

AToL: Collaborative research on ant phylogeny: a comprehensive evolutionary tree for the world's premier social organisms

P.S. Ward¹, Seán Brady², Brian Fisher³ & Ted Schultz²



Introduction

Ants, aculeate wasps in the family Formicidae, are arguably one of the greatest success stories in the history of terrestrial Metazoa. These eusocial organisms, numbering 12,000 described species and perhaps as many undescribed, monopolize 15-20% of the total animal biomass in many ecosystems, and thus serve as major conduits of energy and organic material. They are among the leading predators of invertebrates in most communities, and in the Neotropics they are the principal herbivores as well. Ants participate in symbioses with plant species in over 52 families, thousands of arthropod species, and as-yet unknown numbers of fungi and microorganisms. Taken as a whole, ants display remarkable adaptive strategies and specializations—agriculture of fungi, seed harvesting, herding and “milking” of other invertebrates, communal nest weaving, cooperative hunting in packs, social parasitism, slave-making—which have fueled scientific and public curiosities alike. A clearer picture of the stepwise evolution of the major ant lineages will shed light on the factors, both ecological and historical, that contributed to the ecological dominance and behavioral diversity of the ants.

Objectives

The primary goals of this 5-year project are to:

- Infer the phylogeny of all major lineages of ants. The data gathered for this analysis will include ~10kb of DNA sequence from a total of 11 genes, and a morphological data set of ~300 characters. These data will be obtained from ~340 ant species, representing all extant subfamilies and tribes, and 10 outgroup taxa.
- Estimate divergence times for the origin of ants and major events in ant evolution by incorporating fossil information with current molecular dating methods. This analysis will also allow the testing of specific biogeographic hypotheses.
- Use the inferred phylogeny as a framework for reconstructing the evolutionary histories of key biological features of ants, including caste polymorphism, life history traits, and symbioses with plants and animals.
- Develop the AntTree interface to AntWeb (www.antweb.org), to provide internet-accessible resources on the phylogeny and diversity of ants. This will include the first interactive online key to the world genera of ants.
- Provide training in insect systematics to students and other researchers, who will be exposed to both morphological and molecular methods, diverse approaches to phylogenetic and comparative analyses, and a variety of application tools in bioinformatics.



Methods

We will develop a comprehensive phylogeny of the ants using a combination of morphological and molecular data. The morphology of multiple castes of approximately 350 species, representing all major ant lineages and outgroups, will be freshly examined for newly-discovered characters as well as for those already described in the literature. For the same species, and for individuals from the same nest series whenever possible, molecular data will be generated from ~10 nuclear genes and one mitochondrial gene, selected for their phylogenetic utility. These data will be analyzed using a variety of criteria (parsimony, maximum likelihood, Bayesian inference) and strategies geared toward large data sets (e.g., MCMC, genetic algorithms, parallel processing). Divergence times for major events in ant evolution will be inferred by combining fossil information with molecular dating methods that do not assume clocklike evolutionary rates. Dating analyses will also permit the testing of specific biogeographic hypotheses addressing ant distributions. The evolution of caste polymorphism and other key life history traits will be reconstructed using a variety of methods

Preliminary Results and Future Prospects

Some provisional findings are shown in Figure 1, which is based on a study of the phylogenetic position of the ant genus *Leptanilloides* (Ward, in prep.). Using 5 nuclear genes (~5.1 kb of sequence) we find that (1) the enigmatic subterranean ant *Leptanilla* appears to be sister to all other extant ants; (2) there is an early diversification of poneroid ants (represented today by *Amblyopone*, *Paraponera*, etc.); and (3) most modern ants belong to the formicoid clade, which arose later within the poneroids. Monophyly of the formicoid clade is very strongly supported, but relationships among the early poneroid lineages and among the subfamilies within the formicoid clade are poorly understood and will be a primary focus of future research efforts. Additional genes and wider taxon sampling promise to provide better resolution of these relationships and new insight into the main features of ant evolution.

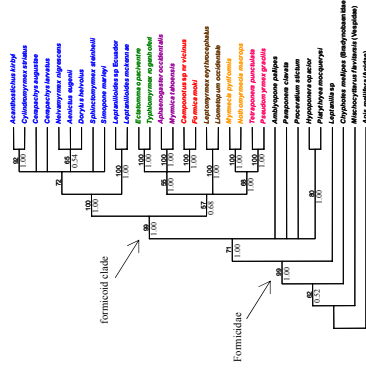


Figure 1. Phylogenetic relationships among selected ant taxa, based on analysis of five nuclear genes (18S, 28S, *wg*, *1 W Bt*, and *46d-4*). Numbers above each node are parsimony bootstraps; those below are Bayesian posterior probabilities. Taxa with blue labels are dorytomorph ants. Other color-identified members of the formicoid clade are members of the same subfamily, as follows: green = Ecitoninae; purple = Myrmecinae; red = Formicinae; brown = Dolichoderinae; orange = Myrmecinae; pink = Pseudomyrmecinae.

¹University of California, Davis, CA, USA ²Smithsonian Institution, Washington, DC, USA ³California Academy of Sciences, San Francisco, CA, USA