

the present holotype, was recollected in a nearby patch of primary rainforest.

Discussion. We assume that the present specimen of *M. heureka* is a worker, because it lacks ocelli, the enlarged mesosoma and the extra sclerites associated with wings (Figs. 1 and 2). In addition, the specimen was collected in the leaf litter suggesting foraging activity usually performed by the worker caste. However, queens with worker-like morphology have been reported from several poneroids and socially parasitic Formicinae and Myrmicinae (26–29). Because we did not perform a dissection of the single specimen no statement can be made about palpal segmentation or internal anatomy.

Inferred Biology. On the basis of the specimen's external morphology, we are able to infer some aspects of the species' biology. The pale integument and the absence of eyes suggest that *M. heureka* lives hypogaeically or in covered low-light environments, like leaf litter or rotting wood. The fact that the first two *M. heureka* individuals were collected in soil core samples during the day, and the present specimen in leaf litter at dusk, supports this hypothesis. Possibly, *M. heureka* surfaces during the night to forage. The unusually enlarged procoxae and long front legs could potentially be an adaptation to prey capture. Presumably, they are used less for digging activities, because the legs are relatively thin and lack the characteristic erect setae of actively digging species. We speculate that *M. heureka* might take advantage of preexisting underground cavities, like hollow rotten roots (Fig. 2). The forceps-like mandible type is not seen in any other ant species. These long, filigree instruments could be used to drag soft prey items out of cavities. Annelids, termites, insect larvae, and other soft-bodied arthropods are possible prey. We do not expect *M. heureka* to prey on heavily sclerotized invertebrates.

Phylogenetic Study. To infer the phylogenetic position of *M. heureka* and to evaluate competing phylogenetic hypotheses, we sequenced 4.2 kb of *Martialis heureka*'s nuclear ribosomal and single-copy nuclear DNA. DNA sequence data were added to a previously published molecular data set of 151 ant species from 20 subfamilies and 11 aculeate outgroup taxa (20), except for four single-copy nuclear genes, which we could not amplify from the limited amount of DNA extract. The phylogeny was inferred using maximum likelihood (ML, 30) and Bayesian inference (BI, 31). Both approaches place *Martialis* as sister to the remaining extant ants and support the monophyly of all ants, including *Martialis* (Fig. 3). *Martialis* did not associate with any extant subfamily in the molecular phylogeny, supporting the designation of the Martialinae as a distinct subfamily on morphological grounds. The basal position of *Martialis* had a Bayesian posterior probability (BPP) of 0.912, a maximum likelihood bootstrap proportion (ML BP) of 0.76 (Fig. 3), and was strongly supported by Bayes factors (BF, 32–34) over the next most strongly supported rooting (Leptanillinae as basal to all extant ants; $2\ln(\text{BF}) = -16.4$; Fig. 4). However, the more conservative Shimodaira-Hasegawa (SH, 35, 36) test did not reject the alternative rootings (Fig. 4). Even though the BPP and ML BP were only moderately high, the basal positions of *Martialis* and the Leptanillinae were robust to taxon sampling (Figs. S1 and S2). When *Martialis* was removed from analyses, the leptanillines were recovered as sister to all extant ants. The converse was true when the leptanillines were removed. Because the basal position of neither *Martialis* nor the leptanillines changed in the absence of the other, we suggest that their basal position is not because of a particular taxon-sampling scheme.

The basal position of *Martialis* is not likely caused by long-branch attraction (LBA), as was previously suggested of the leptanillines (20), because *Martialis* has a substantially shorter

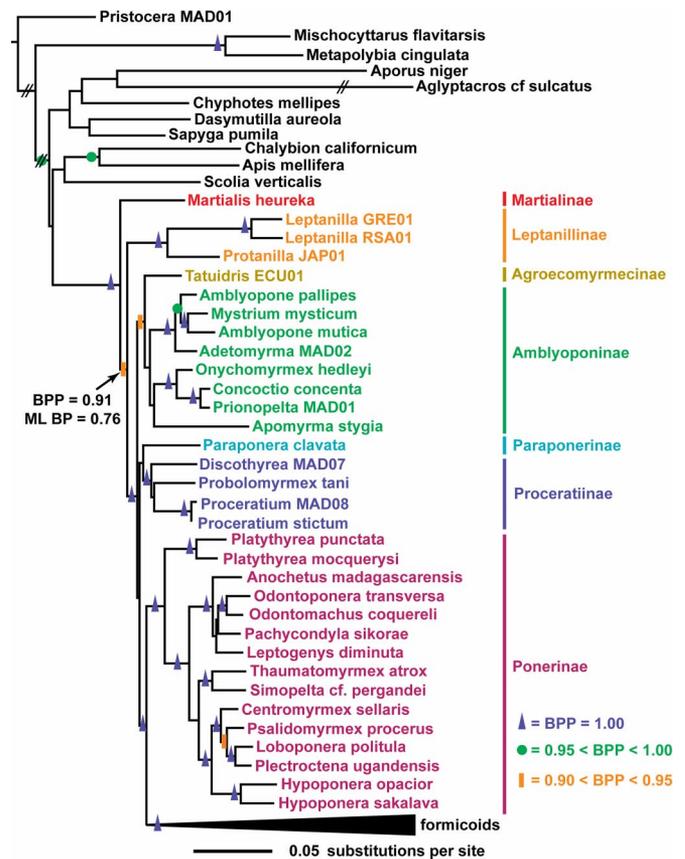


Fig. 3. Maximum likelihood (ML) tree with Bayesian posterior probabilities (BPP) and ML bootstrap proportions (ML BP) support values. Tree is rooted on the branch leading to the outgroup, *Pristocera*. The formicoid clade has been collapsed to increase resolution of relationships among basal ant groups (*Martialis*, Leptanillinae, and poneroids). Bipartitions with strong Bayesian support are indicated by blue triangles (BPP = 1.0), green circles (0.95 < BPP < 1.0) or orange rectangles (0.90 < BPP < 0.95).

branch than all outgroup taxa and the Leptanillinae (Fig. 3). Additionally, the ribosomal DNA sequences in this study (87% of our data set) are the most slowly evolving of the genes used by Brady *et al.* (20) (58% of their data set) and are least likely to contribute to LBA artifacts (37). Taxon sampling was also increased by one important lineage over previous studies, breaking the long branch that subtended the extant ants in previous studies (20, 21). However, the reconstruction of the molecular ant phylogeny still faces at least two sources of uncertainty that could introduce analytical artifacts. First, even though *Martialis* breaks the long branch leading to the remaining extant ants, the branch connecting the ingroup to the aculeate outgroup taxa remains long (Fig. 3). Second, the basal ant lineages seem to have originated in a relatively short period (20, 21), potentially making the unambiguous resolution of their relationships quite difficult and sensitive to methodological error. Increased gene and taxon sampling for both ants and outgroup aculeates should reduce the potential for statistical artifacts in future analyses.

Our phylogeny supports paraphyly of the poneroids (Fig. 3). The Ponerinae were strongly supported as sister to the formicoids by Bayesian analysis (BPP = 1), although less strongly by ML bootstrap analysis (ML BP = 68). Relationships among the remaining poneroid subfamilies were more ambiguous. The best estimate from both ML and Bayesian analyses (Fig. 3) has an Amblyoponinae/Agroecomyrmecinae clade basal to all other poneroids, followed by a Paraponerinae/Proceratiinae clade, although support is weak (BPP = 58, ML BP < 50). Paraphyly of