

A TAXONOMIC REVISION OF THE NEW WORLD *HYPOPONERA*
SANTSCHI, 1938 (HYMENOPTERA: FORMICIDAE)

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Dedication

To my mother Joyce Dash, as she was and is always encouraging of my exploits and understanding of my Naturalist's behaviors. My family was always loving and supportive though they have no idea what being a "bug doctor" means. A special recognition must be given to all of my teachers and professors, who did not let the system get them down, or be discouraged from the many stresses from students. I am where I am today because they guided me and introduced me to the path of the roving scholar. In addition, two major influences in my life who were professors, mentors, and friends: Charles Bartlett and Jake Bowman did so much to shape who I am and what I wish to become.

PREVIEW

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by

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Abstract

The New World taxa of the pantropic ant genus *Hypoponera* (Ponerinae: Ponerini) is revised for the first time. The 55 previously recognized taxa have been evaluated using morphological and, when possible, ecological and biogeographical data to resolve taxon validity and species limits. Currently I recognize 42 species of *Hypoponera*, a number of which are new. I propose the following taxonomic outline: *Hypoponera agilis* (Borgmeier), *Hypoponera aliena* (F. Smith), *Hypoponera antoniensis* (Forel) stat. nov., *Hypoponera apateae* sp. nov., *Hypoponera capilosa* sp. nov., *Hypoponera clinei* sp. nov., *Hypoponera clavatula* (Emery) [= *fiebrigi* (Forel) syn. nov., = *neglecta* (Santschi) syn. nov.], *Hypoponera coveri* sp. nov., *Hypoponera creola* (Menozzi), *Hypoponera distinguenda* (Emery) [= *argentina* (Santschi) syn. nov., = *distinguenda dispar* (Santschi) syn. nov., = *distinguenda histrio* (Forel) syn. nov.], *Hypoponera faceta* (Menozzi) *incertae sedis*, *Hypoponera fallax* (Forel) stat. nov., *Hypoponera famini* (Forel) stat. nov., *Hypoponera fenestralis* (Gallardo) *incertae sedis*, *Hypoponera foeda* (Forel) [= *gracilicornis* (Menozzi) syn. nov.], *Hypoponera foreli* (Mayr), *Hypoponera gleadowi* (Forel), *Hypoponera idelettae* (Santschi), *Hypoponera iheringi* (Forel), *Hypoponera ignigera* (Menozzi), *Hypoponera impartergum* sp. nov., *Hypoponera inexorata* (Wheeler), *Hypoponera inexpedita* (Forel) stat. nov., *Hypoponera leninei* (Santschi), *Hypoponera leveillei* (Emery) comb. nov., *Hypoponera menozzii* (Santschi) *incertae sedis*, *Hypoponera nitidula* (Emery), *Hypoponera opaciceps* (Mayr) [= *opaciceps gaigei* (Forel) syn. nov., = *opaciceps postangustata* (Forel) syn. nov.], *Hypoponera opacior* (Forel) [= *opaciceps jamaicensis* (Aguayo) syn. nov., = *opacior chilensis* (Forel) junior syn.], *Hypoponera pampana* (Santschi) stat. nov. [= *opaciceps cubana* (Santschi) syn. nov.], *Hypoponera parva* (Forel) [= *reichenspergeri* (Santschi) syn. nov.], *Hypoponera perplexa* (Mann), *Hypoponera punctatissima* (Roger) [= *beebei* (Wheeler) syn. nov., = *ergatandria* (Forel) syn. nov.], *Hypoponera schmalzi* (Emery), *Hypoponera schwebeli* (Forel), *Hypoponera stoica* (Santschi), *Hypoponera subsarissa* sp. nov., *Hypoponera transiens* (Santschi) stat. nov., *Hypoponera trigona* (Mayr) [= *distinguenda vana* (Forel) syn. nov., = *trigona cauta* (Forel) syn. nov., = *collegiana* (Santschi) syn. nov., = *collegiana paranensis* (Santschi) syn. nov.], *Hypoponera vernacula* (Kempff) and *Hypoponera viri* (Santschi). All recognized species are illustrated and described with notes on natural

history and biogeography. Additionally, type images for these species are provided, serving as a photographic record. Also present is the first key to treat the New World species.

This assessment provides a framework that will aid in biodiversity surveys since *Hypoponera* is one of the most commonly collected ants in Neotropical regions. *Hypoponera* is a good candidate for conservation efforts because of the genus' importance in brown food webs, its abundance, and the fact that numerous species are known only from type localities. Additionally, distributional patterns suggest *Hypoponera* is limited to tropical and subtropical climates with limited ranges in temperate areas. When found in temperate areas, microhabitat selection favors warm areas. I propose the use of *Hypoponera* monitored in ant assemblages as a metric for evaluating the effects of climate change on ant communities. The revised taxonomy of the New World *Hypoponera* and the recent treatment of the African fauna is a major leap forward in understanding the diversity of *Hypoponera* and the Ponerinae as a whole.

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Chapter 1: Introduction

BACKGROUND

The Formicidae is a diverse hymenopterous taxon with more than 12,000 described species (Bolton et al. 2006). This family is considered a derived clade within the aculate superfamily Vespoidea, whose species are all eusocial (Grimaldi et al. 1997, Brothers 1999, Moreau et al. 2006). Ants are major components of terrestrial ecosystems; dominating habitats by their biomass (Hölldobler and Wilson 1990, Kaspari 2000), filling numerous niches, such as predators, granivores, mutualists and resource specialists (Hölldobler and Wilson 1990, LaSalle and Gauld 1993, Agosti et al. 2000). Furthermore, ants manipulate species composition, influence trophic interactions, possess numerous mutualistic and symbiotic relationships, and shape both the abiotic and biotic components of communities (Agosti et al. 2000).

Understanding ecological roles and documenting natural histories has mostly been afforded to pest, widespread, “interesting” or charismatic species. The red imported fire ant (*Solenopsis invicta*), for example, is the subject of numerous books and over 25,000 publications (Taber 2000, Tschinkel 2006), whereas related species of *Solenopsis* have few articles or only portions of monographs devoted to them (e.g., Tschinkel 2006, Pacheco 2007). Taxa that are common or of biological curiosity, such as the fungus-growing ants (Wheeler 1907, Weber 1937, 1938, 1966, 1970; Rabeling et al. 2007), army ants (Watkins 1982, 1985; Gotwald 1979, 1985, 1995; Brady 2003, Snelling and Snelling 2007) and harvester ants (Cole 1968, Hölldobler 1971, Taber 1990, 1998) have received comprehensive treatments. However, for the majority of ant species little more than a collection locality is known. Additionally, many genera have not received contemporary revisions, resulting in confused taxonomy and poorly documented biodiversity (Davidson et al. 2003, Armbrrecht et al. 2004). The majority of contemporary studies have focused on the evolutionary relationships of higher taxonomic categories (Shattuck 1992, Ward and Brady 2003, Astruc et al. 2004, Ward et al. 2005, Brady et al. 2006, Ward 2010), with limited attention devoted to particular genera.

One such genus that has very limited taxonomic work and no systematic study is *Hypoponera*. Often referred to as one of the most “confused” taxa, *Hypoponera* Santschi, 1938 is an obvious candidate for study. *Hypoponera* is often described as lacking any defining characters and being rather featureless. Longino (2010) related the genus to the potato in the Mr. Potato Head Game. The body forms are very similar to other ponerines so detailed study of meristic and morphometric parameters is required to accurately distinguish between species. Morphometric measurements are hypothesized as being important for revealing phylogenetically and taxonomically informative characters. However, even though *Hypoponera* species are very similar, noncongruent and distinct meristic characters such as sculpturing and pilosity are also informative. Because a contemporary taxonomic revision has not been attempted, species limits are unclear, variability of morphology has not been documented, validity of known taxa has not been tested, distributional patterns have not been explored, and collection of ecological data is lacking. The taxonomy is riddled with nebulous subspecies and varieties. Species described based on reproductives that are lacking worker associations in addition to the presence of intercastes have only added to the confusion of *Hypoponera*’s taxonomy.

Many ecological studies focused on ants found in leaf litter rarely denote species of *Hypoponera*, instead utilizing morphospecies groupings (e.g., King et al. 1998, Soares and Schoereder 2001, Berghoff et al. 2003, Theunis et al. 2005, Longino 2010, Calcaterra et al. 2010). Wild’s (2007b) study of the Paraguayan ant fauna found a number of taxa not assignable to known *Hypoponera* species. The lack of assigned species restricts future research as well as freezes the documentation and recording of natural history. This obstacle can be thought of as an “ignorance cycle” because taxonomy is so poor and thus so is the ecological data. Then the lack of ecological characters retards species discrimination, which in turn limits identification thereby continuing the cycle. Without accurate species determination, the accumulation of natural history is limited, as no information can be assigned to a particular species. This interrelationship of lost or ignored data and undefined species results in a further continuation of the cycle. A complete review of this genus is not only long overdue, but is crucial to understanding ant taxonomy and

ecology. Proper taxonomic keys and notes on biogeography will facilitate study of not only the genus *Hypoponera* but entire communities in which they are members.

This project represents the only alpha taxonomic analysis of the New World *Hypoponera*. Once species are recognized and evolutionary relationships are resolved, the door is open for more advanced studies. For example: How does localized high species richness relate to niche partitioning? Does the spread of tropical species into North America support theories of global climate change? What taxa may be of future concern with regards to pest status? The legacy of this revisionary study is the foundation for future research in ecology, evolution, and taxonomy. This research is guided by two domains of investigation: 1) Does the current taxonomy (Table 1) actually reflect species richness of *Hypoponera*? and 2) Can modern methodology produce a functional taxonomy? The resulting monograph represents a complete taxonomic assessment of the New World fauna.

Table 1. Specific and subspecific taxa of New World *Hypoconera* with country of type country.
This table represents the alpha taxonomy as of 2005.

<i>H. agilis</i> (Borgmeier, 1934): Surinam	<i>H. inexorata fallax</i> (Forel, 1909): Guatemala
<i>H. aliena</i> (Smith, 1885): Brazil	<i>H. leninei</i> (Santschi, 1924): Brazil
<i>H. argentina</i> (Santschi, 1922): Argentina	<i>H. menozzii</i> (Santschi, 1932): Costa Rica
<i>H. beebei</i> (Wheeler, 1924): Ecuador	<i>H. neglecta</i> (Santschi, 1923): Brazil
<i>H. clavatula</i> (Emery, 1906): Argentina	<i>H. nitidula</i> (Emery, 1890): Costa Rica
<i>H. collegiana</i> (Santschi, 1924): Brazil	<i>H. opaciceps</i> (Mayr, 1887): Brazil
<i>H. collegiana paranensis</i> (Santschi, 1924): Brazil	<i>H. opaciceps cubana</i> (Santschi, 1930): Cuba
<i>H. creola</i> (Menozzi, 1931): Costa Rica	<i>H. opaciceps gaigei</i> (Forel, 1908): Colombia
<i>H. distinguenda</i> (Emery, 1890): Venezuela	<i>H. opaciceps pampana</i> (Santschi, 1925): Argentina
<i>H. distinguenda dispar</i> (Santschi, 1925): Brazil	<i>H. opaciceps postangustata</i> (Forel, 1914): Paraguay
<i>H. distinguenda histrio</i> (Forel, 1912): Brazil	<i>H. opaciceps jamaicensis</i> (Aguayo 1932): Jamaica
<i>H. distinguenda inexpedita</i> (Forel, 1911): Brazil	<i>H. opacior</i> (Forel 1893): West Indies
<i>H. distinguenda vana</i> (Forel, 1909): Guatemala	<i>H. parva</i> (Forel, 1909): Guatemala
<i>H. ergatandria</i> (Forel, 1895): West Indies	<i>H. perplexa</i> (Mann, 1922): Honduras
<i>H. faceta</i> (Menozzi, 1931): Costa Rica	<i>H. punctatissima</i> (Roger, 1859): Germany
<i>H. fenestralis</i> (Gallardo, 1918): Argentina	<i>H. reichenspergeri</i> (Santschi, 1923): Brazil
<i>H. fiebrigi</i> (Forel, 1908): Paraguay	<i>H. schmalzi</i> (Emery, 1896): Brazil
<i>H. fiebrigi antoniensis</i> (Forel, 1912): Colombia	<i>H. schmalzi fugitans</i> (Forel, 1912): Brazil
<i>H. fiebrigi famini</i> (Forel, 1912): Colombia	<i>H. schmalzi paulina</i> (Forel, 1913): Brazil
<i>H. fiebrigi transiens</i> (Santschi, 1925): Argentina	<i>H. schwebeli</i> (Forel, 1913): Brazil
<i>H. foeda</i> (Forel, 1893): West Indies	<i>H. stoica</i> (Santschi, 1912): Uruguay
<i>H. foreli</i> (Mayr, 1887): Brazil	<i>H. trigona</i> (Mayr, 1887): Brazil
<i>H. gleadowi</i> (Forel, 1895): India	<i>H. trigona cauta</i> (Forel, 1912): Brazil
<i>H. gracilicornis</i> (Menozzi, 1931): Costa Rica	<i>H. vernacula</i> (Kempf, 1962): Brazil
<i>H. idelettae</i> (Santschi, 1923): Brazil	<i>H. viri</i> (Santschi, 1923): Brazil
<i>H. ignigera</i> (Menozzi, 1927): Costa Rica	<i>H. wilsoni</i> (Santschi 1924): Brazil
<i>H. iheringi</i> (Forel, 1908): Brazil	
<i>H. inexorata</i> (Wheeler, 1903): USA	

INTRODUCTION TO *HYPOPONERA*

Taxonomy and Systematics

Santschi (1938) described *Hypoponera* as a subgenus of *Ponera* Latreille, 1804; the subgenus *Ponera* (*Ponera*) was defined as having a distinct mesometanotal suture ("suture mesoepinotale") and *Ponera* (*Hypoponera*) lacks this suture, with the type species designated as *Ponera* (*Hypoponera*) *abeillei* André, 1881 (Santschi 1938: 79). Taylor (1967) noted that the absence of an incised mesometanotal suture lacked any diagnostic value, as this character is variable across taxa but *Ponera* (*Hypoponera*) and *Ponera* (*Ponera*) can be separated by several other diagnostic morphological differences (Table 2). Taylor (1967) employed these characters to raise the subgenus (*Ponera* (*Hypoponera*)) to full generic status.

Hypoponera (Ponerinae: Ponerini) is comprised of small to medium sized ants ranging from 1–4 mm in length. This genus contains 138 nominative species-level taxa (including subspecies or varieties, 183 taxa comprise the genus) (Bolton et al. 2006). In *Ponera*, the subpetiolar process has a fenestra and a pair of posteriorly directed teeth, but in *Hypoponera* the subpetiolar process lacks both a fenestra and posterior teeth (Taylor 1967). I document, however, that a number of *Hypoponera* species have a fenestra (ex: *H. reichenspergeri* (Santschi, 1923), *H. perplexa* (Mann, 1922), *H. pruinosa* (Emery, 1900), and *H. zwaluwenburgi* (Wheeler, 1933)). No species of *Hypoponera* have paired posterolateral teeth on the subpetiolar process as in *Ponera* (Fig. 1). Other ponerine genera also have some species with a fenestra, including some *Pachycondyla* (=Emeryopone) and *Gnamptogenys*.