

# Newly discovered sister lineage sheds light on early ant evolution

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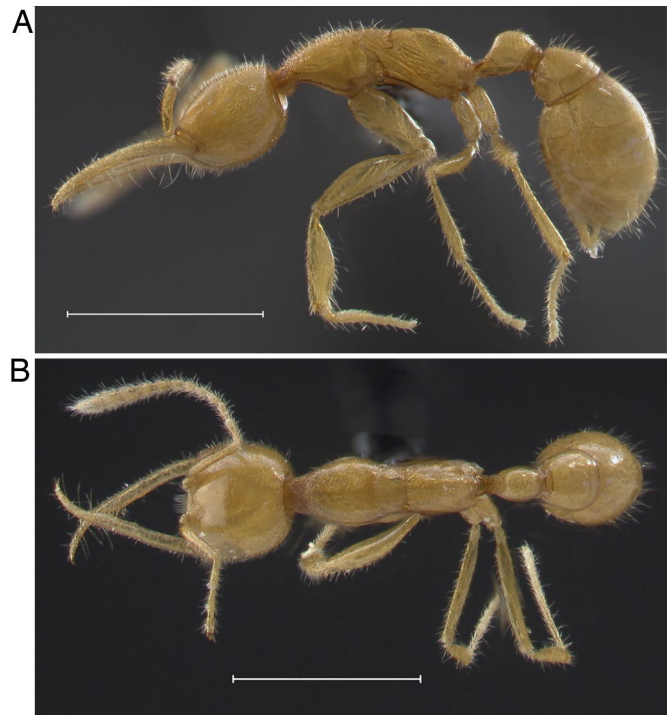
Ants are the world's most conspicuous and important eusocial insects and their diversity, abundance, and extreme behavioral specializations make them a model system for several disciplines within the biological sciences. Here, we report the discovery of a new ant that appears to represent the sister lineage to all extant ants (Hymenoptera: Formicidae). The phylogenetic position of this cryptic predator from the soils of the Amazon rainforest was inferred from several nuclear genes, sequenced from a single leg. *Martialis heureka* (gen. et sp. nov.) also constitutes the sole representative of a new, morphologically distinct subfamily of ants, the Martialinae (subfam. nov.). Our analyses have reduced the likelihood of long-branch attraction artifacts that have troubled previous phylogenetic studies of early-diverging ants and therefore solidify the emerging view that the most basal extant ant lineages are cryptic, hypogaeic foragers. On the basis of morphological and phylogenetic evidence we suggest that these specialized subterranean predators are the sole surviving representatives of a highly divergent lineage that arose near the dawn of ant diversification and have persisted in ecologically stable environments like tropical soils over great spans of time.

biodiversity | Formicidae | long-branch attraction | phylogeny | soil biology

Since the Cretaceous, ants have evolved to become one of the most diverse and abundant animal families to ever appear on Earth (1–5). A robust phylogeny is indispensable for elucidating the evolutionary origin of ants and for exploring the selective forces that have produced their extraordinary specializations. Previously published studies, however, led to contradicting views of early ant evolution, in part because of high levels of morphological convergence, the secondary loss of characters, and a lack of informative paleontological data (5–14). As a result, numerous taxa have been proposed as the most basal lineage (15–23). Two recent, comprehensive molecular studies have reconstructed the formicid phylogeny, resulting in largely congruent topologies that agree that ants as a family and most of the subfamilies are monophyletic (20, 21). In contrast with previous morphological studies (5–14), the blind, subterranean subfamily Leptanillinae was recovered as sister to all extant ants, as suggested by two earlier partial molecular studies (22, 23), implying an early origin and diversification of cryptic, blind species with hypogaeic foraging habits.

## Results and Discussion

Here we describe a new ant species, *Martialis heureka* (Figs. 1 and 2), comprising a new subfamily, the Martialinae, and discuss the implications of this discovery for the early evolution of ants. Morphological results confirm that *M. heureka* is clearly a member of the family Formicidae because of the presence of the metapleural gland orifice, geniculate antennae, and a morphologically differentiated petiole (Figs. 1 and 2). However, it cannot be placed within any extant or extinct subfamily (20–22, 24). *M. heureka* is close to, but not within, the subfamily Leptanillinae, because it exhibits several autapomorphies (see diagnosis below) and retains the plesiomorphic condition for other mor-



**Fig. 1.** Holotype worker of *Martialis heureka* gen. et sp. nov. The single specimen has been collected in the leaf litter of a terra firme rainforest near Manaus, Amazonas, Brazil. *Martialis heureka* is inferred to be the sister lineage to all extant ants. (A) Lateral and (B) dorsal view of the worker. (Scale bar: 1 mm.) Photographs courtesy of C. Rabeling and M. Verhaagh.

phological characters, like the flexible promesonotal suture and the exposed antennal sockets. Hence, we place *M. heureka* in its own subfamily, the Martialinae.

## Taxonomic Treatment

Family Formicidae Latreille, 1809 (25)

Subfamily **Martialinae** Rabeling & Verhaagh, subfam. nov.

***Martialis heureka*** Rabeling & Verhaagh, gen. et sp. nov.

**Martialinae** Rabeling & Verhaagh, subfam. nov.

Worker diagnosis: small, blind, pale, presumably subterranean ants with the following combination of characters. Putative

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Data deposition: The sequences reported in this paper have been deposited in the GenBank database (accession nos. EU913472–EU913474).

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