



What Do Molecular Clocks Tell Us About the Evolution of Ants?

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Within the last decade, the interest in using molecular clock methods for divergence dating has greatly increased, including within the ant community. Due to the rich fossil record of ants and the ever-increasing amount of molecular data available, the ants have become the focus of several divergence dating studies (summarized in Moreau 2009). The fossil record of ants dates back ~100 million years (Grimaldi et al. 2002; Perrichot et al. 2007) and in some formations contains thousands of individual ant fossils (Dlussky and Rasnitsyn 2009), providing numerous fossils to serve as minimum calibration points in molecular clock analyses.

The first attempt to use a molecular clock to date the age of modern ants was implemented by Crozier et al. (1997) using only sequence divergence information between six ant species and a vespid wasp; the results suggested a Jurassic origin for the crown group ants. The first major attempt to incorporate fossil information into a large-scale divergence dating study on the phylogeny of the ants was completed by Moreau et al. (2006), and recovered an age of 140–168 million years for modern ants. Later that same year, Brady et al. (2006) also published a phylogeny of the ants including molecular clock analyses recovering an age of 115–135 million years for the crown group ants. Although these two studies used the same molecular clock method (penalized likelihood, which requires at least one fixed node in the phylogeny), similar fossil information, and similar molecular data, the different ages recovered for modern ants are likely due to the fixed maximum age placed on the root node of each study (Moreau and Bell, unpublished).

To determine if newer Bayesian divergence dating methods (Drummond and Rambaut 2007), which do not require a fixed dated node within the phylogeny and also allow for simultaneous estimation of the topology during inference, are more stable across analyses, the molecular data of Moreau et al. (2006), Brady et al. (2006), and Rabeling et al. (2008) were combined. Within a Bayesian framework using 45 fossils as minimum age constraints across the ant phylogeny, these combined data were subjected to three separate

molecular clock analyses: 1) topology constrained to the maximum likelihood tree with 185 million years as the maximum age for the root node (following Brady et al. 2006); 2) topology constrained to the maximum likelihood tree and no maximum age for the root node; and 3) topology simultaneously estimated during molecular clock analysis and root node constrained to a maximum age of 185 million years. The results of these analyses suggest that regardless of whether the root node or topology were constrained, a stable age of 139–148 million years is inferred for the crown group ants (Moreau and Bell, unpublished).

In addition to providing a date for nodes of interest across a phylogeny, divergence dating can inform biogeographic reconstruction. Ree and Smith (2008) have created Lagrange, a maximum likelihood-based ancestral range reconstruction method which can account for dispersal probability across time. For example, if a taxonomic group of interest includes species distributed across Africa and South America, a chronogram (phylogeny with branch lengths proportional to time) and the known distributions for each terminal taxa can be used to specify the probability of dispersal between these (and other) biogeographic areas across time. In the case of Africa and South America at 195 million years, dispersal between these landmasses would likely be given a probability of 1.0 because the continents were in direct contact, whereas dispersal probability decreases toward the present as the continents drift apart.

Using the current distributions of each included ant genus and dated chronogram, ancestral range evolution was inferred across the ant phylogeny. Interestingly, the Neotropics are inferred to have played a major role in the evolutionary history of the modern ants. As the Neotropics are currently home to more species and genera of ants, this provides an intriguing picture of ant evolution, and for the first time the biogeographic history of the Formicidae has been inferred using statistical methods (Moreau and Bell, unpublished).

Divergence dating also allows for the inference of patterns of diversification across groups of interest. These can include Lineages



Through Time (LTT) plots, inferring rates of speciation, and looking for the signature of changes in the tempo (or rate) of diversification. Using LTT plots and models of diversification, Moreau et al. (2006) found a rapid burst in diversification of the crown group ants around 100 million years ago and correlated this with the rise of the angiosperms (flowering plants). By inferring the speciation rate of the “hyperdiverse” ant genus *Pheidole*, Moreau (2008) found a very high rate of speciation, which suggests that time alone is not enough to explain the diversity in the most species-rich genus of modern ants. More recently, using a method to detect shifts in diversification rates, we found several cases in which there was a significant change in the tempo of diversification across the ant phylogeny, highlighting instances of rate increases and decreases (Moreau and Bell, unpublished).

Overall recent advances in molecular clock and divergence dating analyses have provided the tools to begin to unlock the evolutionary history of ants and many other taxonomic groups. Not only are we able to use the fossil record to put a timeline on the evolutionary history of many groups, but these same studies have provided the framework to begin to inform biogeographic analyses through time and allow for the tempo of diversification to be studied. With new and improved divergence dating methods becoming available and an interest in finding ways to unite neontological and paleontological data, it is an exciting time to be an insect evolutionary biologist.

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