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First Record of the Army Ant *Cheliomyrmex morosus* in Panama and its High Associate Diversity

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ABSTRACT

The occurrence and distribution of hypogaeic army ants is still poorly known despite their potential importance for tropical soil ecosystems. We present the first record of one of the most cryptic of army ants, *Cheliomyrmex morosus*, in Panama and list a diverse array of associated arthropods. The late discovery of these ants and high diversity of their associates indicates that much remains to be discovered even in one of the most intensely studied research areas.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: Acari; Coleoptera; Diptera; Ecitoninae; Formicidae; hypogaeic; myrmecophile; Zygentoma.

THROUGHOUT THE TROPICS, ARMY ANTS ARE ONE OF THE MOST CONSPICUOUS GROUPS OF ANTS. Species with large epigaeic mass raids, such as *Eciton* and *Labidus* in the New World, *Dorylus* (*Anomma*) in Africa, and *Aenictus* in Asia, are recognized as keystone species in their habitats (Franks & Bossert 1983, Gotwald 1995, Brown & Feener 1998). Army ant colonies host very diverse communities of associated arthropods (Rettenmeyer 1962). These associates may live either directly within an ant colony, utilizing its resources, or by using its refuse, or by accompanying its raids. The majority of army ant species, however, lead a subterranean life, and still very little is known about their occurrence, abundance, and species interactions. These cryptic ants are generally not recorded with standard sampling methods (summarized in Agosti *et al.* 2000), but may be attracted to special baits (*e.g.*, Berghoff *et al.* 2002). Nevertheless, chance encounters are still one of the most valuable opportunities to learn more about the occurrence and ecology of hypogaeic army ants.

Of the New World army ants, the genus *Cheliomyrmex* is the most cryptic. Of the genus' five described species, two are known only from males (Watkins 1976). Certain morphological characteristics set *Cheliomyrmex* apart from all other New World army ants: the workers are eyeless, their mandibles have a number of spine-like teeth, and their waist is uninodal (see Gotwald 1995 and O'Donnell *et al.* 2005 for illustrations). These characteristics relate *Cheliomyrmex* to the Old World Dorylinae, with all of the remaining New World army ant genera having at least a single eyespot, negligible teeth, and a binodal waist. These findings as well as the genetic phylogeny of army ants (Brady 2003) support the hypothesis that the hypogaeic lifestyle is the ancestral state for army ants, and *Cheliomyrmex* represents a sister taxon to the remaining New World army ant genera (Gotwald 1995). Given the long time for possible associations (*i.e.*, up to 100 MYR; Brady 2003), arthropods found with *Cheliomyrmex* may provide information on the origins and evolution of other New World army ant associates. Here, we report the first record of a *Cheliomyrmex morosus* colony in Panama and give a summary of associates collected from the ant column.

We conducted extensive daily ant surveys in the Barro Colorado Nature Monument and Soberanía National Park (Panama, 9°10′ N, 79°51′ W) between March and May 2005. Walked trails were mostly forest footpaths of 1.0–1.5 m width. The one exception was Pipeline Road, which represented a 3–5 m wide dirt road partially devoid of tree cover. We encountered *C. morosus* only at this site. On 14 March at 1130 h we found a *C. morosus* trail crossing Pipeline Road approximately 400 m north of Rio Limbo. The trail surfaced 30 cm to one side of the road and disappeared again in the soil 40 cm at the other side of the road. The apparently originally intact soil cover of the trail seemed to have been broken by cars driving over the trail prior to our observation. The trail had not been at this site at 1600 h the previous day and had disappeared at 0930 h the next day. We collected ants and associates with an aspirator from a trail section where the tunnel had been destroyed for 30 min at 1130 h and for another 60 min at 1630 h. During this time, we saw, but unfortunately missed, one Phorid fly and collected 24 *Limulodes* cf. *mexicanus* (Ptiliidae) beetles, 11 *Vatesus berghoffae* beetles (Staphylinidae: Tachyporinae), and 3 *Trichatelura* bristletails (two juvenile and one female, Nicoletiidae). Quick inspection of approximately 50 ants revealed two workers each carrying a phoretic mite: one *Imparipes lapillatus* (Scutacaridae) female and one *Acinogaster panamanus* (Pygmephoridae) female. Another three workers had conspicuously bloated abdomens, which may indicate Mermithid endoparasites (Poinar *et al.* 2006). Except for the mites, all associates were running along the trail under their own power and all obviously hesitated before proceeding onto the open trail parts. The associates did not avoid the ants, nor were they attacked by them. We further collected four worker ants, each carrying an ant larva beneath its body. Following the description of Wheeler and Wheeler (1974) the larvae were most similar to those of *C. megalonyx*. This finding and the absence of prey items carried in the trail indicate that the observed trail was part of an emigration of *C. morosus*. This

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TABLE 1. *Known host records for the here reported associates of* Cheliomyrmex morosus.

Associate species	Previously known hosts	Known hosts of the genus/subgenus	References
Limulodes cf. mexicanus (beetle)	*Cheliomyrmex*	*Eciton, Cheliomyrmex, Myrmecinae* species, *Formicinae* species	G. Hall, pers. comm.
Vatesus berghoffae (beetle)	none	*Eciton, Labidus, Neivamyrmex, Nomamyrmex*	Borgmeier 1961, Kistner and Berghoff 2006
Trichatelura sp.[a] (silverfish)		*Eciton, Labidus, Nomamyrmex*	Kistner 1982, Rettenmeyer 1963
Acinogaster panamanus (mite)	*Eciton, Labidus, Neivamyrmex, Nomamyrmex*	*Eciton, Labidus, Neivamyrmex, Nomamyrmex*	Ross and Cross 1979
Imparipes (I.) lapillatus (mite)	*Eciton*	*Eciton, Labidus, Neivamyrmex, wasps, bees, beetles, soil and litter samples*	Bedano 2004, Ebermann and Hall 2003, Mahunka 1977

[a]Further identification of our single adult specimen is not possible, as the two existing *Trichatelura* species are differentiated by their cerci, which are missing in our female, and color, for which a series of specimens would be needed.

represents only the second record of a *Cheliomyrmex* emigration, the first being Wheeler's observation published in 1921.

Our observations represent the most diverse and extensive list of associates for any strictly subterranean army ant. All of the collected associates belong to genera that have a broad host spectrum (Table 1). Three of these genera are only known from New World army ants and, with the exception of *Trichatelura* bristletails, are now known from all five such army ant genera (Table 1). The vast majority of *Neivamyrmex* species, the only missing host genus of *Trichatelura*, live in the soil and associate species collections are extremely rare. It is therefore conceivable that *Trichatelura* is associated with this ant genus but has so far escaped detection. The observed restriction of these associates to army ants, their wide distribution within the ant subfamily, and their occurrence with the evolutionarily basal *Cheliomyrmex*, could be related to old associations. In such a case, the ancestors of these arthropods might have already been associates of army ants around the time of their New World radiation. If true, the reported arthropods should also represent basal lineages within their taxa. No relevant phylogenetic data are available, although for the beetle *Vatesus berghoffae* we find a relation to the phylogenetic relationships of its host. The beetle is most closely related to a number of *Vatesus* species associated with *Neivamyrmex* and one with *Nomamyrmex* (Kistner & Berghoff 2006). This relationship corresponds to the close phylogenetic relationship between the host genera (Brady 2003) and could point to coevolutionary relationships.

In contrast to these apparently obligate army ant associates, *Limulodes* beetles and *Imaripes* mites are also associated with other ants and arthropods (Table 1). In the case of *Limulodes* this points to a high adaptability to differences in host biology. The adult females of *Imparipes* represent the phoretic stage and use the host as means of transportation. The mites' occurrence in soil and litter samples points to a facultative association with army ants. On the species level, only two of the four identified species appear to be host specific to *Cheliomyrmex* (Table 1). As very little is known about the biology of any of the associates, behavioral studies and further collections from the more cryptic army ant species are needed before any useful speculation can be made about the nature of the associations.

A total of five associated species and 39 individuals collected during only 90 min of observations indicates that the associate diversity of subterranean army ants might be comparable to that of epigaeic species, which represent some of the most diverse arthropod associations ever recorded (*e.g.*, Rettenmeyer 1962, Kistner 1982).

Cheliomyrmex has been recorded from Mexico through Honduras (*C. morosus*) and from Columbia further into South America (*C. andicola*, *C. audax*, *C. ursinus*, and *C. megalonyx*). To our knowledge, no records of *Cheliomyrmex* have yet been published from the countries connecting these two regions (*i.e.*, Nicaragua, Costa Rica and Panama). This is all the more remarkable because some of the oldest and most frequented field stations in the Neotropics are found in Panama and Costa Rica. This first record of *C. morosus* for Panama indicates that efforts need to be increased to reveal the occurrence of hypogaeic ants and to study their possibly important role for soil ecosystems.

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LITERATURE CITED

AGOSTI, D., J. D. MAJER, L. E. ALONSO, AND T. R. SCHULTZ. 2000. Ants. Standard methods for measuring and monitoring biodiversity. *In* D. E. Wilson (Ed.). Biological diversity handbook series, p. 280. Smithsonian Institution Press, Washington DC, and London, UK.

BEDANO, J. C. 2004. Soil prostigmatid mites (Acari: Prostigmata) of Argentina: An annotated checklist. System. Appl. Acarology 9: 45–52.

BERGHOFF, S. M., A. WEISSFLOG, K. E. LINSENMAIR, R. HASHIM, AND U. MASCHWITZ. 2002. Foraging of a hypogaeic army ant: A long neglected majority. Ins. Soc. 49: 133–141.

BORGMEIER, T. 1961. Beitrag zur Kenntnis der ecitophilen Staphylinid-Gattung Vatesus Sharp, nebst Beschreibung von sieben neuen Arten (Col Staphylinidae). Acad. Brasil. Cien. 33: 189–208.

BRADY, S. G. 2003. Evolution of the army ant syndrome: The origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. Proc. Nat. Acad. Sci. USA 100: 6575–6579.

BROWN, B. V., AND D. H. FEENER, JR. 1998. Parasitic phorid flies (Diptera: Phoridae) associated with army ants (Hymenoptera: Formicidae: Ecitoninae, Dorylinae) and their conservation biology. Biotropica 30: 482–487.

EEBERMANN, E., AND M. HALL. 2003. First record of Sporothecae within the mite family Scutacaridae (Acari, Tarsonemina). Zool. Anz. 242: 367–375.

FRANKS, N. R., AND W. H. BOSSERT. 1983. The influence of swarm raiding army ants on the patchiness and diversity of a tropical litter ant community. *In* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (Eds.). Tropical rain forest: Ecology and management, pp. 151–163. Blackwell Publishing, Oxford, UK.

GOTWALD, W. H., JR. 1995. Army ants: The biology of social predation. Cornell University Press/Comstock Press, Ithaca, New York.

KISTNER, D. H. 1982. The social insects' bestiary. *In* H. R. Hermann (Ed.). Social Insects III, pp. 1–244. Academic Press, New York, New York.

KISTNER, D. H., AND S. M. BERGHOFF. 2006. First species of *Vatesus* captured with *Cheliomyrmex* (Coleoptera: Staphylinidae) (Hymenoptera: Formicidae). Sociobiology 48: 385–394.

MAHUNKA, S. 1977. The examination of myrmecophilous Tarsonemid mites based on the investigations of Dr. C. W. Rettenmeyer (Acari). I. Acta Zool. Acad. Sci. Hung 23: 99–132.

O'DONNELL, S., M. KASPARI, AND J. E. LATTKE. 2005. Extraordinary predation by the Neotropical army ant *Cheliomyrmex andicola*: Implications for the evolution of the army ant syndrome. Biotropica 37: 706–709.

POINAR, G. J., J. P. LACHAUD, A. CASTILLO, AND F. INFANTE. 2006. Recent and fossil nematode parasites (Nematoda: Mermithidae) of Neotropical ants. J. Invert. Path 91: 19–26.

RETTENMEYER, C. W. 1962. The diversity of arthropods found with Neotropical army ants and observations on the behavior of representative species. Proc. Entomol. Soc. Am. N Cent. Br. 17: 14–15.

RETTENMEYER, C. W. 1963. The behavior of Thysanura found with army ants. Ann. Entomol. Soc. Am. 56: 170–174.

ROSS, L. J., AND E. A. CROSS. 1979. A revision of the genus *Acinogaster* (Acari: Pygmephoridae). Int. J. Acarol 5: 231–250.

WATKINS, J. F. I. 1976. The identification and distribution of New World army ants (Dorylinae: Formicidae). Markham Press Fund of Baylor University Press, Waco, Texas.

WEELER, G. C., AND J. WHEELER. 1974. Ant larvae of the subfamily Dorylinae: Second supplement (Hymenoptera: Formicidae). J. Kans. Entomol. Soc. 47: 166–172.

WHEELER, W. M. 1921. Observations on army ants of British Guiana. Proc. Am. Acad. Arts Sci. 56: 291–328.