 minor workers, Nest 23, 21 April 1994; 4 major workers, 1 female, 1 male, Nest 24, 21 April 1994; 1 major worker, 1 male, 1 female, Nest 26, 23 April 1994; 1 major worker, 1 male, Nest 27, 24 April 1994; 2 major workers, 1 female, Nest 28, 25 April 1994; 1 major worker, Nest 30, 30 April 1994; 2 major workers, 8 minor workers, 2 females, 2 males, Nest 33, 20 January 1996; 2 major workers, 8 minor workers, 1 male, 1 female, Nest 39, 21 January 1996; 2 major workers, 8 minor workers, 2 males, Nest 48, 4 February 1996. Except where noted, all deposited in NMNH.

Additional specimens, *A. echinatior*:

Panama: Canal Zone, Balboa Heights, 15 May 1923 (J. Zetek): 6 major, 3 minor workers (MCZ); Canal Zone, Ancon, 10 Nov. 1911 (W.M. Wheeler): 15 major, 3 minor workers (MCZ, AMNH); Taboga Island, 16 Nov. 1911, (W.M. Wheeler): 11 major, 1 minor workers (MCZ, AMNH); Canal Zone, Quarry Heights, 16 October 1918 (H.F. Dietz and J. Zetek): 1 major, 7 minor workers (LACM, AMNH, NMNH); Islas Perlas, Isla Cañas, Jan. – April 1978 (C. Campbell): 1 major worker (LACM); Panama City (S.C.H. Barrett): 1 major worker (LACM).

Costa Rica: El Hiquito near San Mateo (P. Biolley): 4 major workers (A. Forel Collection, Muséum d'Histoire naturelle, Geneva, Switzerland): San Jose, 26 Nov. 1911 (W.M. Wheeler): 8 major workers (NMNH, LACM, AMNH): San Jose, 1 Dec. 1911 (W.M. Wheeler): 20 major, 1 minor workers (NMNH, AMNH, LACM): Carrera Nacional, 4650 ft., 17 March 1910 (P.P. Calvert) 4 major workers (MCZ): San José, May 1962 (M.S. Blum): 2 major workers (MCZ): San Jose, 8 May and 8 Aug. 1936 (A. Alfaro): 4 major workers (LACM): Iberia, 18 January 1930 (A. Alfaro #53): 3 major workers (MCZ): Heredia, coffee finca, 29 June 1990 (I. Perfecto): 1 media worker (LACM): Guanacaste, Parque Nacional Santa Rosa, 14 Nov. 1981 (J.J. Howard #81–113): 3 major, 2 minor workers (LACM): Golfito, 24 July 1957 (Truxal and Mencke): 1 major worker (LACM).

Nicaragua: Managua, 29 January 1953 (A.T. Swain 202): 6 major, 12 minor workers (AMNH).

Guatemala: Tsanjuego, 2 March 1935 (W.M. Wheeler): 3 major workers (MCZ): Panajachel, 4 and 5 Jan. 1912 (W.M. Wheeler): 9 major, 3 minor workers (AMNH, LACM); Lake Atitlán, 5000 ft., 5 Jan. 1912 (W.M. Wheeler): 3 major workers (MCZ); Sololá, 5 Jan. 1912 (W.M. Wheeler): 2 major workers (MCZ); Alta Vera Paz, Trece Aguas 9 and 18 April (Barber and Schwarz): 1 alate, 1 dealate female (MCZ).

Mexico: Yucatan: 11 km. s. Progresso, 25 July 1953 (E.O. Wilson): 3 major workers, 2 minor workers, 1 dealate female (MCZ); Ocosingo, Chiapas, Laguna Ocotal Grande, ca. 950 m., 24 July 1954 (R.L. Dressler): 6 major workers (MCZ); Jalisco: Est. Biol. UNAM "Chamela," 9 June 1984 (D.H. Feener #0687): 2 major, 1 minor worker (LACM); Cordoba, Veracruz, 15 July 1964 (E. Fisher and D. Veraty): 2 major, 7 minor workers (LACM); 18 mi. E. of Colima, 1200 ft., Rio Taxpun, 11 July 1966 (J. Dixon, R. Heyer): 2 major workers (LACM); Presidio, Vera Cruz, 12 July 1969 (T.W. Taylor): 3 major workers (LACM); Actún, Chukum, 2 km. S. Mexcanú, Yucatan, 29 November 1974 (Reddel, Wiley, Mitchell, McKenzie): 4 major workers (LACM); Grutas de Tzab-Nah, 2 km. S. Tecoh, Yucatan, 1 Oct. 1974 (Reddell and McKenzie): 3 major, 3 minor workers (LACM); Cenote Aká Chen, 1 km. NE Tixancal, Yucatan, 2 April 1973 (Redell, McKenzie, Murphy, Butterwick): 8 major, 2 minor workers; Holcatzin Camp 3 May 1943 (W.D. Doughty 5017): 2 major, 1 minor worker (NMNH).

Puerto Rico: San Jose (W.M. Wheeler): 3 major workers (NMNH).

Also examined: *Acromyrmex octospinosus sensu stricto*: numerous specimens (NMNH, AMNH, MCZ, LACM); *Acromyrmex octospinosus cubanus*: Type series (MCZ, NMNH); also 18 major, 20 minor workers (LACM); 5 major, 1 minor workers (AMNH, NMNH); *Acromyrmex octospinosus ekchuah*: Type series (MCZ); *Acromyrmex octospinosus inti*: Type series (NMNH, MCZ); *Acromyrmex octospinosus "pallidus"*: Type series (NMNH); *Acromyrmex volcanus*: Type series (MCZ, NMNH).


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