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The Higher Classification of the Ant Subfamily Ponerinae (Hymenoptera: Formicidae), with a Review of Ponerine Ecology and Behavior

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Abstract

The tribal and generic classification of the diverse ant subfamily Ponerinae (Hymenoptera: Formicidae) is revised to reflect recent molecular phylogenetic information and a reappraisal of ponerine morphological diversity. The monogeneric tribe Thaumatomyrmecini (*Thaumatomyrmex*) is newly synonymized under Ponerini (**syn. nov.**), and the diverse genus *Pachycondyla* is fragmented into 19 genera, largely along the lines of its junior synonyms: *Bothroponera*, *Brachyponera* (**gen. rev.**), *Ectomyrmex* (**gen. rev.**), *Euponera* (**gen. rev.**), *Hagensia* (**gen. rev.**), *Megaponera* (**gen. rev.**), *Mesoponera* (**gen. rev.**), *Neoponera* (**gen. rev.**), *Ophthalmopone* (**gen. rev.**), *Pachycondyla*, *Paltothyreus* (**gen. rev.**), *Pseudoneoponera* (**gen. rev.**), *Pseudoponera* (**gen. rev.**), and 6 new genera: *Austroponera* (**gen. nov.**), *Buniapone* (**gen. nov.**), *Fisheropone* (**gen. nov.**), *Mayaponera* (**gen. nov.**), *Parvaponera* (**gen. nov.**) and *Rasopone* (**gen. nov.**). Some junior synonyms of *Pachycondyla* are transferred to junior synonym status under other genera: *Wadeura* as a junior synonym of *Cryptopone* (**syn. nov.**), and both *Termitopone* and *Syntermitopone* as junior synonyms of *Neoponera* (**syn. nov.**). A new genus, *Iroponera* (**gen. nov.**), based on the new species *Iroponera odax* (**sp. nov.**), is described from Australia. Molecular and morphological justifications for these taxonomic changes are given alongside discussions of phylogenetic relationships. Keys to the world genera of Ponerinae are provided, and morphological diagnoses and species lists are given for each genus. Finally, the available information on ponerine ecology and behavior is reviewed and synthesized.

Key words: World revision, ants, taxonomy, Ponerinae

Introduction

The higher taxonomic classification of ants (Hymenoptera: Formicidae) has recently undergone significant changes. Driven by careful reconsiderations of morphological variation (Bolton, 2003; Keller, 2011) and broad molecular phylogenetic studies (Moreau *et al.*, 2006; Brady *et al.*, 2006; Rabeling *et al.*, 2008), the subfamily-level classification of Formicidae is now largely stable and reflective of evolutionary relationships. At the same time, molecular data have demonstrated that tribal and generic classifications remain phylogenetically inconsistent for many ant groups, especially the diverse subfamilies Formicinae, Myrmicinae (Brady *et al.*, 2006) and Ponerinae. These latter groups, along with Dolichoderinae, constitute the “big four” subfamilies of ants in terms of described species diversity. Formicinae, Myrmicinae and Dolichoderinae include the most familiar ants, and together with several smaller subfamilies constitute the formicoid clade (Moreau *et al.*, 2006; Brady *et al.*, 2006). Ponerinae is unique among the major ant subfamilies in being situated outside this clade, and is the focus of this study.

Ponerines are notable for combining generally simple social organization with a high diversity of derived morphological, ecological and behavioral traits. They provide valuable opportunities to examine the incipient evolution of traits considered critical to the success of other major ant lineages such as Myrmicinae and Formicinae. For example, group foraging is characteristic of these latter subfamilies and is probably ancestral within them, but it has apparently evolved repeatedly within Ponerinae. The newly inferred molecular phylogeny of Ponerinae (Figs 1, 2; Schmidt, 2013) provides an historical framework for studying the evolution of group foraging, among many other traits. Because taxonomic classification is expected to reflect phylogeny, a phylogenetically informed ponerine classification system is critical to the success of such studies. The molecular phylogeny of Ponerinae demonstrates the phylogenetic inconsistency of the current tribal and generic classification of the subfamily.

Ponerinae has not received a comprehensive taxonomic revision in nearly a century, since Emery’s (1911) *Genera Insectorum*, though several individual genera have been revised (*e.g.*, Bolton, 1974, 1975b; Brown, 1976, 1978; Bolton & Fisher, 2008a, 2008b, 2008c, 2011). Since Emery’s revision, many additional ponerine taxa have been discovered and some radical and poorly justified taxonomic changes have been made within the subfamily.

relationships among these ants on a global basis. This framework proved invaluable in developing an understanding of the levels of morphological character convergence across the subfamily and in finally cracking the “*Pachycondyla* problem” left behind by Bill Brown. Upon completing his Ph.D. and recognizing that his own new set of commitments precluded proper completion of this work, Chris invited Steve to reenter the project and work with him to complete the current manuscript. Fortunately he agreed, for which Chris is immensely grateful. Thus, the present work represents a combination of Bill’s extensive experience with the world’s fauna, Chris’ detailed and careful thesis research and Steve’s synthesis and expansion to include as broad a range of taxa as possible from the world’s major ant collections. We hope that this work will fulfill the vision Bill had for his “Reclassification” and provide inspiration and a platform for further research on these fascinating ants.

Finally, we would like to thank the numerous colleagues who have given so generously of their time and expertise. This project would be much poorer without their contributions. Many ant researchers influenced our thinking through countless fascinating discussions, but we would like to especially acknowledge Barry Bolton, Seán Brady, John Lattke, Jack Longino, Christian Peeters, Phil Ward, and Alex Wild. Brian Fisher and Ted Schultz kindly facilitated trips to the California Academy of Sciences and Smithsonian Institution, respectively. Barry Bolton, Stefan Cover and Gary Alpert hosted us during numerous visits to the collections in their care, and we are most grateful for hospitality. Numerous people contributed the ponerine specimens which made the molecular work possible, and we are deeply indebted to them: Nugroho Budianggoro, Lloyd David, David Donoso, Bhaktiar Effendi, Katsuyuki Eguchi, John Fellowes, Brian Fisher, Kim Franklin, Anne Hartmann, Bob Johnson, Mike Kaspari, David King, Paul Krushelnycky, John Lattke, Jürgen Liebig, Jack Longino, David Maddison, John Mangold, Joachim Moog, Wendy Moore, Corrie Moreau, Maruyama Munetoshi, Jeff Oliver, Omid Paknia, Chantal Poteaux, Christian Rabeling, Airlan San Juan, Justin Schmidt, Chris Smith, Marcus Stüben, Andy Suarez, Phil Ward, Alex Wild, Seiki Yamane, and Masashi Yoshimura. Many of the images were provided by Brian Fisher through AntWeb.org and Gary Alpert, and we thank them for their outstanding efforts in bringing modern imaging techniques to the world of ant systematics. Useful comments on the manuscript were received from many of the above as well as Brendon E. Boudinot and Brian Heterick. Distribution information was generously provided by Benoit Guénard and Mike Weiser and we are most thankful. Students from the Ant Course 2012 and 2013 gave extensive and valuable feedback on the African and New World keys and we thank Brian Fisher for allowing us to test them on his students. Funding for this research was provided by the University of Arizona GIDP Insect Science, Center for Insect Science, and Department of Entomology, as well as Sigma Xi, NSF (via the AToL Formicidae group of Phil Ward, Seán Brady, Ted Schultz, and Brian Fisher, who helped fund the development of CAD), Andy Suarez and Neil Tsutsui (who helped fund the *Anochetus/Odontomachus* study) and CSIRO (Australia).

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