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## Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae)

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### Abstract

Recent molecular phylogenetic studies of ants (Hymenoptera: Formicidae) have revolutionized our understanding of how these ecologically dominant organisms diversified, but detailed phylogenies are lacking for most major ant subfamilies. I report the results of the first detailed phylogenetic study of the ant subfamily Ponerinae, a diverse cosmopolitan lineage whose properties make it an attractive model system for investigating social and ecological evolution in ants. Molecular sequence data were obtained from four nuclear genes (*wingless*, *long-wavelength rhodopsin*, *rudimentary* [CAD], 28S rDNA; total of ~3.3 kb) for 86 ponerine taxa, representing all three ponerine tribes, 22 of the 28 currently recognized genera, and 14 of the 18 informal subgenera of *Pachycondyla*, a heterogeneous grouping whose monophyly is doubtful on morphological grounds. Phylogenetic reconstructions using maximum likelihood and Bayesian inference support the monophyly of Ponerinae and tribe Platythyreini, but fail to support the monophyly of the large tribe Ponerini due to its inclusion of the unusual genus *Thaumatomyrmex*. *Pachycondyla* is inferred to be broadly non-monophyletic. Numerous novel generic and suprageneric relationships are inferred within Ponerini, which was found to consist of four major multi-generic clades (the *Ponera*, *Pachycondyla*, *Plectroctena* and *Odontomachus* genus groups) plus the single genera *Hypoponera* and *Harpegnathos*. Uncertainty remains in some regions of the phylogeny, including at the base of Ponerini, possibly reflecting rapid radiation. Divergence dating using a Bayesian relaxed clock method estimates an origin for stem Ponerinae in the upper Cretaceous, a major burst of diversification near the K/T boundary, and a rich and continual history of diversification during the Cenozoic. These results fail to support the predictions of the “dynastic-succession hypothesis” previously developed to explain the high species diversity of Ponerinae. Though model-based reconstructions of historical biogeography and trait evolution were not attempted in this study, the phylogeny suggests that ponerine evolution was marked by regionalized radiations and frequent faunal exchange between major biogeographic provinces. The reported results also imply multiple origins of cryptobiotic foraging, mass raiding behavior, and gamergate reproduction within Ponerinae, highlighting the value of the subfamily as a model for studying the incipient evolution of these and other ecological and behavioral traits.

**Key words:** relationships, radiations, systematics, phylogenetic inference, divergence dating

### Introduction

A common theme in the study of terrestrial ecosystems is the ecological importance of ants (Hymenoptera: Formicidae). Though they make up only a small fraction of total insect species diversity (with roughly 12,500 described species; Agosti and Johnson, 2009), ants have few rivals among animals in their abundance, total biomass, range of ecological interactions, and influence on ecosystem-level processes (Fittkau and Klinge, 1973; Wilson, 1990; Hölldobler and Wilson, 1990; Agosti *et al.*, 2000; Kaspari *et al.*, 2000; Wilson and Hölldobler, 2005). Much of the ecological success of ants can be attributed to their advanced sociality, which provides greater efficiency and the exploitation of otherwise unavailable niches (Wilson, 1971; Oster and Wilson, 1978; Hölldobler and Wilson, 1990). Recent molecular phylogenetic studies of ants (*e.g.*, Brady, 2003; Ward and Brady, 2003; Saux *et al.*, 2004; Ward and Downie, 2005; Moreau *et al.*, 2006; Brady *et al.*, 2006; Ouellette *et al.*, 2006; Rabeling *et al.*, 2008; Ward *et al.*, 2010) have revolutionized our understanding of the basic course of ant evolution. Ward *et al.* (2010) recently published the first detailed genus-level phylogeny of one of the “big four” ant subfamilies, the Dolichoderinae, but comprehensive phylogenies are still lacking for Myrmicinae, Formicinae, and Ponerinae.